A VARIABLE LIFE-TABLE FOR *Illinoia pepperi* (MacGillivray)

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ABSTRACT

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A variable life-table approach is used to design and parameterize a population dynamics model for the blueberry aphid, *Illinoia pepperi* (MacGillivray), in Michigan's commercial highbush blueberry agro-ecosystem. The model addresses aphid growth and maturation, seasonal fecundity, morph determination, vertical within bush distribution, parasitism, and rain induced mortality. Degree day durations for parthenogenic life stages are presented. Fecundity was found to decline seasonally from 24 to 3 young per female for both viviparous morphs. The proportion of alates in the population decreased sigmoidally from 79% at 1400 $^{o}D_{38}$ to less than 5% by 2000 $^{o}D_{38}$. Although seasonal changes in the aphid's vertical distribution followed changes in host plant phenology; parasitoids remained, predominantly, in the lower third of the bush. While rates of parasitism remained below 3% at a chemically treated site, parasitism exceeded 15% at an unsprayed site. Storms proved to be an important mortality factor. At times, individual thunderstorms accounted for over 50% reductions in aphid numbers.

To my father,
who shared the dream
but is not alive to see it fulfilled.

I'd rather learn from one bird how to sing
than teach ten thousand stars how not to dance.
e.e. cummings

Deadlines and commitments,
what to leave in what to leave out.
Bob Seiger

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CHAPTER 1. INTRODUCTION

1.1 Why Study an Aphid?

The aphid investigated herein, Illinoia pepperi (MacGillivray), is the only known vector of blueberry shoestring virus (BBSSV), an important disease of cultivated highbush blueberry and the most serious virus disease of blueberry in Michigan (Varney 1977, J. Nelson pers. comm.). Berry production of bushes infected with BBSSV declines drastically before the bush is eventually removed as unproductive. Once a bush is infected, nothing can be done to stop or slow the progress of the disease. For this reason efforts to stop the spread of BBSSV must focus on preventing new infections and identifying and removing existing sources of innoculum. To be effective research directed towards such control must investigate all three components of the plant-virus-vector relationship.

Of the three components, the virus vector is the least understood. The virus itself has been the subject of study for almost thirty years and some cultivars partially resistant to BBSSV have been known for over a decade (Varney 1970). On the other hand, I. pepperi was implicated as the vector of BBSSV only eight years ago (Ramsdell 1979a).

Since that time several aspects of the aphid's biology have been investigated. Laboratory studies have been conducted to determine the lower developmental temperature threshold, developmental rate, generation time, and

fecundity of apterous viviparous I. pepperi (Elsner 1982). Field investigations to determine the aphid's life cycle and seasonal history, alternate host plants, and the identity of natural enemies have been initiated (Elsner 1982). The seasonal timing of alate flights has also been studied (Elsner 1982, Morimoto 1984).

The virus-vector component of the disease cycle has also been investigated. Field studies have explored the seasonality of new virus infections and the viruliferousness of the aphid population (Morimoto 1984). Laboratory research has identified the time course of BBSSV acquisition by (Morimoto 1984) and localization within the aphid vector (Peterson 1984).

1.2 History of Blueberry Shoestring Disease

The probable viral nature of blueberry shoestring disease was first demonstrated by grafting experiments in the mid 1950's (Varney 1957). The disease had first been reported in highbush blueberry, Vaccinium corymbosum L., seven years earlier by Hutchinson (Varney 1970). BBSSV was only one of several blueberry diseases first recognized during the 1950's. Although native blueberry species had been partially cultivated in North America since the early 19th century, few diseases of Vaccinium species were known before the introduction of the cultivated blueberry cultivars V. australe Small and V. corymbosum in the 1920's (Varney 1970, 1977). Even more interesting is the fact that

all known virus diseases of cultivated highbush blueberry are believed to be indigenous to New Jersey (Varney 1970).

This historical pattern suggests that blueberry shoestring disease spread from native plants to introduced cultivars. This hypothesis is supported by grafting experiments conducted on native lowbush blueberry, V. angustifolium Ait. (Lockhart & Hall 1962). In that study buds from lowbush blueberry plants were grafted to highbush blueberry cv. 'Jersey' test plants. Although very few of the lowbush plants exhibited symptoms of shoestring disease, all of the 'Jersey' test plants eventually developed typical shoestring systems. BBSSV has also been discovered in wild populations of both V. angustifolium and V. corymbosum at several sites in Michigan (Ramsdell et al. 1984). These sites are sufficiently isolated from cultivated fields that it is doubtful the disease spread from cultivated to wild populations.

In his 1957 article Varney stated that shoestring was of minor importance, but he warned that it was a potential threat to the emerging cultivated highbush blueberry industry in North America. Since that time BBSSV has indeed become a very real threat to the industry. The disease has been reported from Michigan, North Carolina, and Washington, USA (Ramsdell 1979b) and Nova Scotia, Canada (Lockhart & Hall 1962). Financial losses to the blueberry industry from reduced yield and bush removal in Michigan alone amounted to

more than three million dollars in 1980 (Ramsdell et al. 1980).

Blueberry shoestring was established as a 'new' virus when isometric particles about 27 nm in diameter were implicated as the disease causing agent (Hartmann et al. 1973, Lesney & Ramsdell 1976, Ramsdell 1979a, 1979b). Transmission electron microscopy (Hartmann et al. 1973) revealed these particles in leaf and root tissue but not in phloem. Root xylem contained the largest crystalline arrays of particles indicating that the disease is a systemic root infection. Apparently, the disease only attacks Vaccinium species. All attempts to innoculate herbaceous plants by sap, dodder, or graft transmission have been futile (Varney 1977, Ramsdell 1979b).

Since 1980 researchers from the departments of Botany and Plant Pathology, Horticulture, and Entomology at Michigan State University have been coordinating BBSSV research. In addition to the biological studies of the aphid mentioned above, investigations have focused on developing serological assays to the virus (Morimoto 1984, Peterson 1984), localizing the virus within its aphid vector (Peterson 1984), and screening blueberry cultivars for resistance to both the virus and its aphid vector (Hancock et al. 1982, Schulte et al. 1984, Ramsdell et al. 1984). To date, three serological assays have been developed for detecting blueberry shoestring virus. These techniques are enzyme-linked immunosorbent assay (ELISA), radioimmunoassay

(RIA), and immusorbent scanning electron microscopy (ISEM). Of these techniques ISEM is most sensitive for detecting purified virus while RIA is superior for detecting the virus in individual aphids or aphid extract (Gillett et al. 1982). In 1984 a program was instituted to screen blueberry varieties for resistance to BBSSV using the ELISA technique (Schulte et al. 1984, Ramsdell et al. 1984).

1.3 Disease Symptomatology and Host Range

Typical BBSSV symptoms consist of elongate reddish streaks on current and one-year-old stems. Streaking is most noticeable on the side of the stem exposed to the sun (Ramsdell 1979b). Affected leaves are often narrow and strap-like (hence the name 'shoestring'), curled, or crescent shaped. Occasionally leaves may exhibit red vein-banding or oak-leaf patterns. Immature berries on affected bushes develop a purplish cast. This abnormal color disappears as the berries mature with no apparent loss in quality. Often only a portion of an infected bush exhibits disease symptoms and symptomless infections are common. Environmental conditions may alter symptom expression. As a result bushes that exhibit obvious symptoms one year may be symptomless the following year (Elsner 1982). After a few years the yield from infected bushes is dramatically reduced and the bush is eventually removed.

BBSSV has been observed in the following cultivars: Burlington, Coville, Earliblue, Jersey, June, Rancocas,

Rubel, and Weymouth (Ramsdell 1979b). Under field conditions the disease has never been observed to infect the cultivars Atlantic, Bluecrop, Bluejay, and Northland. However, low percentages of the cultivars Atlantic and Bluecrop do become infected if they are manually inoculated with purified virus (Ramsdell 1979b).

1.4 Disease Spread

The disease tends to spread bush by bush along the row (Lesney et al. 1978). This pattern of spread suggests that apterous aphids are responsible for most of the within field disease transmission. A compound interest rate for disease spread has been calculated at 0.269 bush per year (Lesney et al. 1978). The infection rate is also influenced by bush size. 'Jersey' seedlings infected with purified virus develop symptoms in five to six months (Lesney et al. 1978), but healthy bushes planted in a diseased field may not show symptoms for up to four years (Ramsdell 1979b). The quantity of virus (and therefore the number of aphids) needed to infect a mature blueberry bush is not known.

1.5 Virus-Vector Relationship

BBSSV is transmitted to soft-wood cuttings by I. pepperi after a 10 minute acquisition feeding period and an inoculation period of 100 hours (Morimoto 1984). Longer acquisition feeding periods increase the efficiency of

transmission with a maximum reached after about 24 hours (Morimoto 1984).

Scanning electron microscopy autoradiography (SEM AR), light microscopy autoradiography, and ferritin labeling techniques have revealed that BBSSV is transmitted by the aphid in a semi-persistent, circulative manner (Peterson 1984). In the SEM AR experiments ^{125}I-labeled BBSSV ingested by aphids was detected (1) in the stomach six hours after feeding, (2) in stomach and intestines 12 hours after feeding, and (3) throughout the alimentary canal to the anus 72 hours after feeding. Light microscopy autoradiography supported these findings and also indicated that an interaction occurred between embryos and the ^{125}I-labeled BBSSV. The exact meaning of this interaction is not presently known. Finally, indirect ferritin antibody labeling visualized BBSSV particles in the salivary glands of aphids fed on sachets containing virus preparation in sucrose.

1.6 Biology of I. pepperi

I. pepperi is a holocyclic species of aphid, spending its entire life cycle on Vaccinium species. During population outbreaks the aphid has been observed to feed and reproduce on a few woody plants present in blueberry fields (Elsner 1982). However, none of these colonies was ever observed to survive for more than two weeks. Reproduction has never been observed in the field on herbaceous hosts.

Five morphs of I. pepperi are recognized. These include (1) apterous, viviparous, fundatrix females; (2) apterous, viviparous females; (3) alate, viviparous females; (4) apterous, oviparous females; and (5) alate males (MacGillivray 1958). All morphs are normally green in color; however, a biotype of red morphs has been collected in parts of southwest Michigan (Elsner 1982). In greenhouse colonies green, viviparous females have been observed to produce red progeny, but red females were never observed giving birth to green young (Elsner pers. comm.).

The seasonal life cycle of this aphid begins in late April or early May with the hatching of overwintering eggs laid in or near the base of a blueberry bush. This first, or fundatrix, generation consists entirely of apterous, viviparous females. The fundatrix, in turn, give birth to both apterous and alate viviparous females. From June to August several such viviparous generations are produced. Most of the alate individuals are produced early in the growing season when the blueberry bush is growing actively. In late August and September the viviparous females begin giving birth to oviparous females and alate males that mate to produce overwintering eggs.

1.7 Thesis objectives

For several years the recommendations for controlling the spread of BBSSV have been (1) rouge out **all** bushes exhibiting BBSSV symptoms, (2) plant resistant cultivars,

(3) plant only certified stock, and (4) limit numbers of the aphid vector with chemical suppression. More recently, an aphid labeling study has indicated that mechanical harvesters can be very important in the dispersal of apterous aphids (Ramsdell et al. 1984). This study reiterates the important of harvester sanitation as a means of stopping the spread of BBSSV to uninfected fields.

On the other hand, it is not possible to kill all of the aphids in a blueberry field with chemical suppression strategies. At certain times during the growing season it may be very difficult to even halt their increase. If vector populations in BBSSV infected fields are to be controlled below some threshold level (eg. a minimum level for disease spread, or perhaps, aphid movement) more must be known about the mechanisms that control this aphid's population dynamics. To best utilize all mortality factors, chemical applications must be timed to augment rather than disrupt the actions of predators and parasites. Since many blueberry growers apply pesticides from the air we must also be aware of the within bush distribution of the aphid, and how such applications affect this distribution. For instance, pesticide applications directed against aphids may not be very effective if most of the aphids are at the base of the bush where residues from aerial applications are lowest.

In light of these facts, several objectives providing more information for better aphid control were identified:

1. determine the phenologies of aphid predators and parasites;
2. determine the seasonal within bush distribution of the aphid and its natural enemies;
3. describe seasonal changes in aphid fecundity; and
4. determine the impact of rainfall as an aphid mortality agent.

Research was directed towards designing and parameterizing a life-table that would describe the aphid's population dynamics and could be used to simulate a variety of control strategies.

1.8 Thesis Structure

Due to the diverse nature of the topics contained in this thesis, the work is presented in chapters. Each chapter addresses a different facet of the research. These chapters include discussions of aphid fecundity and mortality, morph determination, spatial distribution, and phenologies of natural enemies. The computer modeling section, in turn, integrates information from the various biological studies to structure a variable life-table for I. pepperi. The thesis ends with general conclusions and suggestions for future research.

CHAPTER 2. NATURAL ENEMIES

2.1 Introduction

The first step in utilizing natural enemies in pest control, whether the insect is a direct or indirect pest, is identifying these biotic mortality agents. The second step is to understand, and to be able to predict, when given predators and parasites will be active in the field. Finally, the impact that individual species or species complexes have on pest density must be assessed.

Both the work of Tuttle (1947) and Elsner (1982) provide information on the identity of potential natural enemies of I. pepperi. Table 2.1 lists potential predators and parasitoids identified by these two researchers.

In his research, Elsner observed individuals from seven insect families attacking the blueberry aphid. Of these, coccinellids were important early in the season during the months of May and June. Larvae of flies in the families Syrphidae and Cecidomyiidae were both found to be effective aphid predators. Elsner found syrphid larvae to be common from June to September. Cecidomyiid larvae, while much less common, were found to be very effective predators during July and August. Chrysopids, hemerobiids, and anthocorids were found throughout much of the growing season, but they appeared to have little impact on aphid populations. Whalon and Elsner (1982) have suggested that these three families

Table 2.1 Potential predator and parasitoid species of *I. pepperi* in Michigan.

Order	Family	Genus	Species[1]
Coleoptera	Coccinellidae	Adalia	bipunctata
		Anatis	15-punctata
		Chilocorus	bivulnerus
		Coccinella	novemnotata[2]
			sanguinea
			trifasciata
		Coleomegilla	maculata lengi[2,3]
		Hippodomia	convergens[2,3]
			parentesis
			13-punctata
		Hyperaspis	signatabinotata
Diptera	Cecidomyiidae	Aphidoletes	Aphidomyza[2,3]
	Syrphidae	Cartosyrphus	trista
		Eristalis	dimidiatus
			tenax
		Melanostoma	obscurum
		Mesogramma	marginata
			polita
		Metasyrphus	latifasciatus
			wiedemanni
		Pipizella	puchella
		Platycheirus	erraticus
			quadratus
		Sphaerophoria	cylindrica
			robusta
		Syritta	pipens
		Syrphus	knabi
			ribesi
		Toxomerus	geminatus
		Tropidea	quadrata
Hemiptera	Anthocoridae	Orius	insidiosus
Hymenoptera	Eulophidae	Aphelinus	sp.[2]
		Symphiesis	bimaculatipennis
Neuroptera	Chrysopidae	Chrysopa	carnea[3]
			oculata
	Hemerobiidae	Micromus	subticus

[1] Unless otherwise noted, all species are cited from Tuttle (1947).

[2] Elsner (1982).

[3] Whalon & Elsner (1982).

may be limited by chemical control practices. Finally, Elsner observed hymenopterous parasitoids in the family Eulophidae frequently attacking aphids during July and August.

Although Tuttle collected over 400 species of insects from 300 acres of highbush blueberry, he did not specifically note any of these as attacking aphids. Fortunately, most of the families identified by Elsner are composed of species that feed primarily, or solely, on aphids. For this reason all species collected by Tuttle from these seven families are included in the table as potential natural enemies. Undoubtedly, some of these were feeding on other species of aphids in the neighboring habitat and do not have any significant impact on populations of I. pepperi. The table also indicates that two large natural enemy complexes exist in the commercial highbush blueberry agro-ecosystem. These complexes are composed of predators in the families Coccinellidae and Syrphidae.

Tables 2.2 and 2.3 contain more detailed information from the literature concerning aphid predators and parasitoids. These tables list lower developmental temperature thresholds and generation times for natural enemies studied in other aphid ecosystems.

Most of the parasitoids listed in Table 2.2 are in the ichneumonoid family Aphidiidae. Members of the families Ceraphronidae and Pteromalidae are hyperparasitoids. Notice

Table 2.2 Lower developmental temperature thresholds and generation times for several species of aphids and their parasitoids.

Taxa	t[4]	K[5]	Citation
Aphididae			
Acrythosiphon pisum	5.5	100[6]	Campbell & Mackauer, 1975
		119[7]	Campbell & Mackauer, 1975
Masonaphis maxima	3.9	125	Campbell & Gutierrez, 1973
Illinoia pepperi	3.4		Elsner, 1982
Aphidiidae			
Aphidius ervi ervi	6.1	196	Campbell & Mackauer, 1975[8]
Aphidius ervi pulcher	6.1	187	Campbell & Mackauer, 1975[8]
Aphidius rubifolii	5.3	176	Campbell et al., 1974[9]
Aphidius smithi	6.2	178	Campbell & Mackauer, 1975[8]
Praon pequodorum	6.9	200	Campbell & Mackauer, 1975[8]
Ceraphronidae			
Dendrocerus niger	8.1	233	Campbell & Mackauer, 1975[10]
Pteromalidae			
Asaphes lucens	6.5	184	Campbell & Mackauer, 1975[10]

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[4] t = lower developmental temperature threshold in ^{o}C.

[5] K = time from oviposition to F_1 emergence in $^{o}D_t$.

[6] apterae

[7] alatae

[8] Parasitoid of the pea aphid, Acyrthosiphon pisum.

[9] Parasitoid of the thimbleberry aphid, Masonaphis maxima.

[10] Hyperparasitoid of both Acyrthosiphon pisum and Masonaphis maxima.

that the parasitoids listed have higher developmental temperature thresholds than their hosts. The table also indicates that all of the parasitoids studied have generation times of approximately 200 degree days. What the table does not show is that the adults are relatively long lived. For example, Gilbert and Gutierrez (1973) were able to keep Aphidius rubifolii Mackauer alive in the laboratory for one to two weeks when honey was provided as a carbohydrate food source. A. rubifolii is the primary parasitoid of Masonaphis (=Illinoia) maxima (Mason), an

Table 2.3 Lower developmental temperature thresholds and generation times for several species of aphid predators.

Taxa	t[11]	K[12]	Citation
Coccinellidae			
Adalia bipunctata	9.0	263	Obrycki & Tauber, 1981
	6.8d		Obrycki et al., 1983
Coccinella septempunctata	12.1	197	Obrycki & Tauber, 1981
Coccinella transversoguttata	12.2	218	Obrycki & Tauber, 1981
Coleomegilla maculata lengi	11.3	236	Obrycki & Tauber, 1978
	13.8	199	Wright & Laing, 1978
Hippodamia convergens	9.0		Baumgaertner et al., 1981
Chrysopidae			
Chrysopa carnea	8.3		Baumgaertner et al., 1981
	4.4	170	Tauber & Tauber, 1973
Chrysopa harisii	10-14	314	Tauber & Tauber, 1974
Hemerobiidae			
Hemerobius pacificus	4.4c, 0.4e, 4.11, 0.6p		Neuenschwander, 1975

[11] t = lower developmental temperature threshold in ^{o}C; e=eggs; l=larvae; p=pupae; c=complete development; d=post-diapause, pre-reproductive adults.

[12] Time of oviposition to F_1 emergence in $^{o}C_t$.

aphid closely related to I. pepperi. Frazer & Forbes (1968) reported that levels of parasitism from this species can reach 15%. The species also has the potential for very rapid rates of increase. Females lay 400 eggs in the laboratory and up to 90 eggs per female have been observed in the field (Gilbert & Gutierrez 1973, Gilbert et al. 1976). Potential fecundity for other species of aphidiid wasps ranges from a low of 30 to a high of over 1500 eggs per female (Hagen & Van den Bosch 1968). Two species listed in the table, A. smithi Sharma & Subba Rao and A. ervi ervi Haliday, are not native to North America. Both species were imported, mass reared, and released in 1958 in an attempt to control the pea aphid, Acyrothosiphon pisum (Mackauer & Finlayson 1967).

In general, primary parasitoids of monoecious aphids tend to be species specific. Dioecious aphid species, on the other hand, often have different complexes of parasitoids on each of their host plants. Hyperparasitoids are usually not species specific. Aphid predators also tend to be generalists; feeding on mites, Lepidoptera larvae, and insect eggs in addition to a variety of aphid species (Hagen & Van den Bosch 1968).

Several of the aphid predators listed in Table 2.3 have been observed in commercial blueberry fields. These species include Adalia bipunctata L., Coleomegilla maculata lengi Timberlake, Hippodamia convergens Guerin-Memeville, and Chrysopa carnea Stephens. Most of the predators listed in

the table have lower developmental temperature thresholds much higher than I. pepperi. Exceptions to this generalization include C. carnea and Hemerobius pacificus. C. carnea overwinters as a pupa. Data from Ithica, NY, indicates that, at least in an apple ecosystem, chrysopid adults are one of the first predators to appear in the spring (Tauber & Tauber 1973). Laboratory studies revealed that post diapause females required only 100 degree days above 4°C to develop into reproductive adults. H. pacificus is a confer dwelling hemerobiid in the Pacific Northwest.

Although the same families of predators appear time and time again in studies of different aphid ecosystems, the relative importance of each family is quite variable. For instance, while studying Myzus persicae (Sulz.) in potatoes Mack and Smilowitz (1980) found coccinellids to be the primary predator. On the other hand, syrphids were found to be the most important predator of M. maxima on thimbleberry (Gilbert & Gutierrez 1976). Both syrphids and cecidomyiids were important predators of the cabbage aphid, Brevicoryne brassicae (L.), on Brussels sprouts in a study conducted in southern England (George 1957). George also noted, with some surprise, that coccinellids were completely absent from this system. In a later study of this ecosystem, Harris (1973) identified the cecidomyiid Aphidoletes aphidimyza (Rondani) as the predominant predator. During insecticide trials in highbush blueberries here in Michigan Whalon and

Elsner (1982) also found cecidomyiids to be the most common predator.

The current study of I. pepperi's natural enemies has two objectives. The first is to determine the phenologies of the aphid's natural enemies with greater precision. The second objective is to continue the process of identifying I. pepperi's parasitoids.

2.2 Materials and Methods

Rather than devise separate experiments to address questions concerning phenologies of natural enemies, within bush aphid distribution, and other life-table parameters; a systematic sampling scheme that could be analyzed in a variety of ways was developed. In later references this scheme will be referred to as the 'standard sample'.

These studies were conducted at two commercial highbush blueberry, V. corymbosum cv. 'Jersey', sites in Michigan during the summers of 1981 and 1982. Data was collected during both years at site 1 near Charlotte, MI. At a second site near Grand Junction, MI, data was only collected in 1982. Plots were sampled every seven to ten days from early June until September.

Site 1 was located on the Lowel Cook Farm, 3.5 miles southwest of Charlotte, MI, on Kalamo Highway (Eaton Co., T2N, R5W, Sec. 22, SW 1/4). The study area consisted of eight rows of mature blueberry bushes, four to six feet tall, planted on a six by ten foot spacing, about ten years

old, with rows oriented north to south. A 20 foot wide fence row of trees borders the western edge of this field. Fertilizer was applied to the field in the spring of 1982, resulting in more succulent terminal growth during that year. This farm is a commercial you-pick operation covering about four acres. All berries are hand harvested. The site is particularly appropriate for 'natural' distribution and life-table studies because it is not subjected to regular chemical suppression. Only one pesticide spray is applied annually, this being an application of Meserol one week before harvest to discourage birds from feeding on maturing berries. This spray is applied from the ground using an air blast sprayer.

Site 2 was located on the Jones Blueberry Farm, 3/4 mile south of Grand Junction, MI, on 54th Street (Van Buren Co., T1S, R15W, Sec. 9, SW 1/4). The area of the field where the study was conducted consists of mature bushes eight to ten feet tall planted on an eight by ten foot spacing with rows oriented north to south. The field was one of the first blocks of 'Jersey' bushes planted in the state and is over 40 years old. Harvesting is done both by hand (as a you-pick operation) and mechanically. All pesticides are applied from the air. The study area is in the middle of a 400+ acre clearing of cultivated blueberries operated by several growers.

These two sites are about as different as commerical blueberry sites can be. Besides being located about 100

miles apart, four major differences between the sites are worth noting. The first difference is bush size. Bushes at the Grand Junction site are about twice as tall as those at Charlotte. Second, unlike the primary study site near Charlotte, the Grand Junction site receives regular aerial pesticide applications. Third, no mechanical harvesting is done at the Charlotte site. Finally, while the first site is protected from the elements by a fence row of trees along its western edge; the second study area is located in the center of several hundred acres of blueberries.

Weather data for these studies consists of daily maximum and minimum temperatures, and rainfall. Weather data for site 1 was obtained from the NOAA weather station located at the Charlotte water treatment plant, approximately 3.5 miles east northeast of that site. Data for site 2 was obtained from the cooperating agricultural weather station located at the headquarters of the Michigan Blueberry Grower's Association in Grand Junction, MI. This station is situated 0.2 mile northwest of the study area in the same large clearing. For purposes of comparing data from different sites and years, calendar time was converted to physiological time, ie. degree days (^{o}D), using Baskerville and Emin's (1969) sine wave approximation with a lower developmental threshold of 38F (3.4^{o}C) (Elsner 1982). Since the aphid's lower developmental threshold is considerably lower than many other insects, seasonal degree day accumulations were begun January 1st rather than on

April 1st as is commonly done for many insects with lower thresholds near 50F (10°C). Daily rainfall was measured in inches.

Each study area consisted of seven rows of 50 bushes each. Rows 1, 3, 5, and 7 were buffer rows and were not sampled. This resulted in an effective sample size of three rows by 25 bushes. The sample unit was one terminal, ie. six to eight inches of cane with leaves. The sample was also stratified vertically, meaning that one terminal was randomly chosen from the upper, middle, and lower portions of each bush sampled. For each terminal sampled, counts of the aphid, two parasitoids, and six predators were recorded by life stage. Figures 2.1 and 2.2 illustrate the typical inhabitants of three blueberry terminals (sample from one bush) during a population explosion in mid July.

The sampling scheme contains eight categories of information about the aphid's natural enemies and one disease category. Two categories contain data on aphid parasitoids (Hymenoptera: Aphidiidae). Both parasitoids cause parasitized aphids to become mummified and firmly attached to a leaf. However, they can be easily distinguished in the field because one pupates within the aphid mummy, while the other bores through the mummy and pupates beneath it. Five insect predators are also represented in the data set. These are grouped by family: Syrphidae, Cecidomyiidae (Diptera), Chrysopidae, Hemerobiidae (Neuroptera), and Coccinellidae (Coleoptera).

BLUEBERRY APHIDS

				LARGE		ADULT	
	Egg	Small	Medium	Apt.	Alate	Apt.	Alate
UPPER	0	59	16	9	0	10	1
MIDDLE	0	0	0	1	0	0	0
LOWER	0	27	0	2	0	13	0

PARASITOIDS

	PUPATES WITHIN MUMMY					PUPATES BENEATH MUMMY				
	Egg	Larva	Pupa	P.Em.	Adult	Egg	Larva	Pupa	P.Em.	Adult
UPPER	0	0	0	0	0	0	0	0	0	0
MIDDLE	0	0	0	1	0	0	0	0	0	0
LOWER	0	0	0	0	0	0	0	1	0	0

Figure 2.1 Typical sample of I. pepperi and parasitoids from one blueberry bush (3 terminals) in mid July (first data entry screen).

PREDATORS

	SYRPHIDAE				CECIDOMYIIDAE			
	Egg	Larva	Pupa	Adult	Egg	Larva	Pupa	Adult
UPPER	2	0	0	0	0	0	0	0
MIDDLE	0	0	0	0	0	0	0	0
LOWER	2	1	0	0	0	0	0	0

	CHRYSOPIDAE				HEMEROBIIDAE			
	Egg	Larva	Pupa	Adult	Egg	Larva	Pupa	Adult
UPPER	1	0	0	0	0	0	0	0
MIDDLE	0	0	0	0	0	1	0	0
LOWER	0	0	0	0	0	0	0	0

	COCCINELLIDAE				SPIDERS	
	Egg	Larva	Pupa	Adult	Egg	Other
UPPER	0	0	0	0	0	0
MIDDLE	0	0	0	0	0	0
LOWER	0	0	0	0	0	0

Figure 2.2 Typical sample of predators of I. pepperi from one blueberry bush (3 terminals) during a population explosion in mid July (second data entry screen).

Data was also collected on one category of non-insect predator -- spiders. For details on life stage groupings for each category refer to Figures 2.1 and 2.2. Originally the data contained a category for aphids killed by fungal disease; however, by the time the data entry program described below was being constructed this category had been eliminated because no fungal deaths had been observed in the field.

Due to the enormity of the data set (8,775 numbers per sample, almost one half million numbers total), it was necessary to develop programs to efficiently enter that data into a computer and later to reduce it to a form that could be analyzed using existing statistical packages. These database management programs were written in UCSD Pascal (version IV.0) and run on a Columbia Data Products micro-computer (model Commander 964, 64K memory, 2 floppy disk drives, 256 X 512 pixel bit mapped monochrome graphics). The data entry program is menu driven with sufficient error checking to eliminate fatal program errors. Elaborate error checking was necessary because data entry was done by student employees with little or no previous computer training. Figures 2.1 and 2.2 are reproductions of the two data entry screens used in the program. The data reduction program was written in a command structured format to ensure a maximum of flexibility. The program executes tasks in response to commands consisting of single words or short phrases. User responses can be automated using two levels

of command files so the program can reduce an entire diskette of data at once.

2.3 Results

Results of this 'standard sample' are presented in two sections. The first section discusses I. pepperi's parasitoids, the second addresses aphid predator data. Other results from this sample are analyzed in chapter three.

2.3.1 Parasitoids

Most hymenopterous parasitoids of aphids have similar life cycles. The cycles begins with mating and egg laying. Many of these parasitoids, particularly those in the family Aphidiidae, can reproduce parthenogenically; however, virgin females produce only male progeny (Hagen & Van den Bosch 1968). Adult females search out late instar aphid nymphs in which to oviposit. Usually only one egg per host is deposited. The ability to distinguish between already parasitized and non-parasitized aphids varies between species, but most species can detect active parasitoid larvae (Hagen & Van den Bosch 1968). Young larvae develop within the aphid's abdomen and produce 'giant cells'. These cells absorb nutrients from aphid hemolymph and are fed on by the growing larvae (Hagen & Van den Bosch 1968). Even if the parasitoid larva dies, giant cells continue to grow and will eventually kill the aphid. When ready to pupate, the

larva cuts a small slit in the aphid's venter and affixes the empty shell to the leaf substrate. At this stage the empty aphid exoskeleton appears dry and bloated and is referred to as a mummy. In some species larvae pupate within the aphid mummy. In others, the larva exits the mummy and forms a cocoon between it and the leaf surface. Still others do not affix the aphid to a leaf at all. Instead, the dying aphid falls to the ground where the parasitoid larva crawls out and pupates in the litter. To emerge, adult parasitoids cut a small exit hole in the cocoon. The placement and shape of this exit hole, along with the color and location of the cocoon are commonly used characters in identification keys (Mackauer & Finlayson 1967).

Adult parasitoids reared from mummies collected during the course of this study have been identified to family. The vast majority of specimens in both parasitoid categories are members of the braconid family Aphidiidae. Two individuals reared from mummies collected at site 1 on July 13, 1982, have been identified as ceraphronids (Hymenoptera: Ceraphronidae). Some members of this family are hyperparasites of ichneumonoid parasitoids of aphids (Borror et al. 1981). A third species of parasitoid was reared from shiny, black mummies collected in greenhouse colonies of I. pepperi during December 1982. This species is a small, yellowish wasp in the family Scelionidae.

Parasitoid data collected during the 'standard sample' is summarized in Figures 2.3, 2.4, and 2.5. Each figure is composed of four graphs. Special events such as pesticide applications and mechanical harvesting are indicated by arrows at the top of each figure. The first two graphs in each figure chart daily rainfall and the total number of aphids per sample, respectively. Aphid counts are plotted on a log scale to retain sensitivity on the low end of the scale. The third graph plots the number of aphid mummies containing parasitoids versus degree days for each sample. Since parasitoid larvae pupate very soon after an aphid become mummified, this graph is essentially a pupal sample. Similarly, the fourth graph plots the number of empty aphid mummies in each sample. Empty mummies are those from which adult parasitoids have already emerged. If the mummies remain fixed on the leaves indefinitely this sample should represent cumulative adult emergence of these parasitoids.

Several peculiarities in the data require highlighting. First, data collected in 1981 at site 1 contains only one parasitoid category. The presence of two types of parasitoids was not detected until the 1982 growing season. Second, at site 2 two applications of Cythion in late July resulted in significant aphid mortality. Figure 2.5b shows the complete collapse of the aphid population following these sprays. Third, the sharp peaks in Figures 2.5c and 2.5d are highly unusual. They probably do not represent the

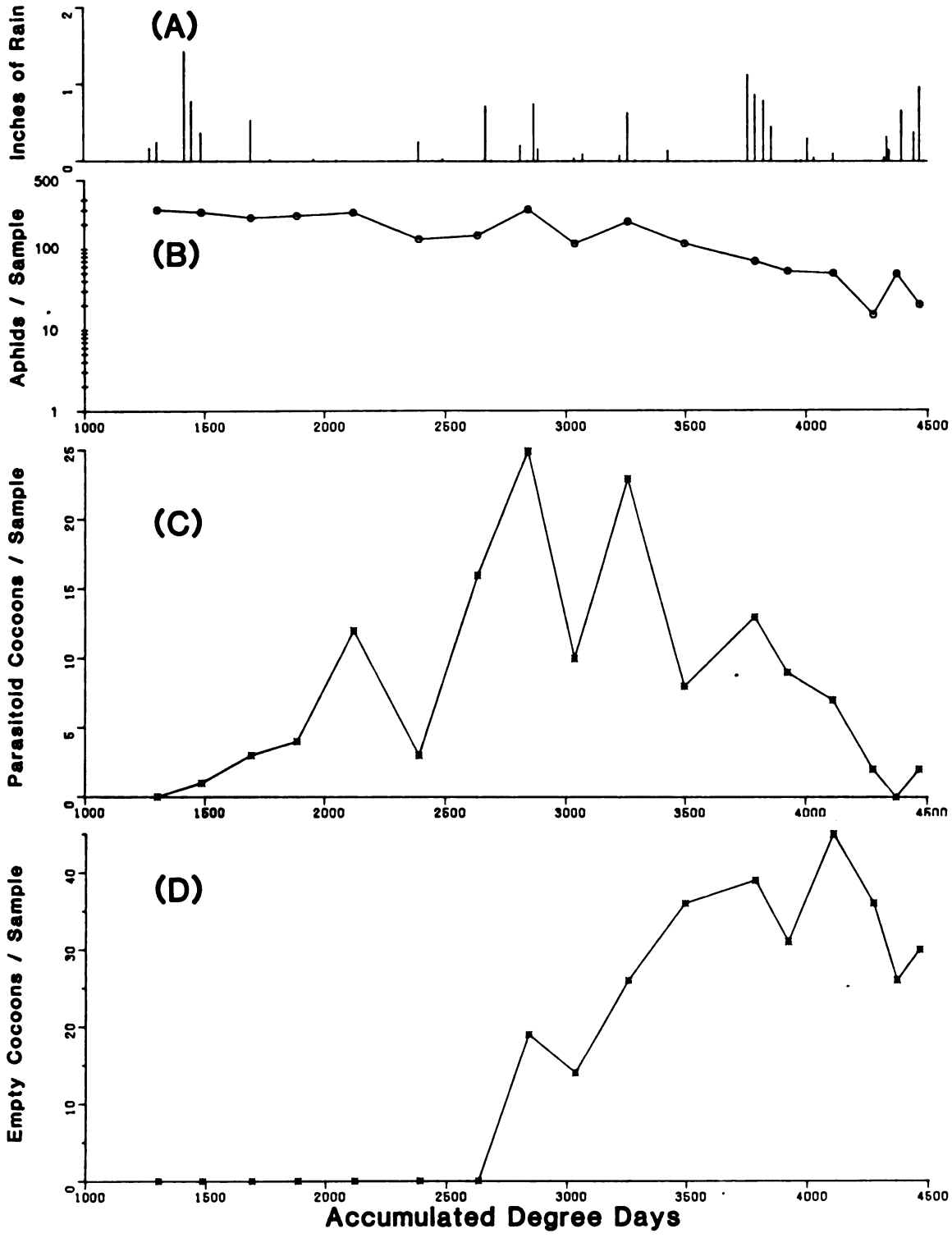


Figure 2.3 Parasitoid summary for site 1, 1981: (a) daily rainfall, (b) total aphids per sample, (c) aphid mummies containing parasitoids, and (d) empty parasitoid cocoons.

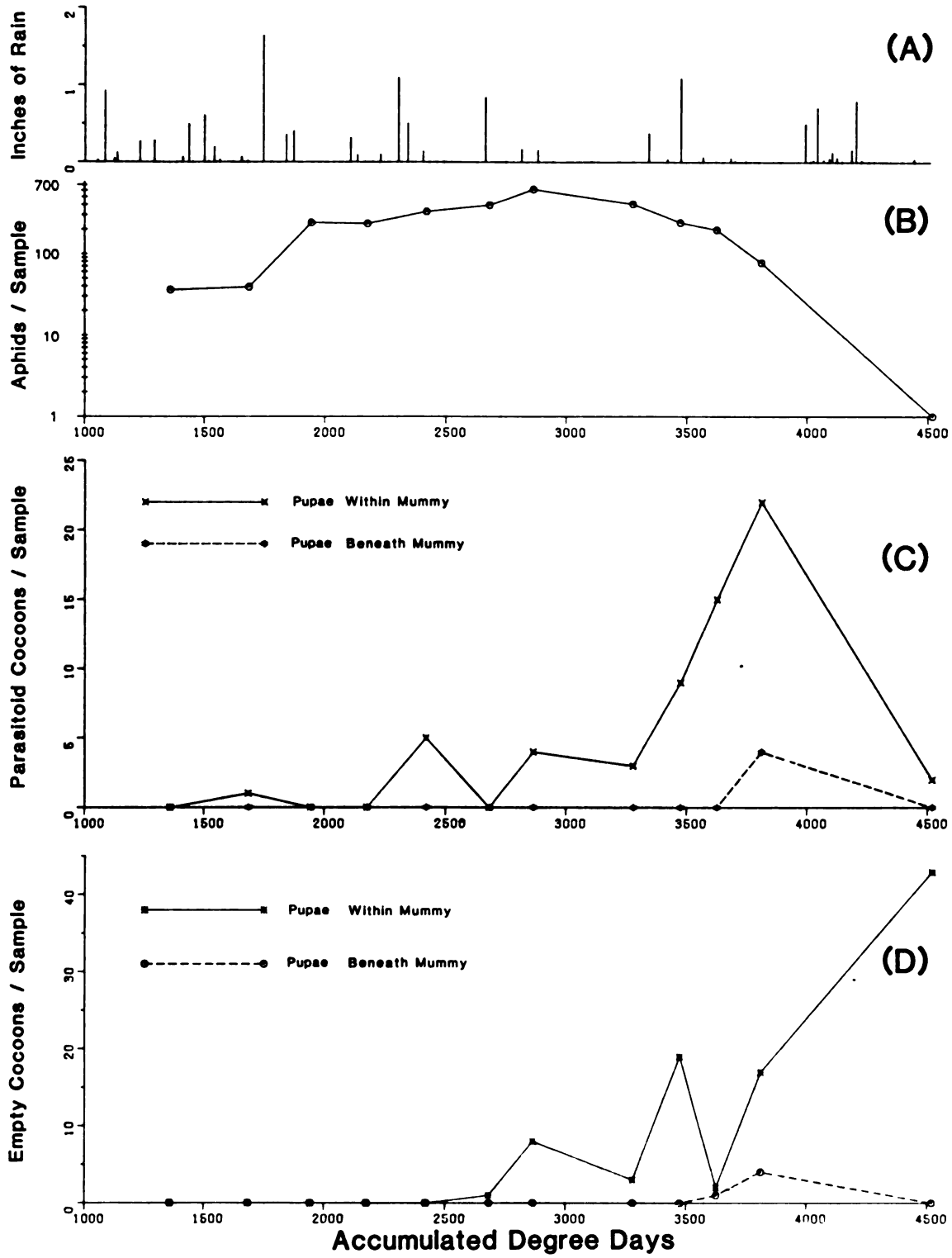


Figure 2.4 Parasitoid summary for site 1, 1982: (a) daily rainfall, (b) total aphids per sample, (c) aphid mummies containing parasitoids, and (d) empty parasitoid cocoons.

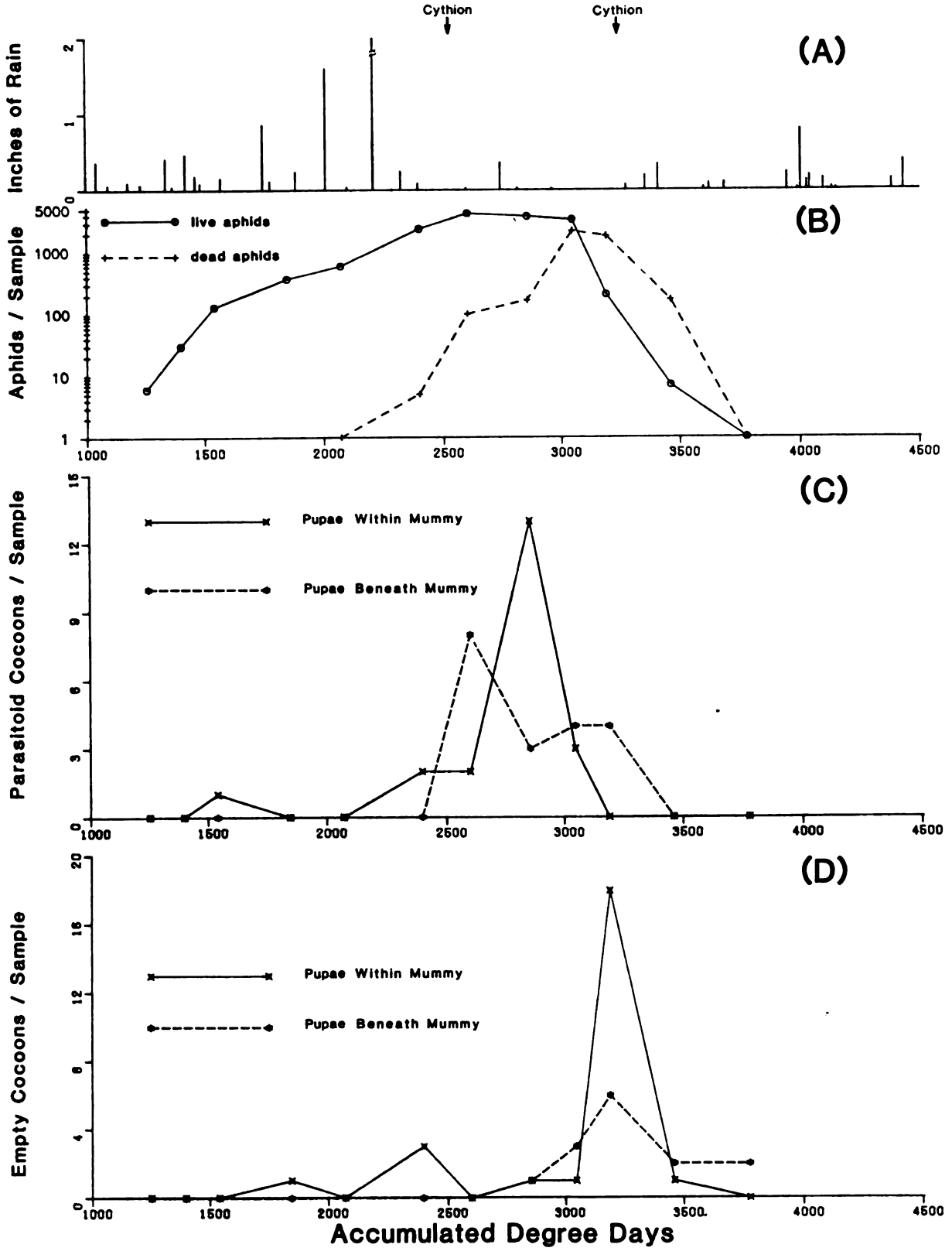


Figure 2.5 Parasitoid summary for site 2, 1982: (a) daily rainfall, (b) total aphids per sample, (c) aphid mummies containing parasitoids, and (d) empty parasitoid cocoons.

synchronized development of a single generation of parasitoids. The rapid disappearance of parasitoid pupae in Figure 2.5c is most likely linked to the collapse of the aphid population. Adult aphidiid wasps require honeydew as a source of carbohydrate fuel (Hagen & Van den Bosch 1968, Gilbert & Gutierrez 1973). Therefore, as the aphid population declined the parasitoids were deprived of both suitable hosts and a food source. On the other hand, the peak in Figure 2.5d cannot be linked to this collapse or to the chemical applications. Since it charts cumulative adult emergence this curve should be sigmoid shaped not bell shaped. The only way to decrease the number of empty parasitoid cocoons in the sample is to physically remove them from the leaves. In this case removal was the result of mechanical harvesting.

Several broad generalizations may be drawn from these diagrams. First, the aphidiid species that pupates within the mummified aphid was observed in all plots throughout much of the growing season. In all cases, they first appeared around 1500 $^{o}D_{38}$ (June 15 to 21). Conversely, the aphidiid species that pupates beneath the aphid mummy was not observed until later in the growing season and then only for a limited time. At site 1 this second parasitoid species was only found on August 31 and September 8. At site 2 it was observed, in larger numbers, from July 27 to September 9.

The figures also indicate that empty parasitoid cocoons are a poor indicator of cumulative adult emergence. Counts of empty parasitoid cocoons declined two or three times during the growing season in all plots. With two exceptions (one of these was discussed earlier), all of these declines were associated with heavy rainfall between samples. In most cases these accumulations exceeded one inch of rain.

Figure 2.6 charts percent parasitism through the growing season for each site. This rate of parasitism combines counts of both kinds of aphidiid parasitoids. Percent parasitism for each sample was calculated as follows:

$$\% \text{ Parasitism} = \frac{\text{Number of parasite pupae}}{\text{Total number of aphids}} \times 100$$

This method of calculating the rate of parasitism is overly simplistic. Since not all aphid life stages are parasitized, the method will tend to underestimate the level of parasitism. One the other hand, since the aphid populations have a relatively stable age distribution (Kriegel & Whalon 1983) more complicated methods of estimation do not alter the general conclusions drawn here. These conclusions are two fold. First, the rate of parasitism increases through the growing season. A similar result was obtained by Gilbert & Gutierrez (1973) in the M. maxima system. Second, the rate of parasitism at the unsprayed plots was an order of magnitude greater than at the sprayed site. Parasitism reached a high of 18% at

Figure 2.6 Percent parasitism versus degree days for (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

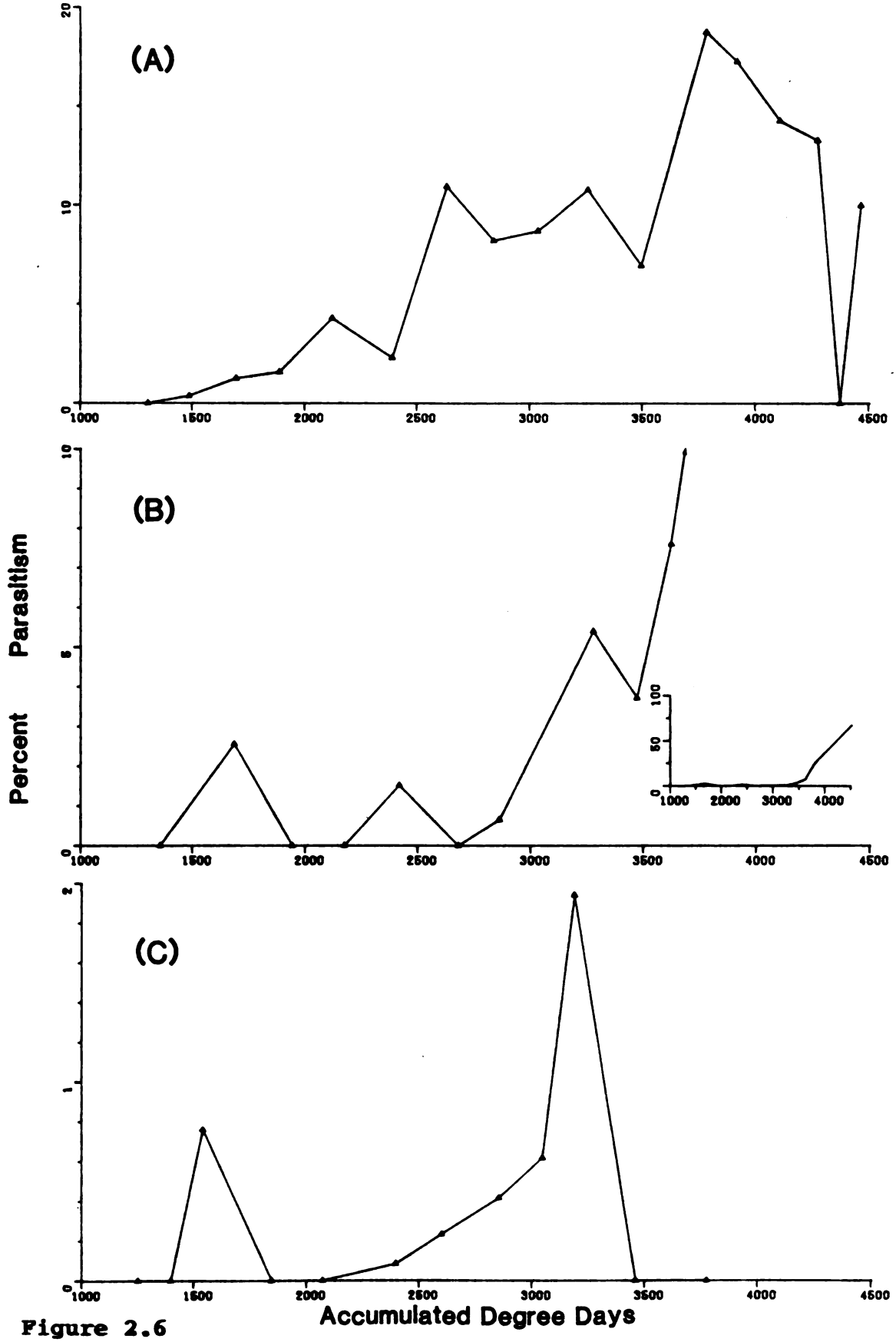

(A)
(B)
(C)
Percent Parasitism
Accumulated Degree Days
1000
1500
2000
2500
3000
3500
4000
4500

Figure 2.6

site 1 during 1981. This plot also contained the largest early season aphid population. At site 2 the rate of parasitism peaked at 2% during the collapse of the aphid population. The figures of 25% and 66% parasitism encountered at the end of the season at site 1 in 1982 (Figure 2.6b) are not reasonable figures. I believe these numbers represent diapausing parasitoid pupae remaining on the leaves after the aphid population had all but disappeared.

2.3.2 Predators

Very little is known about the role that spiders play as direct predators in the highbush blueberry agro-ecosystem. Direct evidence of their consuming aphids was only encountered once during this study -- a shriveled alate was discovered in a web. Most often, a single spider was the lone inhabitant of a blueberry terminal. On the other hand, crab spiders (Araneae: Thomisidae) were observed consuming lepidopterous larvae on several occasions.

The present study is primarily concerned with when spiders and spider egg cases are present in blueberry fields. These results are depicted graphically in Figure 2.7. No attempt was made to differentiate between different families or life stages of arachnids. In general, spiders were present, though not abundant, throughout the growing season. More spiders were observed at site 1 than at

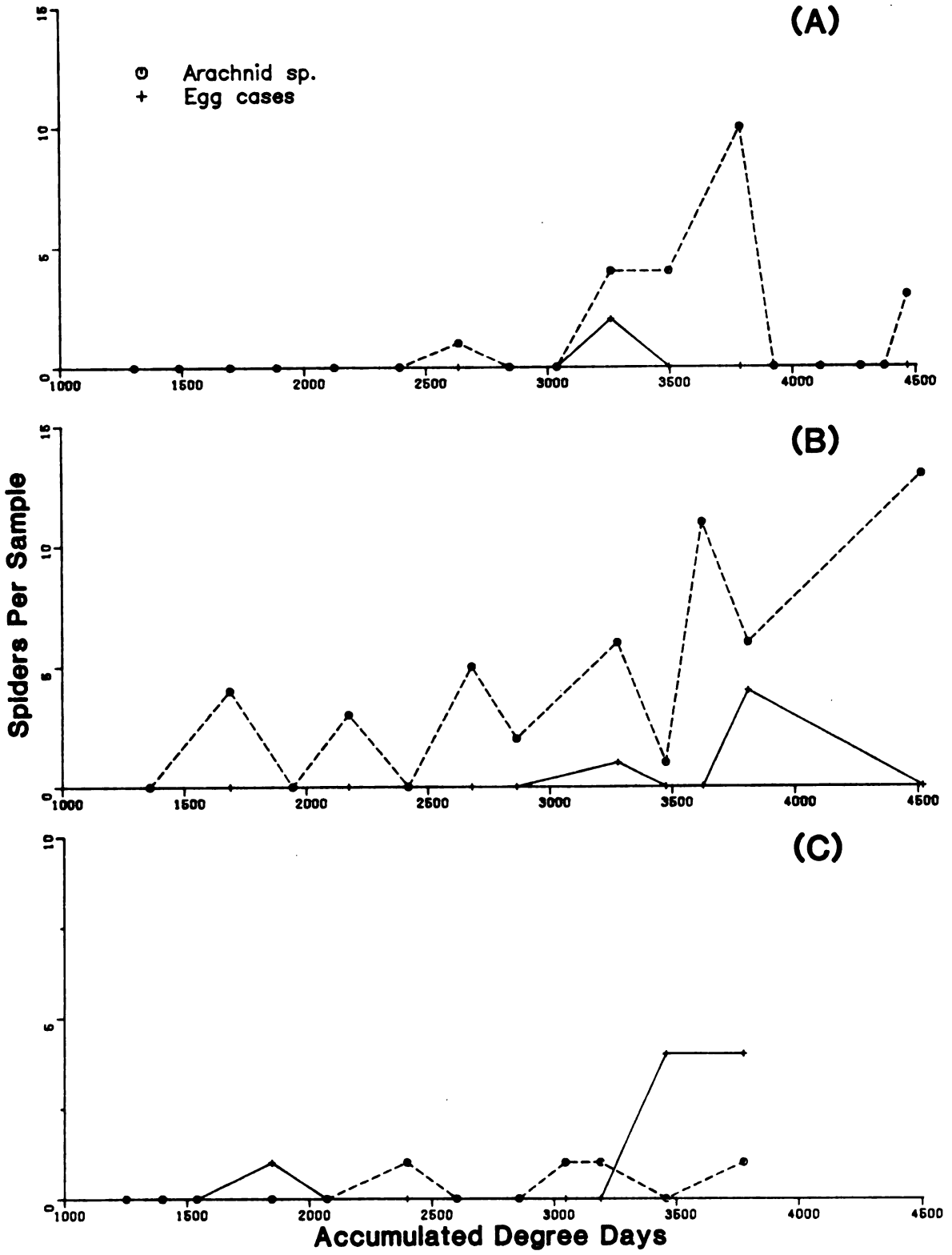


Figure 2.7 Sample counts of spiders and spider egg cases for (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

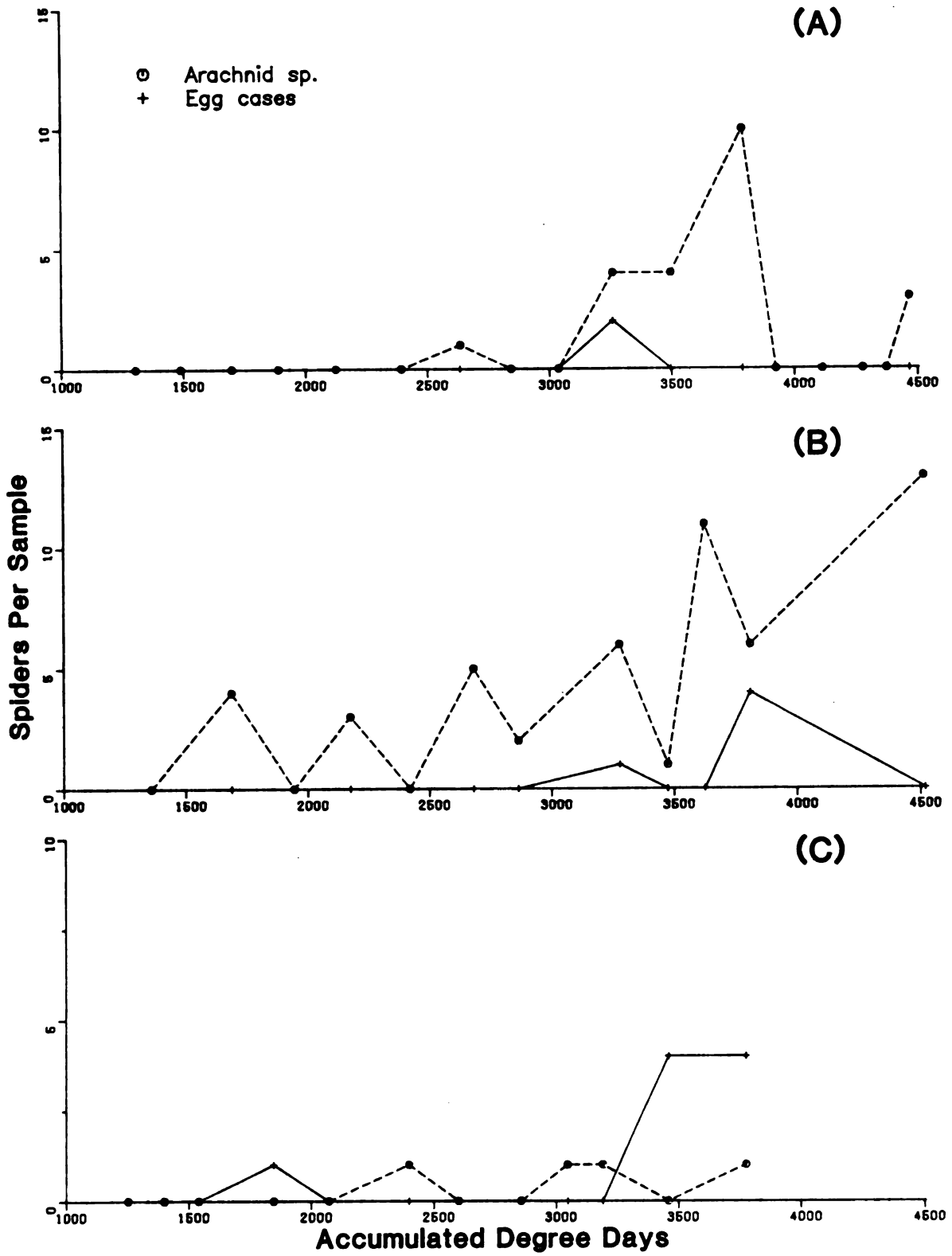


Figure 2.7 Sample counts of spiders and spider egg cases for (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

site 2. Although one egg mass was found in early July, most egg laying appeared to take place in August and September.

Surprisingly few coccinellids were observed during the course of this study. Table 2.4 indicates that all such observations were of isolated adults at site 1. Although larvae were occasionally seen in the fields visited, none were observed during the course of the 'standard sample'. One of the adults collected belongs to a species not previously recorded from highbush blueberries. This new member of the already large complex of predatory coccinellids is Brachyacantha ursina (F.).

Table 2.4 Observations of coccinellid predators during the 'standard sample'.

Site	Date	^{o}D	Life stage	No. Observed
1	JUN-15-81	1487	adults	1
1	JUN-27-82	1686	adults	2
1	JUL-06-82	1943	adults	2

Predatory neuropterans belonging to the families Hemerobiidae and Chrysopidae were collected during the course of this study. Hemerobiids were quite rare and were not collected during the 'standard sample'. However, they and chrysopid larvae were the most abundant predators present in a mechanical harvester at site 2 on August 19, 1982.

Sample counts of chrysopids collected during the 'standard sample' are presented in Figure 2.8. Eggs were the most commonly collected life stage. This observation is

in accordance with Hagen & Van den Bosch's (1968) review of aphid natural enemies. In their review the authors state that eggs and adults are the most commonly encountered life stages. Indeed, adult chrysopids were also commonly observed in blueberry fields. However, they were normally observed in flight and therefore appear only rarely in 'standard sample' counts.

It is very interesting that so few chrysopids were observed at site 2 during 1982 (Figure 2.8c). The reasons why this is so cannot be stated with any certainty. Perhaps they were excluded by chemical suppression strategies practiced throughout the entire 400+ acre clearing. Adult chrysopids are known to be much less resistant to pesticides than their larvae (Bartlett 1964). But why then was such a flush of egg laying observed around 3000 ^{o}D? Hagen & Van den Bosch (1968) note that fecundity of C. carnea is dependent on the amount of honeydew available to adults. They state that very high aphid densities are required to attract the species and induce egg laying. Indeed, by 3000 ^{o}D the number of I. pepperi exceeded 3000 aphids per 225 terminals and honeydew covered much of the foliage. Since the fields were approaching harvest, pesticide applications had also ceased. Therefore, I believe this flush of eggs were produced by immigrant chrysopid adults attracted to the field by large quantities of honeydew on the foliage.

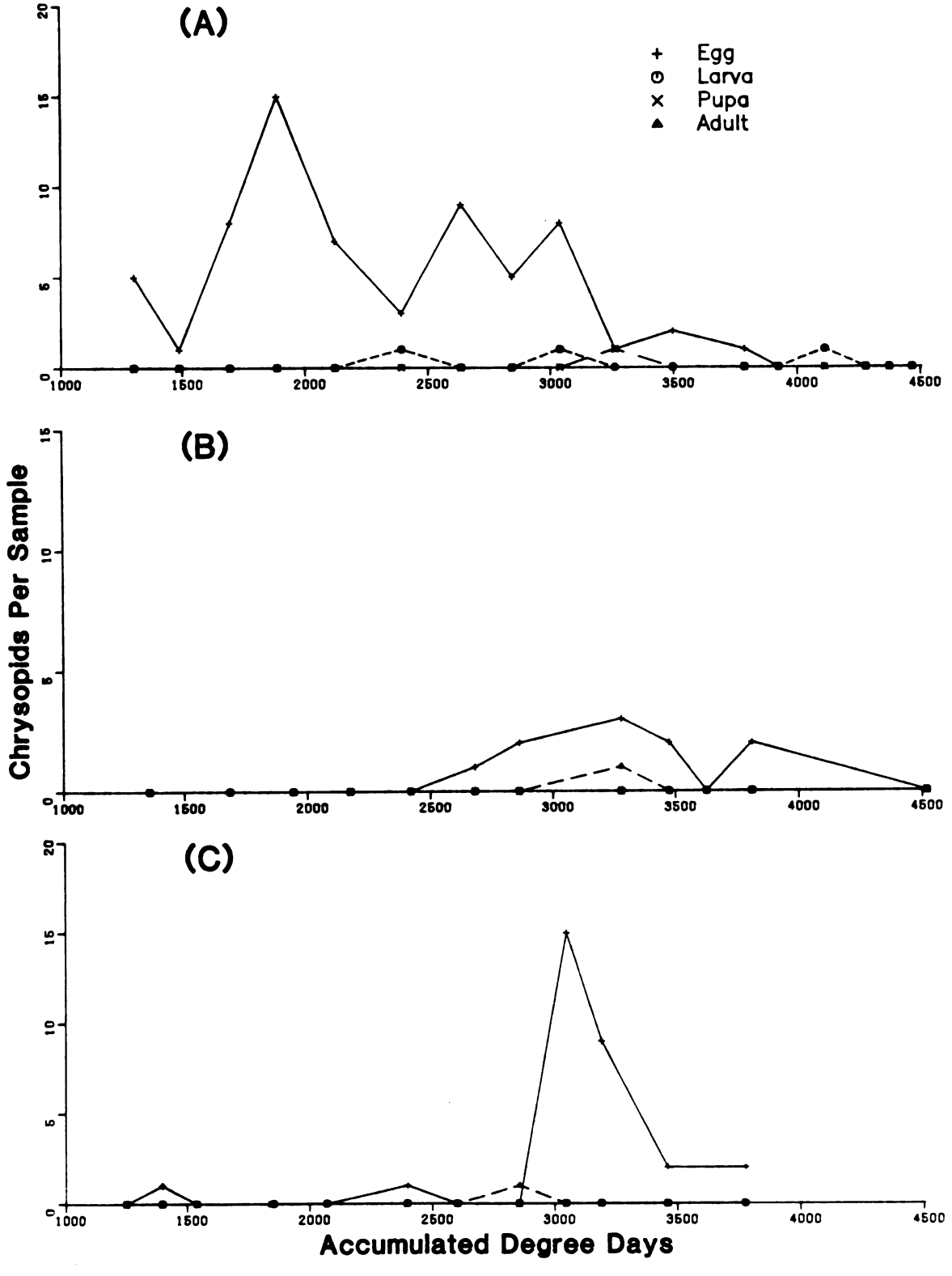


Figure 2.8 Sample counts of chrysopid predators for (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

All dipterans collected during this study are members of the families Cecidomyiidae and Syrphidae. Cecidomyiid larvae were observed only rarely. In fact, during the two years of sampling only three blueberry terminals with cecidomyiid larvae were found. The details of these observations are presented in Table 2.5

Table 2.5 Observations of cecidomyiid predators during the 'standard sample'.

Site	Date	^{o}D	Life stage	No. Observed
1	JUL-27-81	2842	eggs	1
1	SEP-08-82	3811	larvae	1
2	AUG-10-82	2047	larvae	4

Conversely, syrphids were by far the most common aphid predator observed. Sample counts for all syrphid life stages are presented in Figure 2.9. As with some earlier predator species, eggs were the predominant life stage collected in the sample. The only sizeable larval samples were obtained in 1982 at Site 2 (Figure 2.9c). This site also contained aphid counts five to ten times larger than any other plot. In general, both egg and larval counts in Figure 2.9c follow the same pattern. Also, the sharp decline in syrphid numbers between 2500 and 3000 degree days coincides with the applications of Cythion discussed earlier.

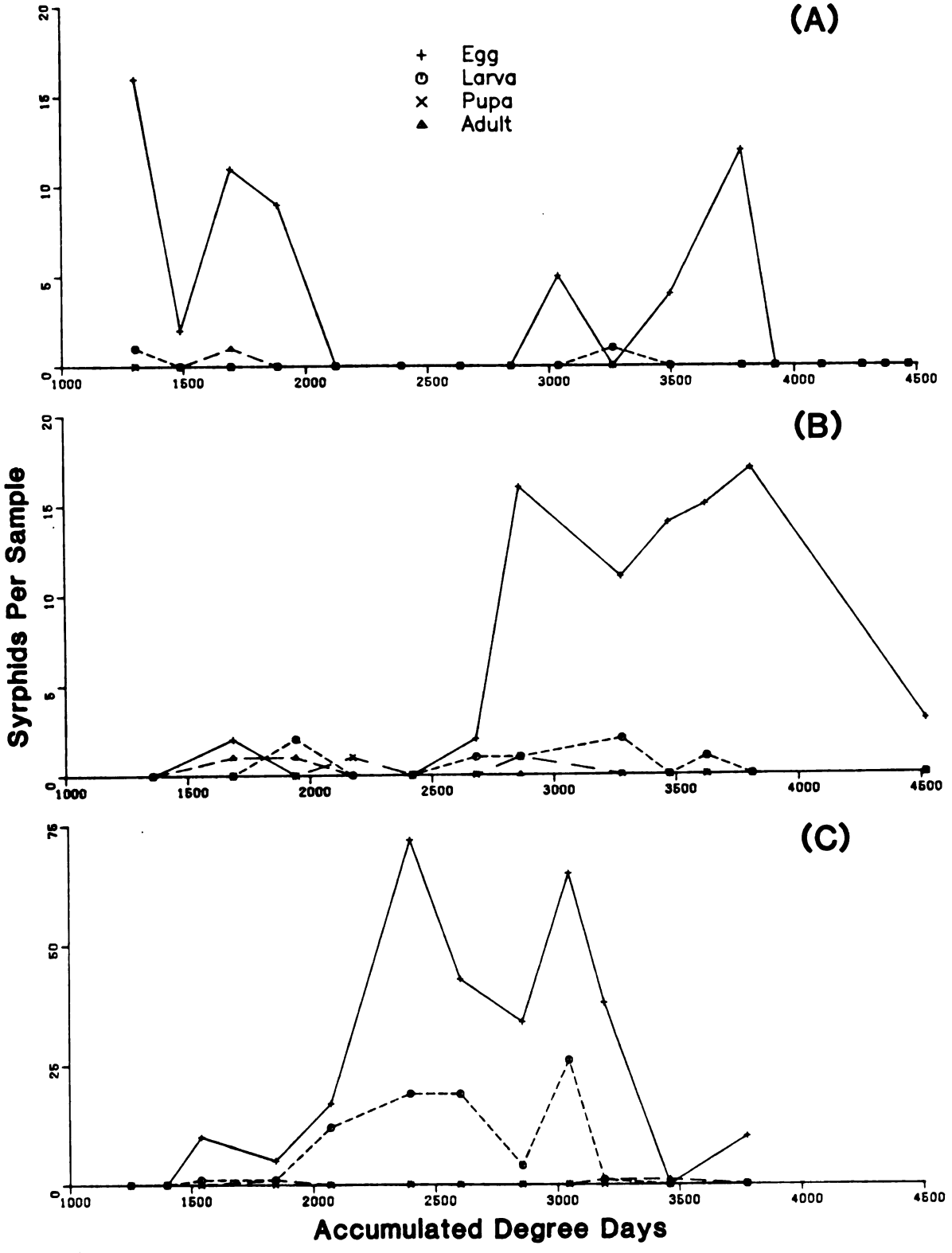


Figure 2.9 Sample counts of syrphid predators for (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

2.4 Discussion

2.4.1 Entomophthora

One surprising result of this study was the complete absence of fungal pathogens. Earlier studies using caged bushes reported significant epizootic outbreaks (Elsner 1982, Morimoto pers. comm.). There are two simple reasons why caging bushes may lead to such outbreaks. First, Entomophthora sp. require high relative humidity for spore germination. Second, according to Hagen & Van den Bosch (1968), epizootic outbreaks appear to be a density dependent mortality factor. Caging blueberry bushes encourages both of these conditions. The results of this study suggest that Entomophthora sp. are not normally a significant mortality factor in the commercial highbush blueberry agro-ecosystem.

2.4.2 Sampling Method

The sampling method used in this study was more successful at capturing some natural enemies than others. Such problems are difficult to avoid when attempting to survey a large number of insect species and life stages with a single sample method. Since it was essentially a static, visual sample, the method was most successful at sampling relatively slow or immobile creatures such as aphids and insect eggs or pupae. The method did not prove useful for sampling highly mobile organisms or life stages. The latter included adults of most natural enemies and larvae of

Coccinellidae and Neuroptera. The difficulties in sampling coccinellids, in particular, has been studied by several authors (Frazer & Gilbert 1976, Gilbert et al. 1976, Mack & Smilowitz 1980).

At present it is unclear exactly how useful the method was in capturing larval Diptera. Substantial numbers of syrphid larvae were only obtained when aphid numbers exceeded 2000 per sample. However, at such high aphid densities the temporal patterns of egg and larval counts were very similar. Either (1) mortality is very high for first instar syrphid larvae, or (2) the sample cannot detect small populations of these larvae. Harris (1973) found that a visual sample was a very poor estimator of the numbers of cecidomyiid larvae in a field of Brussels sprouts. Compared to fixing a leaf sample in 70% EtOH, sieving, and examining under a stereo microscope; a visual examination of the leaves only identified 11% of the larvae present.

2.4.3 Parasitoids

Several interesting conclusions regarding I. pepperi's parasitoids can be drawn from this study:

(1) Parasitoids first appear in the field at approximately 1500 $^{o}D_{38}$.

(2) This parasitoid complex consists of at least two primary parasitoids and one hyperparasitoid. An

additional species was observed to attack I. pepperi in the greenhouse.

(3) Samples of empty aphid mummies are a poor indicator of cumulative adult parasitoid emergence.

(4) Although parasitoids were a significant mortality factor (10-18%) in a highbush blueberry field not subjected to regular chemical suppression strategies, the rate of parasitism remained below 2% in a chemically treated field.

If these estimates of percent parasitism are at all reliable, parasitoids are not a significant mortality factor in most commercial highbush blueberry operations. Before proceeding with the development of a parasitoid sub-model for the aphid simulation program it would be appropriate to obtain a better assessment of the importance of aphid parasitoids in Michigan's commercial highbush blueberry agro-ecosystem. Development of such a sub-model would require that (1) cultures of the major parasitoids be established, and (2) fixed temperature rearing experiments be conducted to determine their lower developmental temperature thresholds and other life-table parameters. On the other hand, a field experiment to asses the importance of aphid parasitoids would be both quicker and less expensive. Such an experiment would also yield additional information on the identity of these parasitoids. It is

very possible that some parasitoid species present in the system were not collected during the above experiment because (1) only two sites were surveyed, (2) they are relatively rare, or (3) they do not affix mummified aphids to blueberry leaves. This assessment could be carried out most economically using an approach modified from Messenger & Force (1963): (1) collect large nymphs of I. pepperi from several locations, (2) rear aphids in clip cages in the greenhouse, (3) place parasite pupae, ie. aphid mummies, in gelatin capsules until adult emergence, and (4) calculate percent parasitism and identify adult parasitoids. Such a sample should be conducted four to five time during the growing season beginning around 1500 $^{o}D_{38}$.

2.4.4 Predators

In general, the phenologies of aphid predators were not consistent among either sites or years. At site 1 chrysopids and syrphids were the most commonly collected predators. Isolated coccinellid adults were also collected during the first half of the growing season. At site 2 syrphids appeared to be the primary aphid predator. Although a previous study found cecidomyiid larvae to be very important, they were very rare in this study.

Just how important each of these predators is in reducing aphid numbers is difficult to say. This study suggests that chrysopids and syrphids are the most common predators in the system. Both families also have a high per

capita consumption rate of aphids. Chrysopid larvae require 200 to 500 aphids to complete their development. Syrphid larvae require from 400 to 800 aphids to complete theirs (Hagen & Van den Bosch 1968). This means that the 25 syrphid larvae observed at site 2 on August 10, 1982, ate ten to twenty thousand aphids during the course of their development! Also, remember that only two species of chrysopids have been reported from highbush blueberries. On the other hand, nineteen species of syrphids have been collected there. To accurately model the population dynamics of I. pepperi it will be necessary to develop methods to account for losses inflicted by these two families of predators.

CHAPTER 3. RANGE AND SPATIAL DISTRIBUTION

3.1 Introduction

This chapter addresses two important questions regarding the distribution of the blueberry aphid, I. pepperi. First, where in Michigan has the aphid been found? Second, how does the within bush distribution of this aphid and its natural enemies change through the growing season?

3.2 Geographical Distribution

Since I. pepperi only infests Vaccinium species, the aphid's range must be a subset of its hosts' ranges. Four blueberry species are found in Michigan: V. corymbosum L., V. angustifolium Ait., V. myrtilloides Michx., and V. vacillans Torr. (Marvin Pritts pers. comm.). Both cultivated and wild stands of the common highbush species, V. corymbosum, may be found throughout the lower half of Michigan's lower peninsula. About 12,000 acres of V. corymbosum are currently under cultivation in the state, with over 90% of this acreage located in southwest Michigan near Lake Michigan (J. Nelson pers. comm.). Late lowbush blueberry, V. angustifolium, is a native species found throughout the upper peninsula and the upper half of the lower peninsula. In some regions of the upper peninsula this blueberry species is the dominant ground cover in coniferous forests and logged areas. I. pepperi feeds on both of these blueberry species and could therefore

potentially be found anywhere in the state. I. pepperi has only been collected from V. myrtilloides on one occasion (E. Elsner pers. comm.). The blueberry aphid has not yet been observed on V. vacillans in Michigan.

Although I. pepperi was not confirmed as the vector of blueberry shoestring until 1979, the aphid was a suspected vector of the disease for many years. As early as 1963 the Michigan Blueberry Grower's Association was encouraging research to identify the BBSSV disease vector (Burger 1966). One result of this research was the first distributional study of aphids in blueberry fields. This study was conducted on ten highbush blueberry farms in southwestern Michigan in Berrien, Van Buren, Allegan, Ottawa, and Muskegan counties. Burger found only two aphid species widely distributed in blueberry fields, Masonaphis (=Illinoia) pepperi and Myzus scammelli (Mason). I. pepperi was collected at all ten sites. While Burger was surveying blueberry fields for virus vectors, Francis Giles (1966) was investigating the geographic distribution of aphid species infesting small fruits in Michigan's lower peninsula. Giles also found I. pepperi to be the prevalent species of aphid in commercial blueberry plantings. Except for one observation in Montcalm County, Giles only found I. pepperi in southwest Michigan near Lake Michigan. Also, he did not report I. pepperi from wild Vaccinium species. Giles' dissertation included a map showing the distribution of I.

pepperi and M. scammelli in Michigan's lower peninsula. Unfortunately, no documentation on the map's construction was included with the work. However, 16 specimens from these two studies were deposited in MSU's Department of Entomology museum.

Since these studies, I. pepperi has been investigated in greater detail. The aphid has been collected from wild V. angustifolium in both the lower and upper peninsulas. During this time blueberry acreage in the state has continued to expand. With these facts in mind it seems appropriate to compile a new list of localities where I. pepperi has been collected (Appendix 2) and construct a new distribution map from this data (Figure 3.1). Data for this map comes from several sources; (1) specimens deposited in the Department of Entomology museum at Michigan State University, (2) I. pepperi study sites used by faculty or graduate students at MSU, and (3) wild Vaccinium sites surveyed by Dr.'s Jim Hancock and Mark Whalon.

The distribution map shown in Figure 3.1 includes all documented sites where I. pepperi has been collected. Vaccinium host species are also indicated. Although I. pepperi has only been collected from 15 of Michigan's 82 counties, the locations of these sitings suggest that the species is found on Vaccinium species throughout the state.

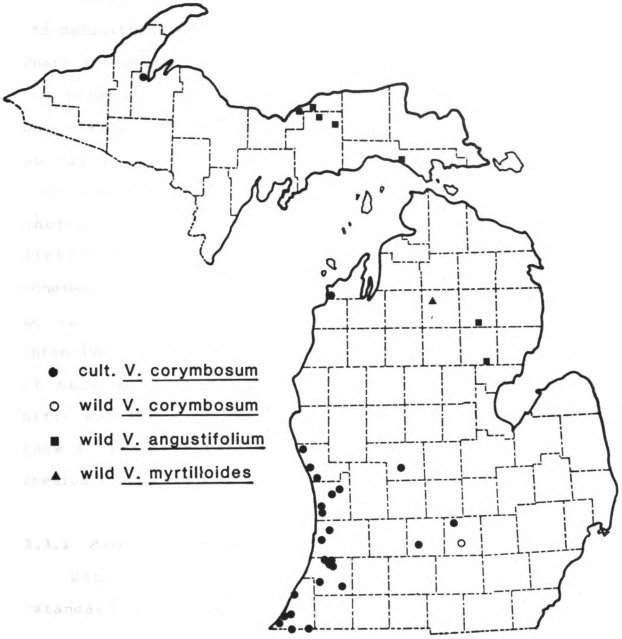


Figure 3.1 Distribution of I. pepperi on wild and cultivated Vaccinium species in Michigan.

3.3 Within Bush Distribution

The remainder of this chapter is devoted to an investigation of the vertical distribution of I. pepperi and its parasitoids within cultivated highbush blueberry bushes. There are several reasons why it is important to understand how this distribution changes through the growing season. One reason, the impact of vertical distribution on aphid survival following aerial pesticide applications, was already discussed in the introductory chapter. But there is another, less obvious reason. Changes in vertical distribution must be accounted for in aphid sampling schemes. During some parts of the year it may be necessary to sample some portions of the blueberry bush more intensively than others. Uneven distribution may even make it necessary to devise different sampling plans for different times of the year. It would also be useful to know if the vertical distribution of the aphid's natural enemies tracks changes in the aphid's vertical distribution.

3.3.1 Materials and Methods

Data for this study was collected as part of the 'standard sample' described in Section 2.2. Blueberry bushes were partitioned roughly into thirds. One terminal was sampled from the upper, middle, and lower portions of each of 25 bushes in each of three rows.

3.3.2 Results

Results for the aphid portion of the vertical distribution study are shown in Figure 3.2. Samples are plotted as percent of the population in a given third of the bush versus degree days. Such graphs can be misleading when the number of aphids actually collected in a sample becomes small. In most samples hundreds of aphids were collected; however, in a few cases aphid populations were almost non-existent. Less than 10 aphids were collected in a sample of 225 terminals at the following times: Site 1, 1982 at 4519 ^{o}D; and Site 2, 1982 at 1253, 3461, and 3777 ^{o}D. The last two dates cited occurred during the collapse of the aphid population following pesticide applications.

The figure indicates that early in the season most aphids were found in the bottom third of the bush. In general, vertical distribution followed a trend of increasing percentages of aphids in the upper third of the bush as the growing season progressed. The middle third of the bush consistently contained the smallest share of the aphid population. A temporary increase in the proportion of aphids in the bottom third of the bush was observed around 3500^{o}D in two of the three plots. Table 3.1 lists summary percentages of vertical aphid distribution in the three plots.

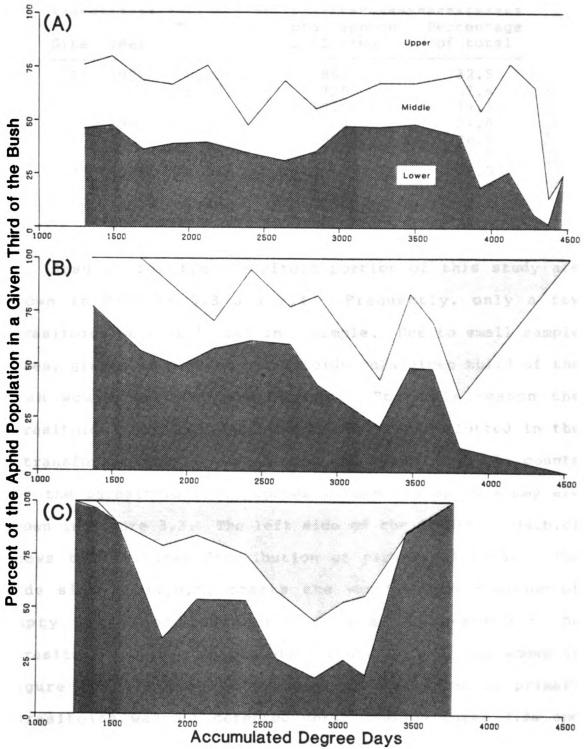


Figure 3.2 Vertical distribution of I. pepperi within highbush blueberry bushes at (a) site 1, 1981; (b) site 1, 1982; and (c) site 2, 1982.

Table 3.1. Overall percentages of aphids in each third of the bush for samples with N > 20 aphids.

Site	Year	Third of bush	Total aphids collected	Percentage of total
1	1981	upper	853	32.5
		middle	726	27.6
		lower	1048	39.3
1	1982	upper	683	24.6
		middle	802	28.9
		lower	1292	46.5
2	1982	upper	3917	33.0
		middle	4381	36.9
		lower	3601	30.1

Results for the parasitoid portion of this study are shown in Figures 3.3 and 3.4. Frequently, only a few parasitoids were collected in a sample. Due to small sample sizes, graphs of percent parasitoids in a given third of the bush would be very misleading. For this reason the parasitoids' vertical distribution have been plotted in the untransformed unit -- parasitoids per sample. Sample counts for the parasitoid that pupates within the aphid mummy are shown in Figure 3.3. The left side of the figure (3.3a,b,c) shows the vertical distribution of parasitoid pupae. The ride side (3.3d,e,f) charts the vertical distribution of empty parasitoid cocoons. Similar diagrams for the parasitoid the pupates beneath the aphid mummy are shown in Figure 3.4. Since the presence of two kinds of primary parasitoids was not detected until 1982, Figures 3.3a and 3.3d contain counts of both parasitoid species.

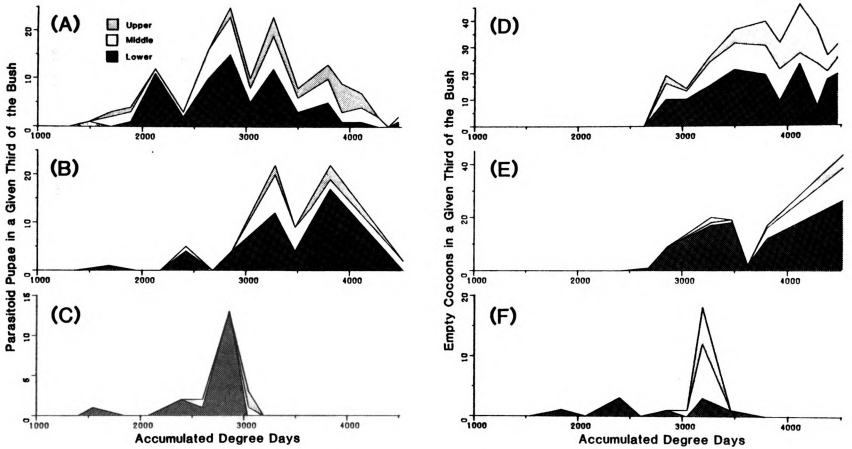


Figure 3.3 Vertical distribution of the aphidiid parasitoid that pupates within the aphid mummy at (a,d) site 1, 1981; (b,e) site 1,1982,; and (c,f) site 2, 1982.

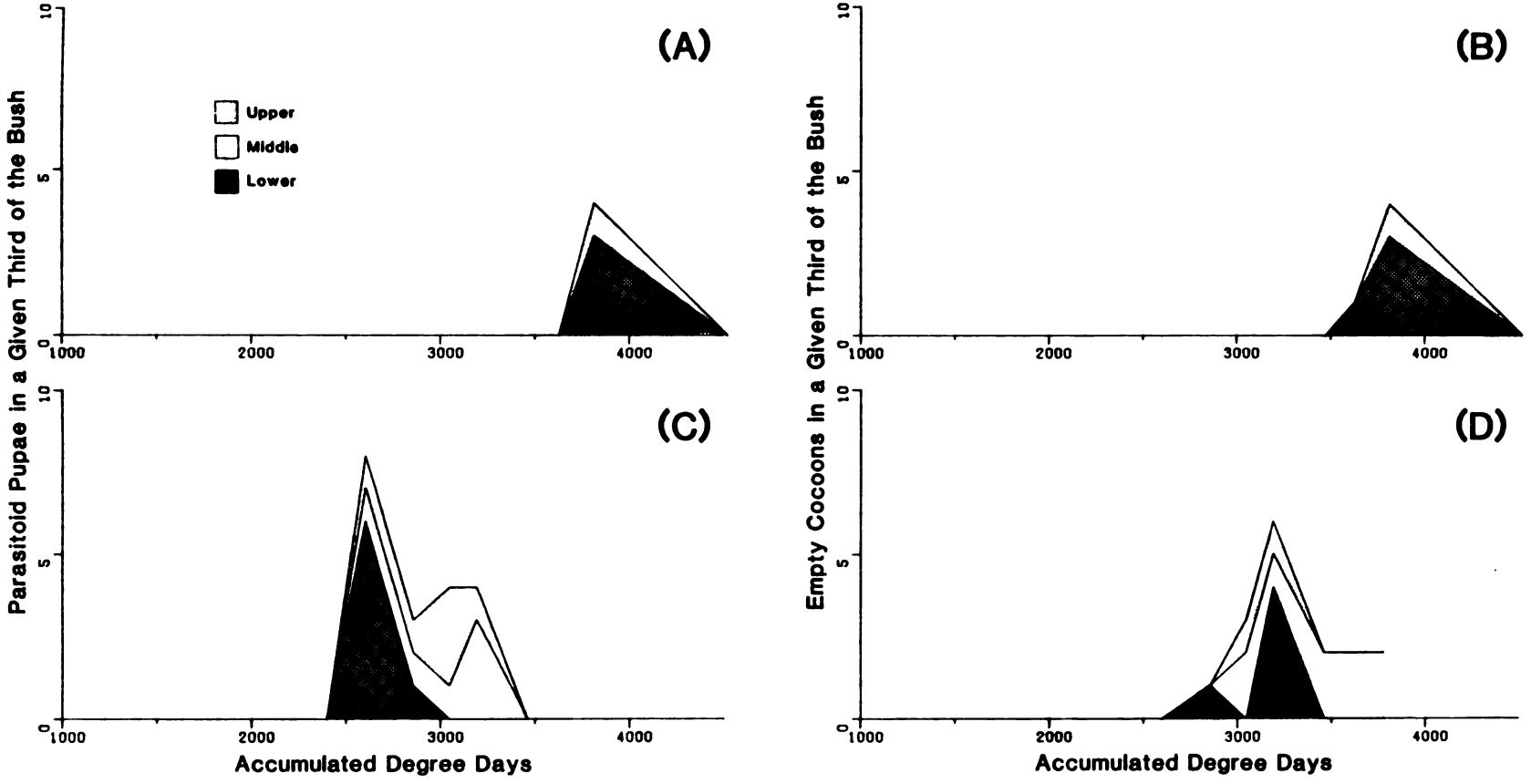


Figure 3.4 Vertical distribution of the aphidiid parasitoid that pupates beneath the aphid mummy at (a,b) site 1, 1981; and (c,d) site 2, 1982.

The most striking aspect of these graphs is the abundance of parasitoids in the bottom third of the bush. Table 3.2 shows that 50% or more of the primary parasitoid pupae were found in the bottom third of the blueberry bush, while 20% or less of the pupae were collected from the upper third of the bush.

Table 3.2. Overall percentages of parasitoid pupae collected in each third of the blueberry bush.

Site	Year	Third of bush	Total aphids collected	Percentage of total
1	1981	upper	24	17.4
		middle	46	33.3
		lower	68	49.3
1	1982	upper	10	11.9
		middle	20	23.8
		lower	54	64.3
2	1982	upper	8	20.0
		middle	8	20.0
		lower	24	60.0

3.3.3 Discussion

Seasonal changes in the vertical distribution of I. pepperi documented in this study agree well with previous knowledge of the aphid's life history. Since fundatrix individuals hatch from eggs in leaf litter or in the crown of the bush, one would expect to find most of the aphids in the bottom third of the bush early in the growing season. As the season progresses aphids become distributed throughout the bush on actively growing terminals. Since most of these terminals are located in the upper portion of

the bush, distribution slowly shifts in favor of aphids being found in the top of the bush. After berries have been harvested the bush experiences a flush of new growth. This late season growth is most noticeable in the crown of the bush. A corresponding increase in the proportion of aphids in the lower third of the bush was observed at this time.

The aphid's parasitoids, on the other hand, display no recognizable shift in vertical distribution through the growing season. Parasitoid pupae are found in increasing numbers as one moves lower in the bush. Usually, more than half of the pupae collected were found in the bottom third of the bush.

These small wasps are not known to be particularly strong fliers. In the M. maxima system, Gilbert & Gutierrez (1973) found different rates of parasitism in patches of thimbleberry separated by as little as 50 meters. From this observation the authors concluded that individual parasitoids do not fly very far. The present study suggests that parasitoids are also less effective in the upper portions of blueberry bushes. One of the following hypotheses seems most likely. Either (1) adult parasitoids spend a greater amount of time searching the lower reaches of the bush, or (2) parasitoids that venture into and above the bush canopy run the risk of dispersal by strong breezes.

CHAPTER 4. APHID GROWTH AND MATURATION

4.1 Materials and Methods

To parameterize the aphid maturation portion of the model the number of degree days required to complete each life stage must be determined. The mean and variance figures needed to parameterize the model's distributed delays were obtained by re-analyzing Elsner's (1982) fixed temperature rearing experiment. Briefly, Elsner's study was a fixed temperature cohort experiment conducted at six different temperatures (5, 10, 17, 23, 26, and 29^{o}C). Aphids were reared individually in small vials on leaf discs floating atop a nutrient solution. Molts and young produced were recorded daily. As they were observed, young were removed to eliminate any complicating density dependent reductions in fecundity. Exuviae were also removed.

The present analysis treats the rearing experiment as a randomized block design with life stage as the treatment variable and temperature as the block variable (after all, temperature is the gradient here). Statistics were done using the SPSS software package. In the course of this analysis, a serious source of experimental bias was discovered. Since the bias will affect the final form of the analysis, it is considered in detail at this time.

4.2 Experimental Bias

Over 90% of the aphids in the experiment died prematurely by drowning. Premature death is readily identifiable during the nymphal stages. Obviously, an aphid that molts has successfully reached the next instar. An aphid that drowns has not been so successful. On the other hand, premature deaths during the adult life stage are more difficult to interpret -- herein lies the rub.

The severity of this drowning bias is most apparent if survivorship curves for reproductive adults are examined. If the experiment was completely unbiased one would expect to obtain very similar curves when survivorship is plotted against accumulated degree days for each temperature block. This expectation is based on the assumption that degree days are an accurate measure of physiological time. Since that assumption breaks down at temperatures near developmental thresholds, a significantly different curve would not be surprising for the 5°C run. Additional knowledge about aphid movement yields yet a third possibility. Both field and greenhouse observations indicate that I. pepperi is more likely to move the higher the temperature. If drowning is the result of temperature induced movement, aphids reared at higher temperatures should drown more frequently than aphids reared at lower temperatures.

Unfortunately, when survivorship of reproductive adults is plotted against accumulated degree days since first birth (Figure 4.1a) the resulting curves do not agree with any of

these hypotheses. Survivorship curves are different for each temperature block. Also, aphids lived progressively longer at each higher temperature. What could have caused this unexpected mortality trend? The answer to this question begins with another graph of survivorship. When percent survivorship is plotted against days since first birth (Figure 4.1b) an interesting pattern emerges. Aphid mortality in the experiment was a function of calendar time not degree days.

Remember, the experiment was sampled daily and any young were removed to eliminate complicating density dependent reductions in fecundity. Similarly, during the nymphal instars daily sampling included removal of exuviae. In this light premature death can be viewed as a function of sample interval. Every time a vial was sampled there was a probability that the sampling process itself would perturb the aphid enough to cause it to move. Movement, in turn, was a risk involving a fixed probability of drowning. In effect, a sampling technique designed to be non-destructive was actually quite destructive.

In the analysis detailed below, only those aphids that lived long enough to reproduce were included. By placing this restriction on the data, any bias due to premature deaths could at least be eliminated from results for the nymphal instars. Unfortunately, this criteria also results

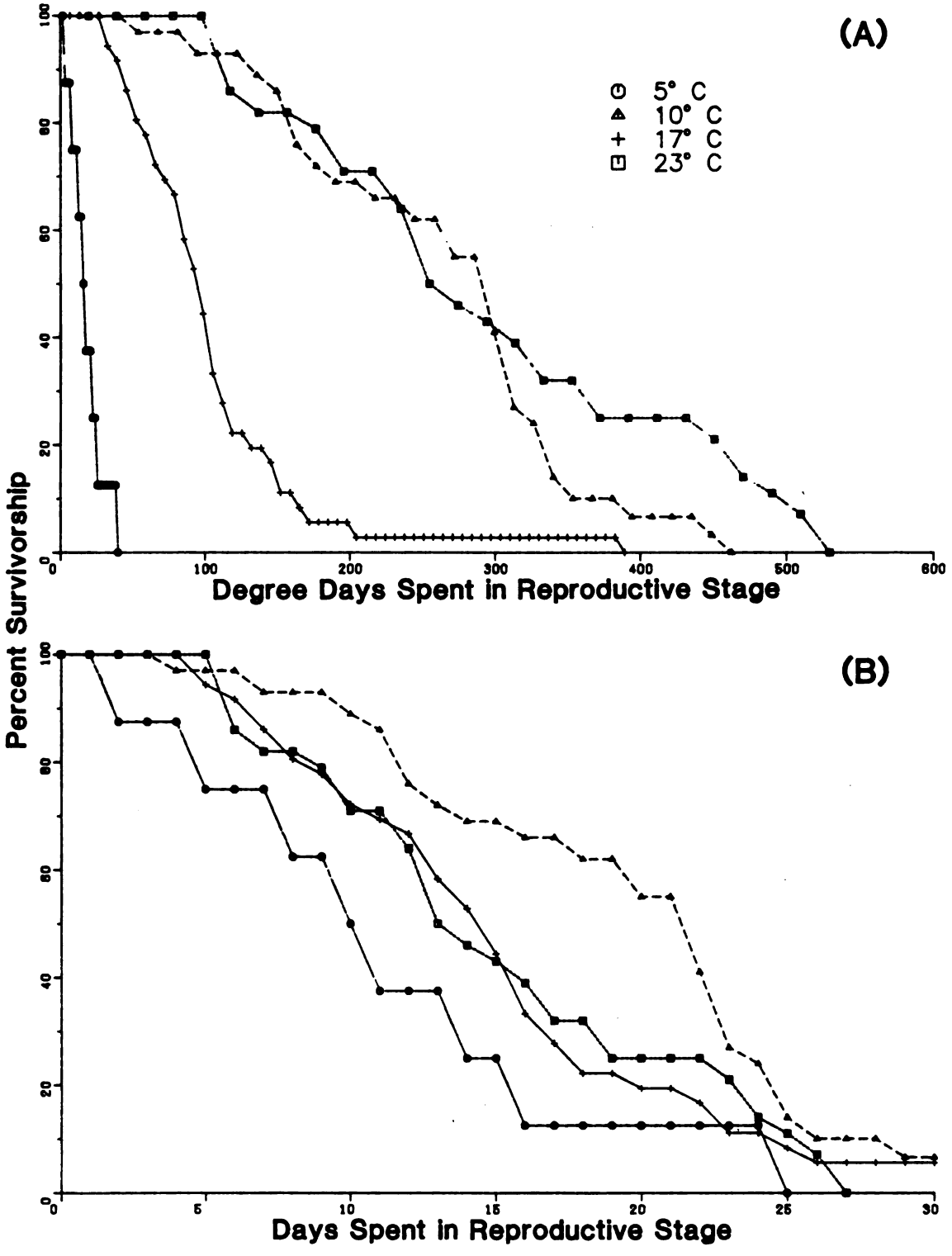


Figure 4.1 Survivorship of reproductive I. pepperi versus (a) physiological time, and (b) calendar time.

in the exclusion of the two highest temperature blocks, 26 and 29°C.

4.3 Results

First, an analysis of variance was conducted to determine the number of degree days required to complete each instar. The ANOVA summary shown in Table 4.1 indicates that the length of the aphid's first three instars is approximately equal. The length of the fourth instar, in turn, is significantly longer ($P \leq 0.05$) than any of the earlier stages. This result agrees with similar data for I. maxima (Campbell et al. 1974, Gilbert et al. 1976).

Table 4.1 ANOVA summary of fixed temperature rearing experiment for four nymphal instars of I. pepperi reared at 5, 10, 17, and 23°C.

Instar	mean	S.E.	95% conf. int. for mean
first	33.34	1.7448	29.86 < x < 36.83
second	37.46	1.4082	34.65 < x < 40.28
third	41.27	1.4979	38.28 < x < 44.27
fourth	53.70	2.3824	48.95 < x < 58.46

The next step was to decide how to convert laboratory data containing four nymphal instars to the three nymphal age classes reported in field samples. I believe the discrepancy between this experiment and field observations lies in the inability to distinguish between the first three nymphal instars. As a result, second instar nymphs were sometimes classified as small nymphs and sometimes as medium nymphs in the field. Therefore, the analysis of variance was conducted again after the data for each aphid

(designated [i]) was transformed from four to three nymphal stages as follows:

$$\text{Small}[i] = \text{First}[i] + \text{Second}[i] / 2.0$$

$$\text{Medium}[i] = \text{Third}[i] + \text{Second}[i] / 2.0$$

$$\text{Large}[i] = \text{Fourth}[i]$$

Analysis of variance for all aphid life stages following this transformation is summarized in Table 4.2. The highly significant F values in this table indicate that different degree day accumulations were required to complete a life stage at different temperatures. Examination of results from Scheffe's multiple range test ($P \leq 0.05$) reveals that the problem lies in the 5°C temperature block. This temperature consistently produced the lowest mean values for degree days spent in a stage. A previous analysis of this experiment (Elsner 1982) indicated that the lower developmental threshold temperature for I. pepperi is approximately 3.4°C. Consequently, the consistently low estimates for mean development time obtained at 5°C are probably the result of being in the non-linear portion of the developmental rate curve. Therefore this block was removed and the ANOVA conducted yet another time for 10, 17, and 23°C.

Table 4.2 ANOVA summary of fixed temperature rearing experiment for all life stages of I. pepperi reared at 5, 10, 17, and 23°C.

Stage	mean	S.E.	F	95% confidence interval
nymphs				
small	52.08	2.010	4.179**	48.06 < x < 56.09
medium	60.01	1.919	25.286***	56.17 < x < 63.84
large	53.70	2.382	5.518**	48.95 < x < 58.46
adults[13]				
pre-repro	55.68	2.501	11.359***	50.69 < x < 61.44
repro	161.04	15.976	19.389***	129.12 < x < 192.95
total	216.72	15.076	16.805***	186.60 < x < 246.84

Table 4.3 ANOVA summary of fixed temperature rearing experiment for all life stages of I. pepperi reared at 10, 17, and 23°C.

Stage	mean	S.E.	F	95% confidence interval
nymphs				
small	53.92	2.073	2.164	49.77 < x < 58.07
medium	63.00	1.771	15.019***	59.46 < x < 66.55
large	56.74	2.355	0.127	52.02 < x < 61.45
adults				
pre-repro	55.89	2.769	15.933***	50.35 < x < 61.44
repro	179.70	16.255	16.748***	147.15 < x < 212.25
total	235.59	15.086	12.569***	205.38 < x < 265.80

---

[13] Abbreviations for adult life stages:
pre-repro = pre-reproductive adults
repro = reproductive and post reproductive adults
total = complete adult life stage

** $P < 0.01$

*** $P < 0.001$

Elimination of the 5°C temperature block improves the results markedly (Table 4.3). There are now no apparent block differences for small and large aphid nymphs. The significant F statistic for medium nymphs may be partly due to the regrouping of data. Notice that block differences are still very significant ($P<0.001$) for the adult life stages. In fact, all three adult categories also fail Bartlett's Box F test for homogeneity of error ($P\leq 0.05$). The statistical difficulties associated with the adult stages are most likely due to the drowning bias discussed earlier.

4.4 Discussion

The drowning bias encountered in this experiment is very serious. The only data available for parameterizing the distributed delays simulating aphid growth and reproduction comes from this fixed temperature rearing experiment. Yet, parameters for the adult life stage (representing over 50% of the aphid's lifetime) obtained from the experiment are dubious at best. The length of the adult stage, presently estimated at 250 °D, could be 350 or possibly even 400 °D. Errors in estimating this parameter will result in error to all model parameters subject to 'tinkering'. Two aspects of the model affected by such error will be the aphid's potential rate of increase and the impact of biotic mortality factors.

The fixed temperature cohort study must be conducted again. Individual aphids could be caged on live plants to eliminate drowning. Since the nutritional quality of individual plants can vary greatly, and relatively few plants will be used in the experiment; measures must be taken to ensure that the nutritional status of the bushes is as uniform as possible. To accomplish this, host phenology should be synchronized by forcing bushes through a dormant period. Bushes should also be replaced at regular intervals.

Once the experiment has been completed, it will be necessary to re-parameterize the aphid growth portion of the model, fit it to field data, and test it against an independent data set. Until these measures have been completed only limited trust should be placed in the simulation.

CHAPTER 5. FECUNDITY

5.1 Introduction

Determining a specie's fecundity is a central component of any effort to understand or predict that organism's population dynamics. Often, a specific number is associated with a birth rate for a given organism. But an insect's reproductive rate is often not a constant but a function of environmental factors. Aphid fecundity in particular is known to be affected by many factors such as crowding (Johnson 1965, Shaw 1970, Dixon 1974, 1975), nutrition (Johnson 1966, Mittler & Sutherland 1969, Dixon 1974, Dixon & Dharma 1980, Wellings et al. 1980), time of year (Way & Banks 1968, Dixon 1975), morph (Dixon 1976a, Wratten 1977, Dixon & Dharma 1980), and size (Dixon & Wratten 1971, Wratten 1977).

To date, several methods have been used to estimate aphid fecundity in the field. The most common methods employed are (1) cohort studies on caged aphids (Way & Banks 1968, Dixon 1975), (2) counting ovarioles (Dixon & Dharma 1980, Wellings et al. 1980), and (3) counting aphid embryos (Gilbert & Gutierrez 1976, Wratten 1977). For several aphid species teneral adult weight has been shown to be a very good predictor of fecundity (Dixon 1970, 1976a, Dixon & Wratten 1971, Taylor 1975, Wratten 1977, Dixon & Dharma 1980, Wellings et al. 1980). For example, Wratten (1977) used relationships involving adult weight within 24 hours of

ecdysis and embryo compliment to predict reproductive potential of apterous and alate morphs of the aphids Sitobion avenae F. and Metopolophium dirhodom Wlk. Conversely, ovariole number alone has been found to be a poor predictor of potential fecundity for several aphid species (Dixon & Dharma 1980, Wellings et al. 1980). Although seasonal changes in ovariole number are very predictable, the number of embryos per ovariole is highly variable. Both of these studies indicate that ovariole number appears to be a programmed feature of aphid life cycles and is not a function of either food quality or adult weight.

5.2 Materials and Methods

Data for these fecundity studies come from two sources. First, data collected by Elsner (1982) was re-analyzed to determine how aphid births are distributed over a stem mother's adult life stage. Methods used in that experiment were summarized in Section 4.1. Since no young were produced at the two highest temperatures used in the experiment (26 and 29^{o}C), the current analysis only incorporates data from the lower four temperature treatments (5, 10, 17, and 23^{o}C).

Data for the seasonal aphid fecundity study was collected during the summer of 1982 at the same two sites where the 'standard sample' was conducted (Section 2.2). In this study individual stem mothers found during the course

of the 'standard sample' alone or with a group of young were collected and the number of young in the colony was recorded. Stem mothers were then carefully dissected to determine the numbers of developed and undeveloped embryos they contained. Developed embryos were defined as those with pigmented eyes (cf. Gilbert & Gutierrez, Wratten 1977). Apterous and alate aphids were recorded separately. Statistically, this study was designed as a two by two factorial experiment with two sites and two aphid morphs. In a similar study, Gilbert & Gutierrez (1976) estimated aphid fecundity as the sum of the young in a colony plus the number of developed embryos. Wratten (1977) however, indicates that developed embryos only represent births that will occur in the next 24 to 48 hours. To determine which of these hypotheses is correct fecundity was calculated using both methods. For convenience the methods will be referred to as 'upper' and 'lower' bounds for seasonal fecundity. The lower bound was estimated as the regression line for young in a colony plus developed embryos, while the upper bound was defined by the regression line for young in the colony plus all embryos. Analysis of variance was done using the SPSS software package. Regression analysis was conducted using SPOCS.

5.3 Results

5.3.1 Frequency Distribution of Births

One consequence of using distributed delays to simulate aphid growth (details of this process will be discussed in Section 8.3.4) is that the computer model requires a discrete frequency distribution describing how fecundity varies during an aphid's reproductive period. Ultimately, this distribution must take the form of a histogram conforming to the following three criteria. First, the time (or X) axis must be in physiological time units, ie. degree days, where

$$X_{max} - X_{min} = \text{mean time spent in reproductive stage} \qquad (5.1)$$

In practice, it is often easiest to set X_{min} equal to 0. Second, the histogram is divided into K equal cells where

$$\text{Cell Width} = \frac{\text{mean time spent in reproductive stage}}{K} \qquad (5.2)$$

K in this case refers to the order of the distributed delay. Finally, the y value of each cell, Y_i, corresponds to the proportion of births that occur during that segment of the reproductive period. It follows by definition that

$$\sum_{i=1}^{K} Y_i = 1.0 \qquad (5.3)$$

To date, aphid fecundity data from the fixed temperature rearing experiment conducted by Elsner (1982) has only been presented in the form of mean young per day versus degree days after molt to adult instar. In this format different temperature treatments cannot be compared. Since insect development rate is different at different temperatures, days after molt is not a uniform measure of time. Therefore, the first step in this analysis was to convert calendar time to degree days using a lower developmental threshold of 38°F (Elsner 1982). Figure 5.1 contains graphs of the number of births per aphid per day versus accumulated degree days since adult molt for the four temperature treatments in which young were produced. It is important to note that since mortality occurs throughout the adult life stage, births per day must be reported on a per aphid basis. One consequence of this strategy is that when the sample size becomes very small a single birth can dramatically alter the histogram. This effect is particularly noticeable in the 10°C treatment (Figure 5.1b) when, after 250 degree days, the sample size has been reduced to one. In subsequent analyses this bias has been eliminated by truncating that data sets when the sample size

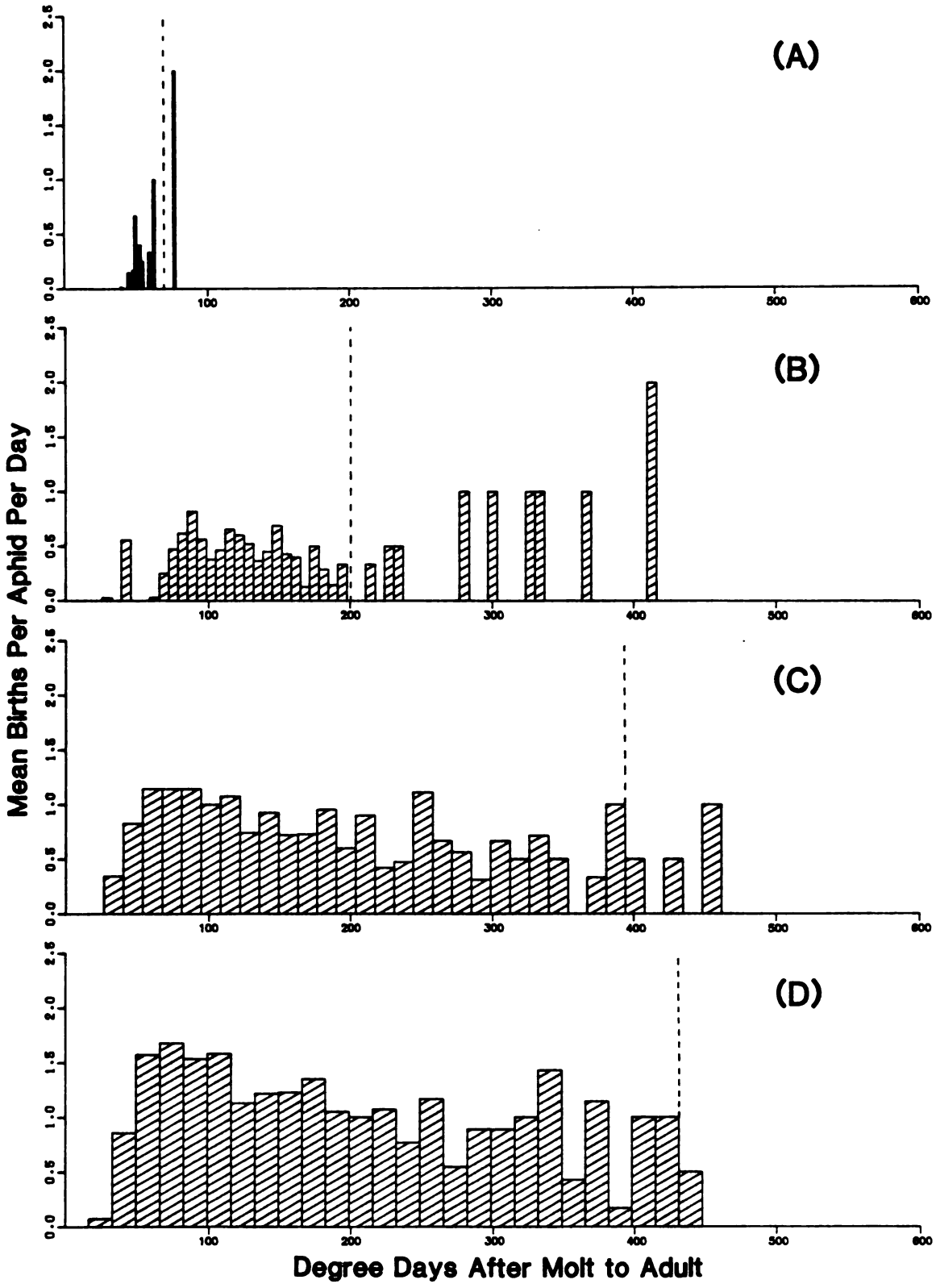


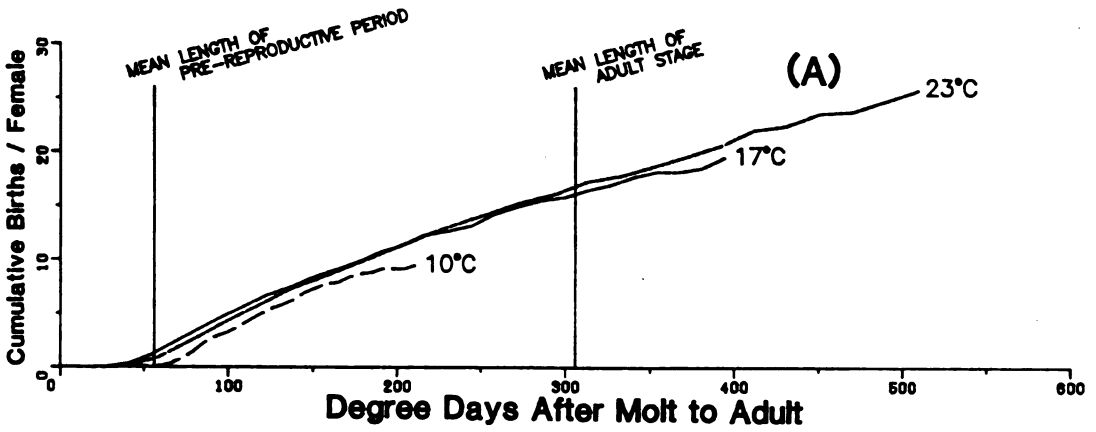
Figure 5.1 Temporal pattern of reproduction for I. pepperi reared at (a) 5°C, (b) 10°C, (c) 17°C, and (d) 23°C. Dotted line marks 90% mortality.

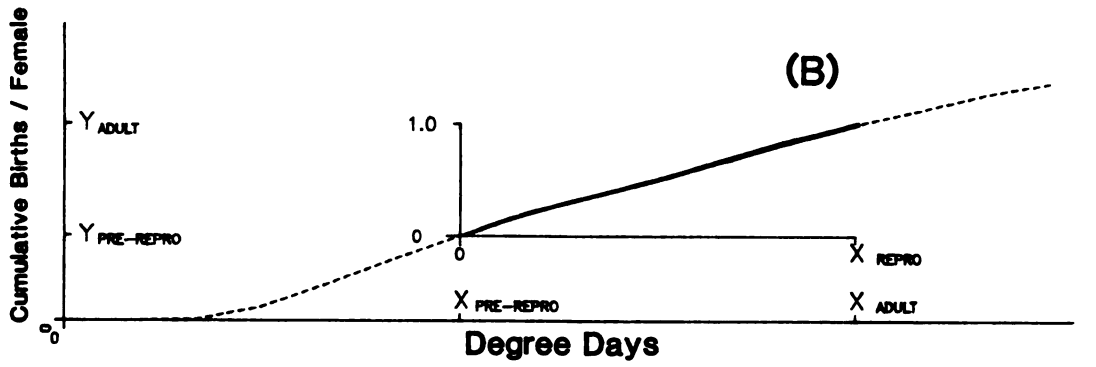
is reduced by 90 percent. Data from the lowest temperature treatment, 5°C (Figure 5.1a), has also been eliminated from subsequent analyses. This data set simply contained little useful information. Undoubtedly, this is primarily due to the fact that aphids in the treatment only spent an average of 6.4 °D in the reproductive stage. Many of these aphids were still alive when the experiment was terminated. At that point some of them were over 100 days old!

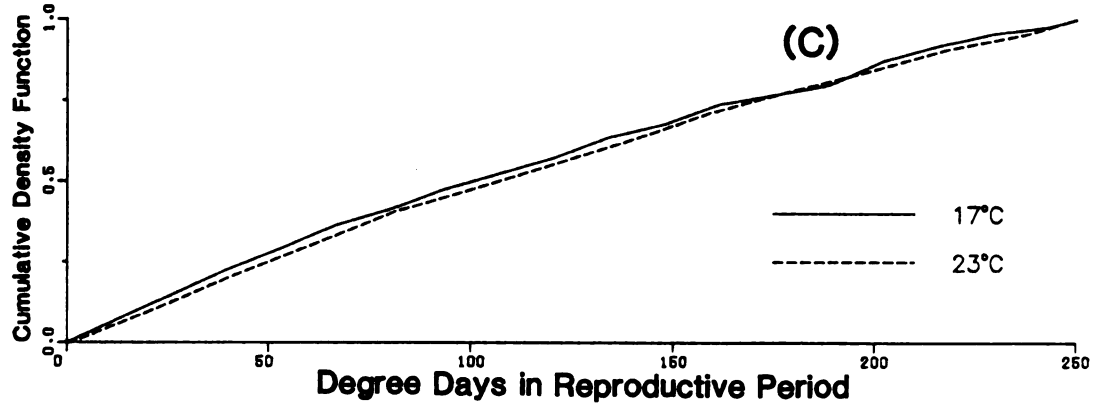
Further examination of Figure 5.1 reveals that these histograms really don't look very similar at all. This is a result of transforming the X axis to physiological time units. Since data was originally collected daily, the transformation results in different cell widths for each temperature. This difficulty is corrected in Figure 5.2a by plotting the truncated data sets as cumulative births per aphid per day versus accumulated degree days since adult molt.

The data is now in a form to begin satisfying the three criteria detailed at the beginning of this section (see Figure 5.2b for a graphical description of this process). First, it is necessary to window data to cover only the mean length of the reproductive phase of the adult life stage. This is accomplished by eliminating data for degree day totals greater than the mean length of the adult life stage and less than the mean length of the pre-reproductive period.

Figure 5.2 Temporal pattern of reproduction: (a) cumulative births/female versus ^{o}D after molt to adult, (b) transforming the cumulative function to a cumulative density function (CDF), (c) aphid fecundity CDF, and (d) discrete probability density fecundity function (PDF).


MEAN LENGTH OF PRE-REPRODUCTIVE PERIOD
MEAN LENGTH OF ADULT STAGE
(A)
23°C
17°C
10°C
Cumulative Births / Female
Degree Days After Molt to Adult


(B)
Y ADULT
Y PRE-REPRO
1.0
0
X REPRO
X PRE-REPRO
X ADULT
Cumulative Births / Female
Degree Days


(C)
17°C
23°C
Cumulative Density Function
Degree Days in Reproductive Period

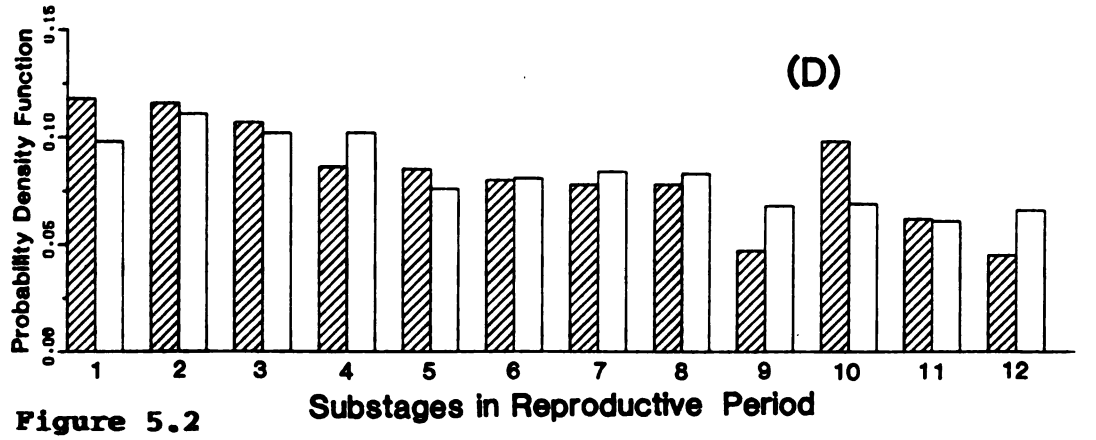

(D)
Probability Density Function
Substages in Reproductive Period

Figure 5.2

Let

$X_{pre\text{-}repro}$ = mean length of pre-reproductive period

X_{adult} = mean length of adult life stage

X_{repro} = mean length of reproductive period

t = time axis, in degree days

then,

$Y_{pre\text{-}repro}$ = cumulative births/aphid/day at $X_{pre\text{-}repro}$

Y_{adult} = cumulative births/aphid/day at X_{adult}

Y_{repro} = cumulative births/aphid/day at X_{repro}

t_new = transformed time axis, in degree days

Since Y values are cumulative it is necessary to transform them as follows:

$$Y_{t\_new} = Y_t - Y_{pre\text{-}repro}$$

This results in the following identity:

$$Y_{repro} = Y_{adult} - Y_{pre\text{-}repro}$$

If X values are transformed in a similar fashion

$$X_{t\_new} = X_t - X_{pre\text{-}repro}$$

The cumulative fecundity function now exists between (0,0) and (X_{repro}, Y_{repro}). To transform this cumulative function into a true cumulative density function calculate

$$Y_{t\_new} = \frac{Y_{t\ new}}{Y_{repro}}$$

Figure 5.2c shows the experimental data following these transformations. All that remains is to convert this cumulative density function to a probability function displayed as a histogram with K cells where

$$\text{Cell Width} = \frac{X_{repro}}{K} = \frac{250}{12} = 20.83\ ^{o}D$$

Values for K and X_{repro} are from Table 8.4. The probability density functions for the 10°C and 17°C temperature treatments are shown in Figure 5.2d. Results from a Kolomagorov-Smirnov test (KS=.03, n=12, ns) indicate that both treatments are from the same distribution. Therefore an average of the two treatments will be used to parameterize the probability density function (Table 5.1) required by the distributed delay.

5.3.2 Seasonal Aphid Fecundity

Data was first analyzed using covariate analysis of variance to determine if (1) seasonal changes, (2) site differences, or (3) morph differences were significant. Upper and lower bounds were analyzed separately. Results of these two ANOVAs are summarized in Tables 5.2 and 5.3.

Table 5.1 Discrete probability density function of the temporal pattern of births for apterous *I. pepperi*.

Degree day interval	% births in interval
0.00 to 20.83	10.80
20.84 to 41.67	11.35
41.68 to 62.50	10.45
62.51 to 83.33	9.40
83.34 to 104.17	8.05
104.18 to 125.00	8.05
125.01 to 145.83	8.10
145.84 to 166.67	8.05
166.68 to 187.50	5.75
187.51 to 208.33	8.35
208.34 to 229.17	6.15
229.18 to 250.00	5.55

Results of the two analyses are very similar. In both cases the covariate, degree days, was the most significant variable ($P<0.001$). Both analyses also indicated no significant difference in fecundity between apterous and alate morphs. The two analyses do differ regarding the question of site differences. When fecundity is defined as the number of young in a colony plus all embryos (upper bound), site differences were highly significant ($P<0.01$). However, when fecundity is defined as the number of young in a colony plus only developed embryos (lower bound), site differences were not significant.

The second step in this analysis was to use linear regression to determine the functions best describing upper and lower bounds for seasonal fecundity. Results from theanalysis of variance indicate that site and degree days are the appropriate variables for the regression.

Table 5.2 ANOVA summary of seasonal fecundity of I. pepperi where fecundity = young in colony plus all embryos.

Source	df	Mean Square	F
Covariates	1	4772.941	125.629***
degree days	1	4772.941	125.629***
Main Effects	2	248.139	6.479**
site	1	455.280	11.983***
morph	1	30.549	0.804
2-Way Interactions	1	0.433	0.011
site X morph	1	0.433	0.011
Explained	4	1316.413	34.649***
Residual	219	37.992	
Total	223	60.924	

Table 5.3 ANOVA summary of seasonal fecundity of I. pepperi where fecundity = young in colony plus developed embryos.

Source	df	Mean Square	F
Covariates	1	2085.118	79.040***
degree days	1	2085.118	79.040***
Main Effects	2	41.309	1.566
site	1	72.929	2.765
morph	1	8.353	0.317
2-Way Interactions	1	5.849	0.214
site X morph	1	5.849	0.214
Explained	4	543.346	20.597***
Residual	219	26.382	
Total	223	35.853	

** $P < 0.01$

*** $P < 0.001$

Therefore, separate multiple regression equations for upper and lower bounds were determined using the following statistical model

$$Y = \sum_{s=1}^{2} a_1*S_1 + a_2*S_2 + a_3*S_1*{}^{O}D + a_4*S_2*{}^{O}D + E(0,\sigma)$$

where,

Y = predicted fecundity per aphid
${}^{O}D$ = accumulated degree days base 38^{O}F
S_1 = 1 if site = 1, 0 if site = 2
S_2 = 0 if site = 1, 1 if site = 2
$a_1..a_4$ = constants determined by regression
$E(0,\sigma)$ = random error term with a mean of 0 and standard error of

Results for these two regressions are summarized in Tables 5.4 and 5.5. The coefficient of variability for the upper and lower bound regressions were 47.2% (F=46.963, P<0.001) and 59.5% (F=28.429, P<0.001), respectively. In both cases the tables reveal that the 95% confidence intervals for slopes and intercepts at the two sites overlap.

5.4 Discussion

I only have one brief comment about the laboratory fecundity study. In general, the form of the analysis used should work for transforming data from other sets of fixed temperature fecundity experiments if one important assumption is met. Births per degree day must be independent of temperature. The data set used here did

Table 5.4 Regression results of seasonal fecundity study where fecundity = young in colony plus all embryos.

constants	S.E.	F	95% conf. int.
a_1 32.015	3.777	0.290^{14}_{***}	24.50 < a_1 < 39.53
a_2 29.980	2.923	105.194_{***}	24.16 < a_2 < 35.80
a_3 -8.040E-3	8.886E-4	82.290_{***}	-9.96E-3 < a_3 < -6.12E-3
a_4 -6.015E-3	1.202E-3	25.059_{***}	-8.63E-3 < a_4 < -3.40E-3

Table 5.5 Regression results of seasonal fecundity study where fecundity = young in colony plus developed embryos.

constants	S.E.	F	95% conf. int.
a_1 22.352	3.141	1.262^{14}_{***}	16.10 < a_1 < 28.60
a_2 18.823	2.431	59.944_{***}	13.99 < a_2 < 23.66
a_3 -5.653E-3	7.371E-4	58.803_{***}	-7.24E-3 < a_3 < -4.06E-3
a_4 -3.740E-3	9.994E-4	14.006_{***}	-5.92E-3 < a_4 < -1.56E-3

---

[14] Due to the way SPSS calculates multiple regressions, this F value really represents the significance of the difference between a_1 and a_2.

*** P < 0.001

indeed meet this assumption; however, only results from 10, 17, and 23°C treatments were used. It will be interesting to see if this assumption is met once the aphid has been successfully reared over a broader range of temperatures.

Several comments about the seasonal fecundity study are in order. The first two comments concern differences in results for the upper and lower boundary conditions. When estimated fecundity is defined as the number of young in a colony plus all embryos (cf. Wratten 1977) site differences are highly significant. However, when fecundity is defined as the number of young in the colony plus only developed embryos (cf. Gilbert & Gutierrez 1976) site differences were not significant. If, as Wratten suggests, developed embryos only represent young born during the next 24 to 48 hours then, indeed, we should expect little difference between sites when potential fecundity is estimated using Gilbert & Gutierrez's criteria. On the other hand, if Gilbert & Gutierrez's criteria is an accurate estimation of potential fecundity then undeveloped embryos must be surplus reproductive material that is a programmed part of the aphid life cycle. If Gilbert & Gutierrez are correct and if site differences do indeed exist, then their method should reveal them and potential fecundity calculated using Wratten's approach should result in no significant difference in fecundity for the two sites. The results from this experiment agree with Wratten's hypothesis and do not support the argument of Gilbert & Gutierrez.

Next, I should like to consider the curious relationship between the F statistics and the multiple regression results for the two boundary conditions. The upper boundary definition for seasonal fecundity resulted in higher F statistics throughout the ANOVA tables. Yet, the multiple regression equation for the upper boundary explained 12% less of the variation in the data than did the multiple regression for the lower boundary condition. Also, site differences in the slopes and intercepts for the multiple regression equations were greater for the lower boundary than for the upper boundary. Nowhere however, were they significant at P=0.05. This pattern suggests that the data has been fitted to an inappropriate regression line. Several transformation were tried; however, none of them resulted in higher coefficients of variability. Nor did they changes the pattern of this statistic for the two boundaries. The most reasonable explanation is that seasonal fecundity is not a linear function at all but a polynomial one. Way & Banks (1968) demonstrated that such is the case for the black bean aphid, Aphis fabae Scop. If changes in the nutritional quality of the host is indeed the primary factor influencing fecundity, then there maybe a very simple biological reason for a polynomial form to the equation. Once the blueberry fruit has matured the bush undergoes a short-lived late season burst of new terminal growth. This abundance of new growth could, in turn, result in a temporary upswing in aphid fecundity.

Throughout this experiment variability in estimated fecundity between aphids collected on the same date was quite high. This high variability is probably the result of aphid movement. During periods of hot weather, ie. above 90°F, aphids were observed actively walking on blueberry leaves. This tendency would result in an underestimation of potential fecundity during generations subjected to hot weather in July and August. Natural enemies could also be responsible for changing patterns of aphid dispersal through the growing season. For instance, Wratten (1976) has shown that lime aphids, Eucallipterus tillae L., are sometimes able to escape predation from coccinellid larvae by jumping, kicking, or running away. The percentage of aphids escaping was dependent on the life stage of both the aphid and the predator and on the mode of escape attempted by the aphid. Frazer & Gilbert (1976) obtained similar results when studying coccinellid predation on pea aphids, Acyrthosiphum pisum. Predator induced movement of adult aphids would also result in underestimates of potential fecundity.

Due to (1) the high variability in the data of this experiment, (2) potential problems due to aphid dispersal, and (3) the great expense (in time and labor) of dissecting large numbers of aphids, I would suggest that future field experiments concerning aphid fecundity be conducted using individually caged aphids. Experiments could be initiated with fourth instar nymphs. This technique should result in

less within date variation, and larger sample sizes can be used with less increase in cost.

CHAPTER 6. MORPH DETERMINATION

6.1 Introduction

The population model detailed in chapter eight includes both apterous and alate, viviparous morphs of I. pepperi. The sole objective of this chapter is to determine how to correctly allocate newborn aphids between these two morphs.

No experiments were conducted to investigate the mechanisms influencing morph determination in this aphid. That project would easily be a thesis topic in its own right. Instead, a review of the existing literature was used to reveal which environmental and biological factors consistently play a role in this process throughout the family Aphididae. Once identified, aphid field data was plotted in terms of these factors and analyzed to arrive at an acceptable mathematical function for the model.

6.2 Literature Review

Scientific literature exploring the causes of aphid polymorphism is quite voluminous. The subject has been debated in more than 100 scientific papers and several review articles (Hille Ris Lambers 1966, Lees 1966, Mittler & Sutherland 1969, Schaefers 1972). Five factors have been demonstrated to be important in the process of morph determination: crowding, nutrition, temperature, photoperiod, and parentage. In general, the literature can be divided into two groups. The first group of papers

explores factors involved in determining whether a female aphid will produce sexual or parthenogenic forms. Photoperiod, temperature, parentage, and to a lesser extent nutrition all play a role in governing the appearance of sexuales (Bonnemaison 1951; Lees 1959, 1960, 1963, 1966; Dixon & Glen 1971; and Dixon 1977). A second, and larger body of research addresses factors influencing whether parthenogenic aphids will be apterous or alate. Only this latter group is pertinent to the present discussion.

The prevailing hypothesis for many decades was that the quality of an aphid's host plant was the primary factor influencing wing development (Schaefers 1972). According to this hypothesis alates were a population's means of escape from deteriorating host plants and apterae were viewed as the true adult form. Crowding was also thought to be a factor but only in so far as it resulted in nutritional deficiencies.

Then, in 1951 Bonnemaison presented evidence indicating that tactile stimulation by other aphids could also promote wing development (Bonnemaison 1951). Since earlier researchers had not controlled for aphid density in their experiments this development placed much of that earlier work in doubt.

The theoretical tide turned again in 1960 when a new theory of the developmental process underlying wing formation was unveiled (Johnson & Birks 1960). This new

hypothesis, later dubbed the diversionist theory, asserted that alates are the ancestral and true adult form of aphids. Apterae, in turn, are a neotenic form occurring when alatiform embryos are irreversibly diverted from their true course by nutritional or density effects. Although this theory is by no means universally accepted today, over the last 25 years it has gained wide support and continues to color many of the developmental questions asked by aphid researchers.

For the last two decades work has focused on questions of how and when the factors of nutrition and crowding affect wing development. Three types of questions have been most prevalent: (1) which chemicals afect aphid growth and wing development, (2) what density levels are required to alter innate developmental tendencies, and (3) when during development can tactile stimmulation affect wing development.

Six amino acids are known to affect wing development, the most important of these being isoleucine and histidine (Mittler & Dadd 1966, Dadd 1968, Sutherland 1969b). Diets lacking these chemicals retard growth and have an apterizing influence on developing aphids. Starvation has also been shown to reduce wing formation in several species (Schaefers 1972). In addition, there is a high correlation between large size (or weight) and the percentage of alates for some species (Tamaki & Allen 1968, Mittler & Sutherland 1969).

Shaw (1970b) has suggested that the level of juvenile hormone present during larval development may be responsible for the continual polymorphism observed between apterous adults and fully developed, functional alates.

The effects of crowding on wing development are more complicated and often contradictory. Some species, such as Aphis fabae, only produce alates when reared in isolation (Shaw 1970b). Others, like B. brassicae, Aphis cracivora, and M. persicae respond to crowded conditions by producing many alate emmigrants (Johnson 1965, Sutherland & Mittler 1971). And a few species such as the strawberry aphid, Chaetosiphum fragaefolii, respond little to changes in density (Dixon & Glen 1971, Judge & Schaefers 1971).

The timing of tactile stimulation also plays an important role in morph determination. Again, different species respond differently. In some species density influences wing formation prenatally, through the crowding of stem mothers (Lees 1961b). In others this development is influenced postnatally, either through the density of stem mothers (Johnson 1965) or nymphs (Shaw 1970b). Still other species are influenced both pre- and postnatally (Dixon & Glen 1971, Sutherland & Mittler 1971).

This wide range of responses reflects the fact that alates play different ecological roles in different aphid species. Schaefers (1972) has identified three ecological function for alates: dispersal, emmigration, and escape

from natural enemies. Two examples will serve to illustrate these functions.

The strawberry aphid, C. fragaefolii, is the first example (Judge & Schaefers 1971, Schaefers 1972). This aphid has a very narrow host range. It exhibits a positive correlation between size and alatism. But only a slight decrease in alate production occurs when aphids are crowded, even at very high densities. Alate production is almost totally a function of nutrition. The sole purpose of alates in this species appears to be dispersal, ie. alates are produced when the host is in the best condition for exploitation by the aphid. Example number two is the bird cherry-oat aphid, R. padi, a host alternating species (Dixon 1976, Schaefers 1972). This species exhibits a negative correlation between adult size and alatism. Crowding results in an increase in the production of alates. In this, and several other species of host alternating aphids poor nutrition and crowding can result in almost an entire generation of aphids being winged emmigrants (Dixon & Glen 1971). However, it would be a mistake to generalize from these two examples that dispersal is the primary role of alates in holocyclic aphid species; while in heteocyclic species their sole purpose is escape, either from a deteriorating host or natural enemies. Contrary examples also exist.

6.3 Materials and Methods

The literature indicates that nutrition and crowding are the most important factors influencing wing development in parthenogenic lines of many aphid species. Blueberry bushes undergo an annual cycle of growth, fruiting, and senescence. Therefore our time axis, degree days, was chosen as the variable most readily associated with these seasonal changes in the nutritional quality of the host. Similarly, the total number of aphids collected in a sample was used as an indicator of crowding.

Partitioning of newborn nymphs will be accomplished by a function relating the porportion of alates produced in a population to aphid density and degree days. Data for the construction of this function was derived from summary statistics of the 'standard sample' described in Section 2.2. Analysis was conducted using (1) SURFACE2, a three dimensional computer plotting package (Sampson 1978), and (2) linear regression techniques (Ruppel & Dimoff 1978).

Make no mistake, this analysis is correlation ecology, plain and simple. As mentioned previously, no effort was made to study the mechanisms governing morph determination in I. pepperi.

6.4 Results

Figure 6.1a contains a contour plot of the three variables in question. The X and Y axes are degree days and

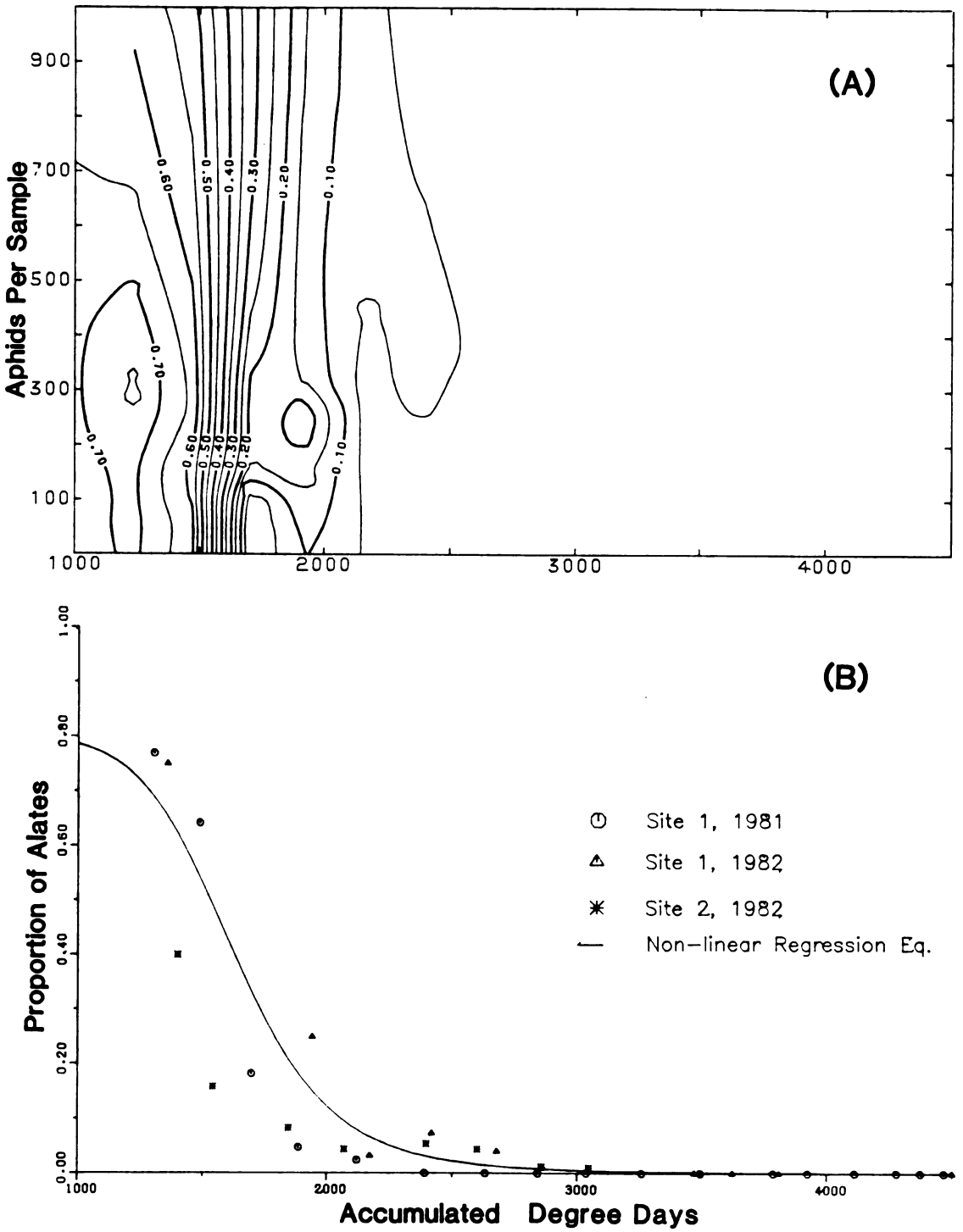


Figure 6.1 Morph determination in I. pepperi: the proportion of alates (a) as a function of crowding and ^{o}D, and (b) only as a function of ^{o}D.

total aphids per sample, respectively. The proportion of alates in a sample is plotted on the Z axis between 0 and 1. Surface contours are drawn at intervals of 0.05 (5%), and labeled in increments of 0.1 (10%). Interpolation of Z values between data points was accomplished using Bessel interpolation (Sampson 1978). The response surface depicted here shows a sharp decline from 75% winged adults early in the growing season to less than 5% alates over an interval of 1500 degree days. Aphid density appears to have little or no affect on the proportion of alate aphids. The area of moderate decline in alate production in the upper left hand corned of the figure is an artifact of the interpolation process. Since very high aphid populations were never observed early in the growing season, this area of the plot is devoid of data. Also, four observation of I. pepperi populations with densities greater than 1000 aphids per sample are not included in this plot. These points were too widely separated to be used in reconstructing the topology of this response surface.

Figure 6.1a indicates that density has little affect on wing production in parthenogenic lines of I. pepperi. This result simplified the analysis since the proportion of alates could then be analyzed as a function of degree days using linear regression. Transformation appropriate for sigmoidally shaped, binomially distributed, proportional data are $\sin^{-1}(P)$, probit, and logit (Anscombe 1948, Rao

1965, and Ruppel & Dimoff 1978). Of these transformations, the logit gave the best results. It was also necessary to specify an upper asymptote for Y values and to transform the X axis by taking the $Log_e(X)$. The final form of this equation reads as follows:

$$P = \frac{e^a * K}{X^{-b} + e^a} \qquad (6.1)$$

where
P = proportion of alate adults
X = accumulated degree days
K = upper Y asymptote
a,b = constants determined by regression

A value of 0.8 was used as the upper Y asymptote. Regression results (R^2=0.83) indicated that the appropriate values for a and b were 61.31 and -8.291, respectively. Therefore the equation used in the model to determine the proportion of alates as a function of degree days is

$$P = \frac{3.42 * 10^{26}}{X^{8.291} + 4.27 * 10^{26}} \qquad (6.2)$$

Figure 6.1b shows both this predictive equation and the data used to generate it. The figure is a plot of the proportion of alates versus degree days using three site-years of data.

6.5 Discussion

The minor role that density appears to play in regulating the number of alates in populations of I. pepperi is quite unexpected. Work with a closely related species, M. maxiam, indicates that crowding is a very important factor in morph determination in that species (Gilbert et al. 1976). In fact, four data points missing from Figure 6.1a suggest that at extreme densities, ie. greater than 2000 aphids per sample, a crowding effect may be present. At such high densities I. pepperi exhibits rates of 1% to 4% alates, at times when smaller samples contained no winged individuals.

CHAPTER 7. ABIOTIC MORTALITY

7.1 Introduction

Several kinds of non-biological, or abiotic, mortality agents can play a role in redcuing the numbers of aphids in highbush blueberry fields. The most important of these are climatic factors and cultural practises. Insecticide applications and mechanical harvesting are undoubtedly the most important cultural practises in this respect. Similarly, climatic mortality effects could be due to excessive heat, precipitation, or high winds.

This chapter focuses on the role of rainfall as an aphid mortality agent. The work was undertaken because previous research (Elsner 1982) suggested that moderate to heavy rainfall may result in significant aphid mortality.

Surprisingly little information on rain induced mortality is present in the aphid literature. Although the impact of predators, parasitoids, and insecticides on aphid populations have been studied intensively, not a single experiment on the effect of rainfall was discovered during the literature search. In fact, the possibility of rain induced mortality was only mentioned in two articles.

In his work with B. brassicae Hughes (1963) found that very heavy rainfalls following prolonged dry periods resulted in the disappearance of almost two-thirds of the aphid population. During dry periods B. brassicae populations develop all over host plants. Subsequent heavy

rains eliminate aphid populations from exposed surfaces. Hughes demonstrated this mechanical effect by holding heavily infested kale plants at an abnormal orientation during a torrential rainstorm. Under these circumstances aphids were washed from leaf surfaces exposed to the rain. Following such storms Hughes also noticed a temporary shift in the age distribution of the population, apparently caused by the re-ascent of late instar aphids that had been washed off the plants.

The second reference to rainfall is no more than a comment. In an article on the population dynamics of M. maxima, Gilbert (1980) notes an apparent correlation between rainfall and year to year variation in aphid numbers. He postulated that such an effect, if genuine, might be due to either the direct effects of wind and rain or to indirect effects on the host plants.

With this background in mind an experiment was conducted to determine the impact of rain induced mortality on aphid populations and to generate predictive equations relating the percent reduction in aphid numbers of daily rainfall between samples.

7.2 Materials and Methods

This experiment was conducted at site 2 (Charlotte, MI) during the summer of 1982. To assess the impact of rainstorms on aphid populations, individual colonies of I.

pepper were tagged and sampled twice weekly until they disappeared. As colonies disappeared they were replaced to maintain a relatively constant sample size. Due to occassional difficulties in finding enough replacement colonies, variations in sample size did occur. The sample was stratified vertically into three regions to determine if the mortality effect was uniform throughout the bush. Sampling consisted of recording the tag identification number and the number of aphids present in a colony. Sample size was generally between 15 to 20 colonies in each third of the bush.

Each of the vertical stratifications was analyzed separately using linear regression. To prepare data for this analysis it was necessary to calculate the rate of change in the population between samples. This was done in several steps. Step number one was to identify which colonies were present at sample time t and t+1. Next, the total number of aphids present in these colonies at the two sample times was calculated. Then a rate of change index (RC) was calculated by dividing the number of aphids present at time t+1 by the number of aphids at time t:

$$RC_t = Number_{t+1} / Number_t \qquad (7.1)$$

Finally, the inches of rainfall that fell during a sample interval was paired with this index value. Only sample

intervals that experienced rainfall were included in the final data sets.

7.3 Results

Inspection of these data sets revealed that not all rainstorms are detrimental to the aphid population. In fact, the heaviest rainfall of the season, 1.75 inches, resulted in no significant mortality. The RC index value remained slightly above 1.0 for all three regions of the bush, just as it did repeatedly when no rain fell. Although only daily weather information was available for Charlotte, hourly data from Lansing airport indicated that light rain had fallen frequently over a two day period. Therefore, although the total accumulation was quite high, each storm was actually very light. Regressions were conducted after this data point had been removed from each data set.

Figure 7.1 contains plots of the rate of change index versus inches of rainfall for the upper, middle, and lower third of the bush, respectively. Both data points and the regression line are illustrated. Solid data points highlight a second, unusual storm. This storm imparted heavy losses to colonies in the upper third of the bush, yet did not affect the rate of increase for populations lower in the bush. If anything the RC index for the bottom third of the bush was elevated slightly. Perhaps the storm is evidence that rainfall may also result in re-distribution of

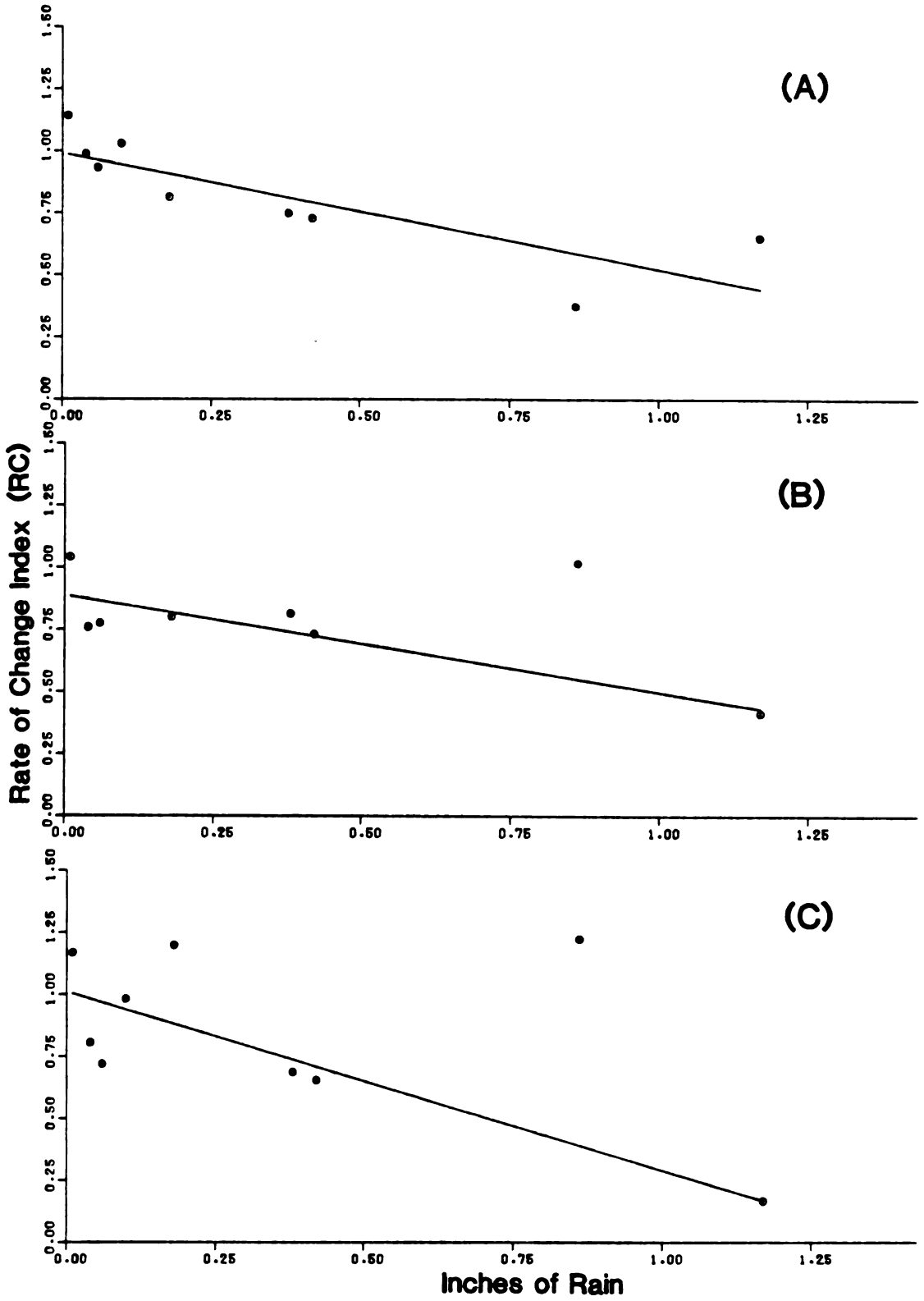


Figure 7.1 Data and linear regression of rain induced mortality for the (a) upper, (b) middle, and (c) lower third of the bush.

aphids within the bush. In any event, removal of this data point from the regression for the bottom third of the bush improved the coefficient of variation by almost 50%, from 23.6 to 70.5%.

Statistics for all three regressions are contained in Table 7.1. The smaller y intercept value for the middle portion of the bush is probably reflection of its suitability to the aphid. A smaller rate of increase for aphids in the middle of the bush, even in the absence of rain agrees well with results from both seasonal fecundity and vertical distribution studies. The seasonal fecundity study highlighted the importance of good nutrition in maintaining high levels of fecundity. The vertical distribution study revealed that the middle of the bush contains the smallest proportion of the aphid population. Since the middle of the bush contains few actively growing shoots, it is not surprising that this region also has the lowest rate of increase. The middle of the bush also has the smallest exterior bush surface are to bush volume ratio. Presumably, aphids away from the bush exterior are afforded some protection from the rain. Therefore it is not surprising that aphids in the middle of the bush are least affected by rain induced mortality. What is surprising is that aphids in the bottom third of the bush are subject to greater rain induced mortality than are aphids in the top of the bush.

Table 7.1 Regression statistics for rain mortality field experiment.

Third of Bush	Y intercept	slope	R^2
Upper	0.990	-0.467	0.677
Middle	0.889	-0.391	0.745
Lower	1.010	-0.721	0.705

7.4 Discussion

The experiment has demonstrated that rainfall can indeed result in significant mortality to I. pepperi populations. It has also shown that increasing levels of rainfall generally mean increasing aphid mortality. However, the present method of prediction was not completely successful. The method failed to identify storms that did not affect the aphid population, even though they dropped significant amounts of rain over a two to three day period. Daily rainfall alone is not the best predictor. Better results should be attainable by incorporating hourly rainfall or wind speed into the prediction.

CHAPTER 8. DESIGNING A LIFE-TABLE FOR I. pepperi

8.1 Introduction

The purpose of this chapter is to distill and synthesize information presented earlier in the thesis to design a predictive population model for I. pepperi. Once completed and tested, the model could be used to simulate strategies for limiting the number of aphids in commercial highbush blueberry fields. One strategy of immediate interest is the proper timing of pesticide applications to limit aphid populations and minimize interference with natural mortality agents.

The idea of constructing a predictive aphid population dynamics model is certainly not new. Several such models have been developed over the last two decades (Hughes 1963, Hughes & Gilbert 1968, Gilbert & Hughes 1971, Lowe 1973, Dixon & Barlow 1979). A few models have also addressed the role of aphids as disease vectors (Gutierrez et al. 1971, 1974a, 1974b, Frazer & Gilbert 1976).

Research on one aphid in particular, Masonaphis maxima, has been instrumental to the development of the present simulation. Although this model is by no means a clone of the M. maxima research, the earlier work pointed out important ecological relationships in a similar aphid ecosystem and provided a source for initial estimates of some model parameters. Since it is important to understand both the similarities and differences between the two

models, a few moments will be spent reviewing the M. maxima system.

8.1.1 A variable life-table for Masonaphis maxima (Mason)

Details of M. maxima's biology are discussed in Frazer & Forbes (1968) and Campbell et al. (1974). Efforts to model this aphid's population dynamics using a variable life-table approach are presented in Gilbert & Gutierrez (1973), Gilbert et al. (1976), and Gilbert (1980).

Like I. pepperi, M. maxima is a holocyclic aphid, spending its entire life cycle on thimbleberry, Rubus parviflorus Nutt. The species range extends along the Pacific coast from British Columbia to California. Although the aphid is not economically important, it is a vector of thimbleberry ring spot virus (Stace-Smith 1958).

The species was originally chosen as the subject for the construction of a variable life-table as a matter of convenience: (1) because of color differences morphs could be distinguished easily; (2) few, distinct generations made the determination of a population's age structure relatively easy; (3) the aphid's life cycle was very closely tied to its host plant; and (4) the aphid had a compliment of natural enemies. The life-table was developed as a deterministic, discrete time model. It is referred to as a variable life-table because many model components (such as fecundity and stage specific mortality factors) are not constants but functions. Aphid fecundity was simulated in

the life-table using three functions. The first function described how M. maxima's birth rate varies during the growing season. This linear decline reflects the influence of food quality on aphid fecundity. A second, negative exponential function described the density-dependent reduction in fecundity caused by competition between stem mothers. A third function reflects the frequency distribution of births suring a stem mother's adult stage. In the earliest forms of the model parasite and predator mortalities were modeled with an arbitrary function. Later, complete submodels were developed to account for syrphid predation and primary parasitism.

The major cricism leveled against this model has been that it was never tested against an independent data set. Although good fit to field data was achieved, the same data had been used to construct the budget in the first place. The modelers' answer to this cricism is that model parameters could only be fitted to a specific population of aphids during one growing season. Because of extreme differences in size, climate, and suitability of different patches of its host, thimbleberry aphid populations have quite different densities, numbers of generations, and proportions of sexual morphs.

8.2 Materials and Methods

Data for the construction of a variable life-table for I. pepperi come from several sources. First, Elsner's (1982) fixed temperature cohort study provided information about the duration of aphid life stages (Section 4.3), and the distribution of births during a stem mother's reproductive period (Section 5.3.1). Second, much of the life-table was parameterized using information collected via the 'standard sample' studies described in Section 2.2. This information included (1) seasonal changes in the aphid's reproductive rate (Section 5.3.2), (2) seasonal within bush distribution (Section 3.2), and (3) both biotic and abiotic mortality factors (Sections 2.3 and 7.3).

As mentioned earlier, where data for a model parameter was not available the parameter was estimated using existing information for M. maxima. The earliest version of this model contained many estimates from the thimbleberry aphid life-table. As the project progressed experiments were devised to replace these estimates with experimental results for I. pepperi. In the current version of the model only the mean development time for large, alate nymphs has been estimated from M. maxima.

The computer program detailing the life-table was written in USCD Pascal (version IV.0) on the Columbia Data Products microcomputer described in Section 2.2.

8.3 Model Design and Parameterization

8.3.1 Overview

Five aspects of I. pepperi's biology are required to simulate its population dynamics: aphid maturation, fecundity, mortality, morph determination, and spatial distribution. The overall design for this variable life-table is flowcharted in Figure 8.1. Following an explanation of this figure each aspect of the model will be discussed in greater detail.

The maturation of each aphid is simulated using five distributed delays, represented in the flowchart by circles. Since the dynamics of apterous and alate aphids are dealt with separately, a total of ten delays are needed to model growth. Although fixed temperature experiments indicate that I. pepperi has four nymphal instars, only three sizes of nymphs can be distinguished readily in the field. These are classified as small, medium, and large nymphs and are modeled using three separate delays. Similarly, the adult life stage is separated into pre-reproductive and reproducitve adults and modeled via two delays. For our purposes the pre-reproductive period is defined as the interval between molt to adulthood and the birth of the first young. Likewise, the reproductive period is defined as the time interval between the first birth and death.

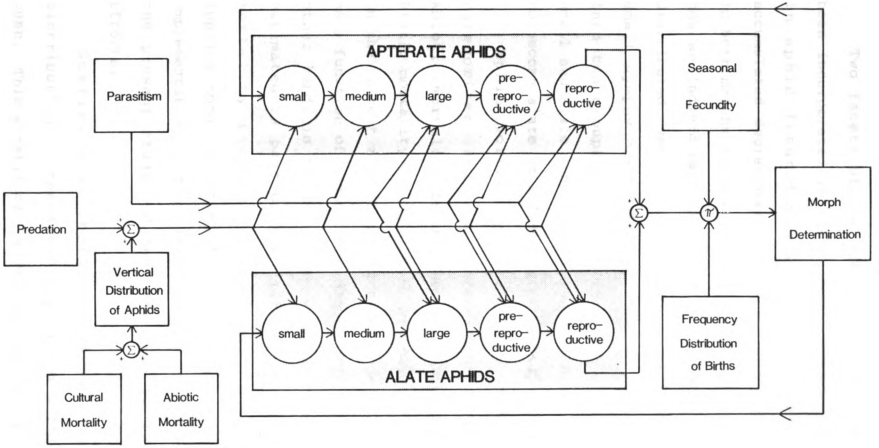


Figure 8.1 Overview of the I. pepperi population dynamics model.

Two facets of the aphid's reproductive strategy have been incorporated into the model. First, seasonal changes in aphid fecundity are estimated as a function of accumulated degree days. Then the numbers of adult aphids in both morphs are pooled and a transfer function describing how an individiual stem mother's reproductive potential is distributed over time is applied to calculate the number of small nymphs born. Finally, newborn aphids are separated into two groups and added to the current populations of small and alate nymphs. The proportion of newborns destined to become alate is a function of accumulated degree days.

Aphid mortality is divided into three causal categories: abiotic, biotic, and cultural mortality. Abiotic mortality is modeled as a function of rainfall. Biotic mortality is the result of predation and parasitism. In the current version of the model, parasitism is estimated as a function of accumulated degree days. Predation, on the other hand, is treated as an unknown quantity and will be estimated as part of the 'tinkering' process. Cultural mortality factors include such things as chemical applications, effects of machine harvesting, etc. The implementation of this last category is beyond the scope of the present study and has been left to future modeling efforts.

Spatial distribution refers to the vertical distribution of the aphid population within a blueberry bush. This stratification changes during the growing season

and is modeled using a table look-up function to linearly interpolate between known values. The effects of both cultural mortality and parasitism are affected by the within bush distribution of aphids.

8.3.2 How the Model Keeps Time

Individuals using the computer program detailing the life-table observe a model that progresses by calendar date. However, the model is also keeping track of time in degree days (variable WEATHER.DD), an estimate of physiological time for the aphid. Although most model variables are updated daily, those relating to aphid growth are updated in discrete steps composed of a fixed number of degree days (variable DD_PER_DT). Each such step is referred to as one DT (delta time step). The portion of the program that controls time in this way reads as follows:

```
LEFT_OVER_DT := 0.0;
FOR J_DATE := FIRST_DAY TO LAST_DAY DO
  BEGIN
    GET_WEATHER( J_DATE );
    LAST_DT_TODAY := TRUNC(WEATHER.DD/DD_PER_DT +
                LEFT_OVER_DT);
    LEFT_OVER_DT := WEATHER.DD/DD_PER_DT - LAST_DT_TODAY;
    FOR DAY_SEGMENT := 1 TO LAST_DT_TODAY DO
      BEGIN
        CALC_STATES( DAY_SEGMENT );
        CALC_RATES( DAY_SEGMENT );
      END;
  END;
```

The FIRST_DAY and LAST_DAY of the current run are entered during the initialization process. J_DATE stands for julian date. Once each day the program reads weather data from a random access file (procedure GET_WEATHER). The program then calculates how many DTs are needed to simulate the current day (variable LAST_DT_TODAY), taking into account any fraction of a DT not run yesterday (variable LEFT_OVER_DT). The actual model is contained within the procedures CALC_STATES and CALC_RATES.

8.3.3 Sequence of Calculations

If the model is to function properly it is important that all variables be calculated in the proper order. Only two correct sequences exist (Manetsch & Park 1980). In either case, during any given DT all state variables must be calculated before corresponding rate variables. To avoid confusion state variables are calculated in one routine and rates in another. Figure 8.2 details the overall sequence of calculations for the entire model. This sequence was chosen because it allows for the greatest flexability in specifying model output.

Note that model output is only available at the end of each day. The actual frequency of such output may be changed during the course of a run via the command line in step (1) of the execution phase. This command line is an important feature for future implementation of control

INITIALIZATION PHASE

1) Default initialization of all user specifiable variables

2) Interactive initialization of user specifiable state and rate variables and specification of run characteristics

3) Initialize internal state variables at T_0

4) Compute internal rate variables at T_0

EXECUTION PHASE

1) Prompt user with command line for possible changes in print frequency and execution interupt control

2) Calculate the number of DT's to run this day

3) Update TIME: T = T + DT

4) Compute STATE variables at T + DT

5) Compute RATE variables at T + DT

6) If not end of current day return to (3)

7) Print output as desired

8) If last day of run terminate simulation and print summary output

9) If an interrupt condition is satisfied return to (1), otherwise return to (2)

Figure 8.2 Sequence of calculations in the blueberry aphid variable life-table. Modified from Manetsch & Park 1980.

strategy simulations. The prompt is the visible portion of an execution interrupt control mechanism that allows users to (1) alter output frequency, (2) view additional model statistics not contained in routine output, (3) specify control measures (not currently implemented), (4) specify how many days the model should run before interrupting execution again, (5) complete the simulation without further interruption, or (6) abort the run.

8.3.4 Modeling Aphid Maturation

As computer usage in biology has become more common place, mathematical models of biological systems have become increasingly complex. This trend is particularly true in the science of entomology where systems science methodology and simulation techniques have played a fundamental role in the design, development, and implementation of many pest management models (Ruesink 1976, Tummala et al. 1976, Welch 1984). One simulation technique in particular, the distributed delay, has been widely employed in the simulation of insect growth and maturation (Gilbert et al. 1976, Welch et al. 1978). In this life-table separate distributed delays are used to model each aphid life stage. Several variations of these delays have been implemented on digital computers (Abkin & Wolf 1976, Manetsch 1976, Manetsch & Park 1980). The delay routine used here is formally classified as a time-invariant distributed delay with storage losses.

A block diagram of the distributed delay used in the present model is shown in Figure 8.3. The parameter MEAN equals the average number of degree days spent in a given life stage. The parameter K is an integer referring to the order of the delay. K describes what form the distribution will take and can be determined directly from experimental estimates of the population MEAN and VARIANCE where

$$K = \frac{MEAN^2}{VARIANCE} \tag{8.1}$$

Output from the delay is the number of aphids that exited a life stage this DT. The rate of recruitment into a life stage is the input variable. Obviously, output from $Stage_i$ is input to $STAGE_{i+1}$. Exceptions to this rule are (1) input to $STAGE_1$ is the number of aphids born during a DT, and (2) output from $STAGE_5$ represents deaths due to old age. The number of aphids in a particular life stage is contained in the variable TOT_STORAGE. The number of aphids in each of K sub-stages is contained in the matrix STORAGE where

$$TOT\_STOR = \sum_{i=1}^{K} STORAGE_i \tag{8.2}$$

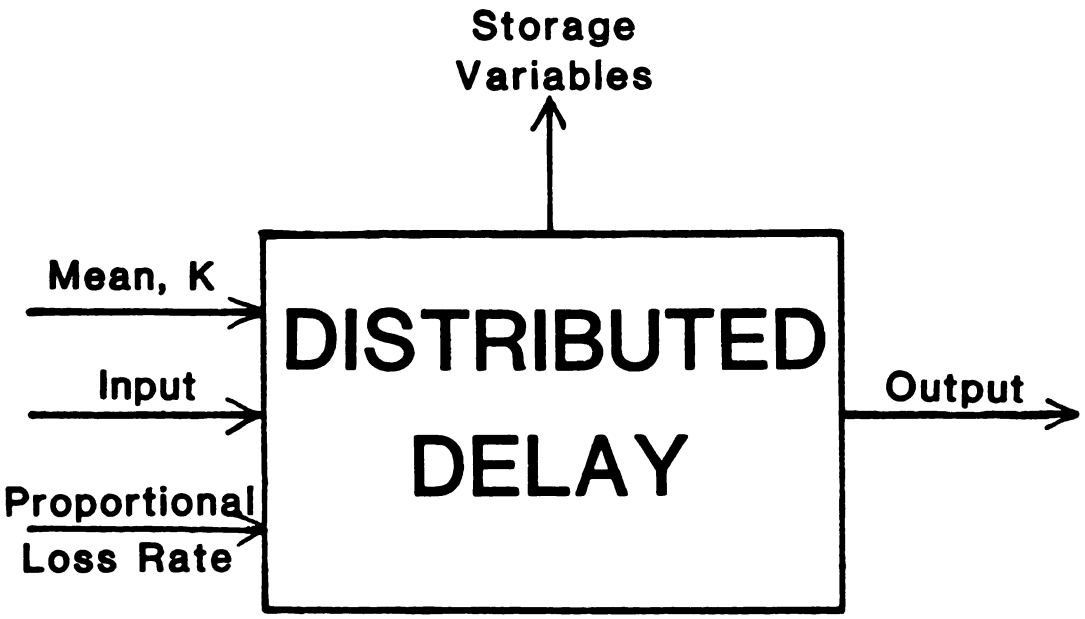


Figure 8.3 Flowchart showing input and output variables for the distributed delay used in the model.

The final two parameters, CONST_PLR and VARIABLE_PLR are the constant and dynamic components of the proportional loss rate. The constant component refers to unexplained stage specific mortality and is entered as an option during the initialization phase of the program. The variable loss rate is the sum of known mortality facotrs such as violent storms, chemical applications, and parasitism acting during one DT.

One final theoretical issue regarding the use of distributed delays remains to be addressed -- model stability. Because of the way distributed delays operate, some choices of DT will result in unstable and unpredictable results. The distributed delay procedure used here employs Euler integration; therefore, allowable DTs must be in the range

$$0 < DT < 2 * (MEAN / K) \qquad (8.3)$$

Such instability is an unavoidable consequence of numerical approximation techniques required to implement differential equations on digital computers. In fact, due to additional feedback from other differential equations scattered throughout the model the maximum allowable DT may be much less than equation 8.3. One facet of model parameterization is the selection of an appropriate DT to ensure that such error remains within allowable limits (for details see Manetsch & Park 1980, vol. 2, p11-14). Whenever changes

involving differential equations are made such stability tests on DT should be conducted again.

Table 8.1 lists MEAN, K, and maximum allowable DT values for each life stage of both apterous and alate morphs of I. pepperi. These values were calculated from Table 4.3 using equations 8.1 and 8.3. Means have been rounded to integer values for simpicity. All aphids in the fixed temperature rearing experiment summarized in Table 4.3 were apterous individuals. However, rearing experiements conducted with M. maxima (Campbell et al. 1974, Gilbert et al. 1976) indicate that the only difference in thermal requirements for alate and apterous individuals is the time required to complete the fourth instar (large nymph

Table 8.1 Distributed delay parameters and maximum allowable DTs for each life stage of apterous and alate viviparous I. pepperi.

Life stage	Mean	K	DT_{max}
apterous morph			
small nymphs	54	12	9
medium nymphs	63	22	6
large nymphs	57	10	12
pre-reproductive adults	56	7	16
reproductive adults	250	12	42
alate morph			
small nymphs	54	12	9
medium nymphs	63	22	6
large nymphs	66	10	12
pre-reproductive adults	56	7	16
reproductive adults	250	12	42

category). Alate M. maxima nymphs require about 17% longer to complete the fourth instar than apterous nymphs. Using this relationship it is estimated that large I. pepperi nymphs require 66.2 degree days to complete development. Both the MEAN and K values for reproductive adults are subjective estimates based on rearing aphids at 23°C. These figures were increased from those contained in Table 4.3 in an attempt to offset the drowning bias present in the rearing experiment. Values of DT_{max} in Table 8.1 indicate that the selection of a DT for the model is limited by stability criteria for medium nymphs. This means that the model variable DD_PER_DT must be less than 6 degree days.

The simulated maturation of one generation of apterous and alate I. pepperi generated using these parameters is shown in Figure 8.4. Output was obtained using an initial population of 100 newborn small nymphs of each morph and a DT of two degree days. Notice that reproduction of alate aphids is delayed slightly because large alate nymphs take longer to mature. Also notice that the aphid spends over half of its lifetime as an adult.

8.3.5 Fecundity and Morph Determination

Figure 8.5 contains a more detailed flowchart of this portion of the model. As discussed previously, both seasonal changes in aphid fecundity and the temporal

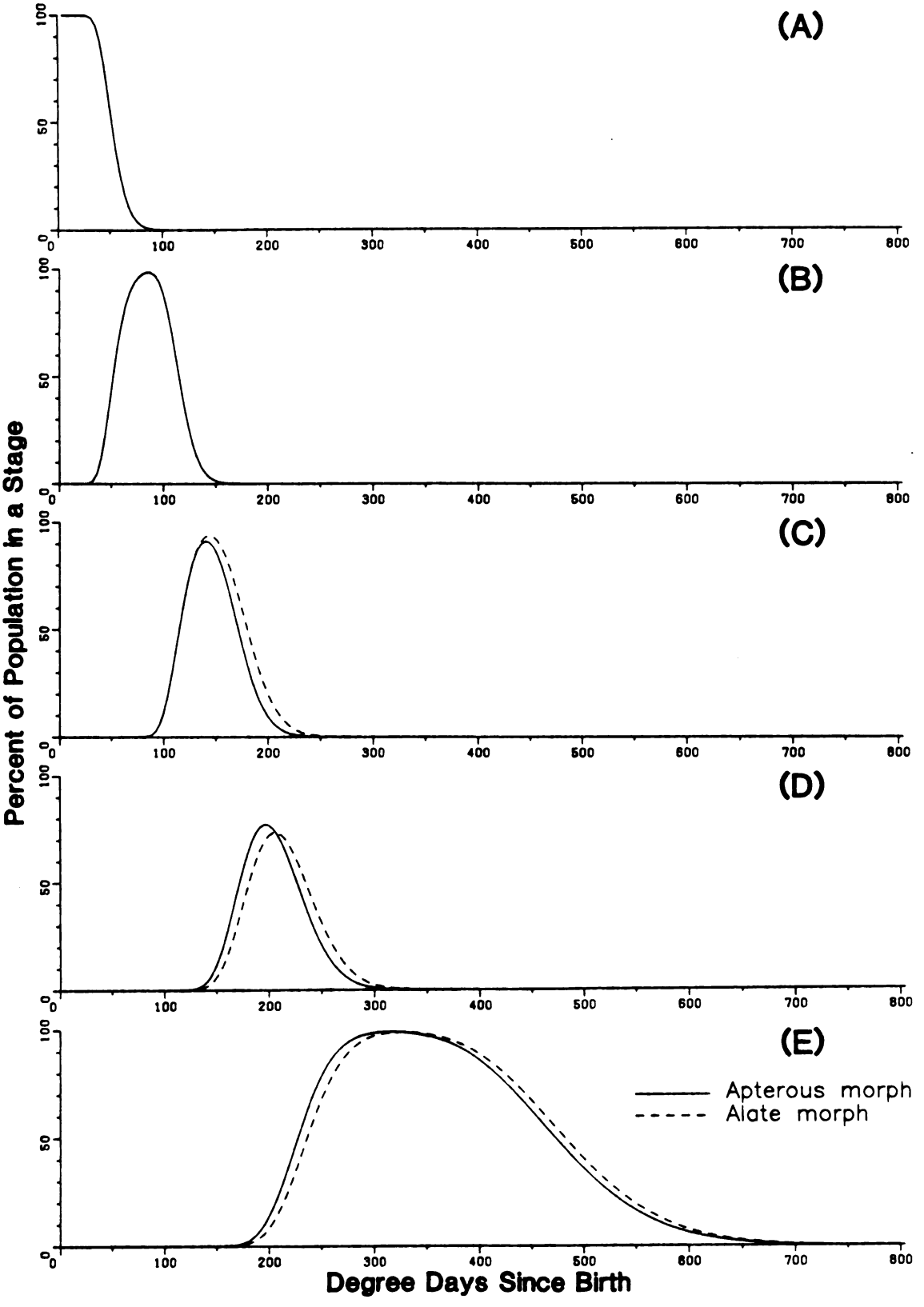


Figure 8.4 Simulated maturation of one cohort of apterous and alate I. pepperi.

distribution of births within a stem mother's reproductive period have been incorporated into the model. The flowchart also shows the relationship of morph determination to other components in this portion of the model. Note that both morph determination and seasonal fecundity are functions of accumulated degree days (TDD).

The seasonal decline in aphid fecundity is simulated using the linear relationships determined in Table 4.4. Since the model will be fitted to data from site 1 (Charlotte, MI), equation 8.4 is used to estimate seasonal fecundity,

$$\text{FECUNDITY} = 32.015 - 0.00804 * \text{TDD} \qquad (8.4)$$

This decline reflects seasonal changes in the nutritional status of the host. Second, the temporal pattern of births during an individual stem mother's reproductive period (REPRO_FREQ) is modeled using the discrete probability function calculated in Section 4.3.1. The values for this matrix were shown in Table 4.1.

The birth rate (per DT) is then determined using equation 8.5. The middle term in this equation reflects that portion of an aphid's reproductive period occurring this DT.

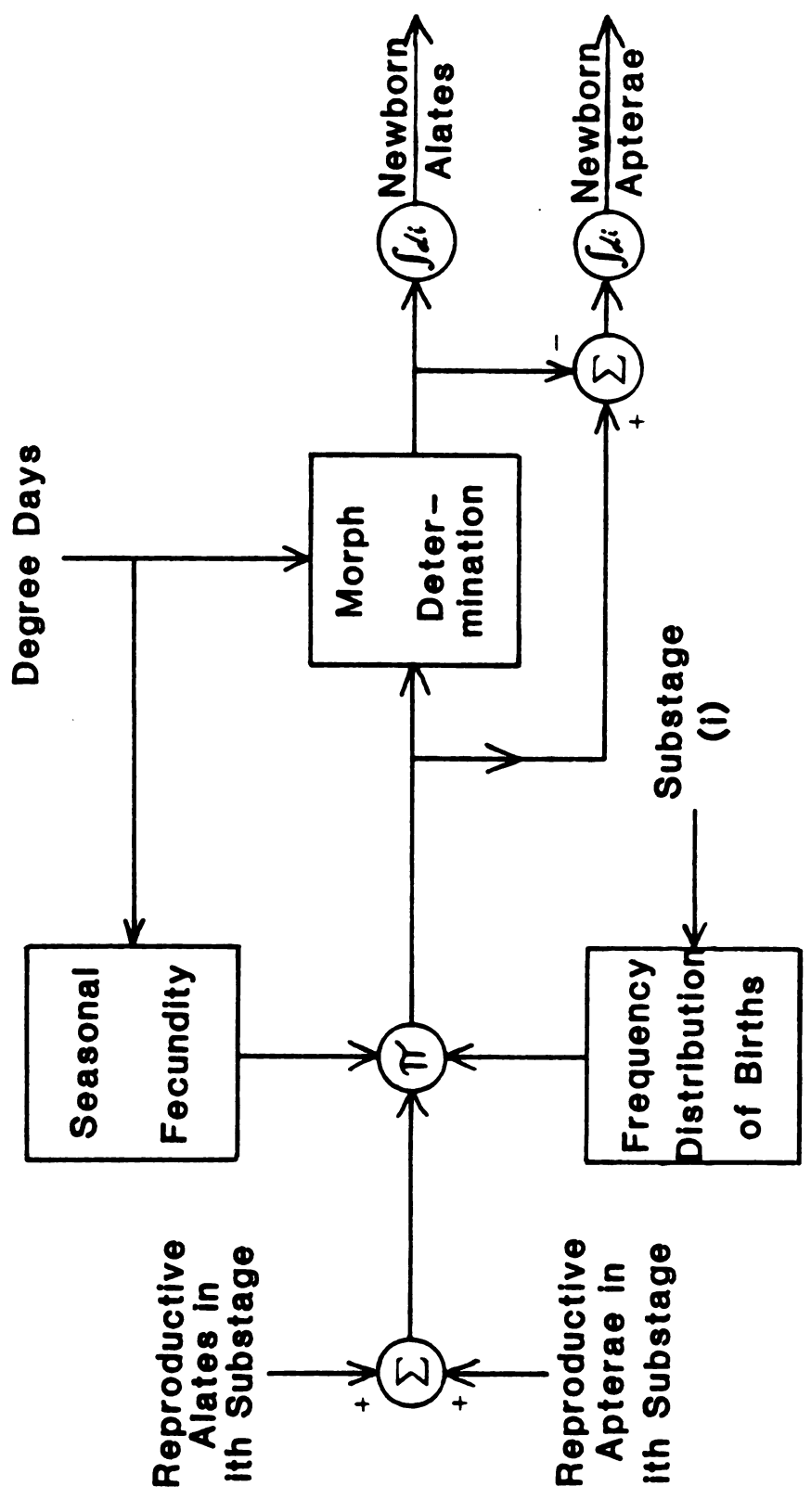


Figure 8.5 Flowchart for the fecundity and morph determination sections of the model.

$$\frac{\text{BIRTHS}}{\text{DT}} = \text{FECUNDITY} * \left[\frac{\text{DD\_PER\_DT}}{\left(\frac{\text{MEAN}}{\text{K}}\right)}\right] * \sum_{i=1}^{K} \text{REPRO\_FREQ}_i * \text{STORAGE}_i \qquad (8.5)$$

where,

K = order of the distributed delay, reproductive stage
MEAN = average degree days spent in reproductive stage
MEAN/K = degree days spent in the $_i$th substage of the reproductive stage
REPRO_FREQ_i = proportion of births occurring during the $_i$th substage
STORAGE_i = number of reproductives in the $_i$th substage

To incorporate alates into the model the proportion of newborn, presumptive alates (P) is determined using equation 8.6 developed in Section 6.4.

$$P = \frac{3.42 * 10^{26}}{\text{TDD}^{8.291} + 4.27 * 10^{26}} \qquad (8.6)$$

As the flowchart for this section of the model indicates, the number of newborn apterae are then calculated as the difference between total newborns and newborn alates.

8.3.6 Modeling Spatial Distribution

Both rain induced mortality and pesticide losses are affected by the vertical within bush distribution of aphids. This distribution is modeled via a table look-up function. The function uses linear interpolation to estimate between table values. Table estimates for each third of the bush are contained in Table 8.2. Table values were estimated from the 'standard sample' vertical distribution results

discussed in Section 3.2. Figure 8.6 illustrates this table in the same fashion in which the data was presented in that earlier discussion.

8.3.7 Mortality Component

Three classes of martality agents are included in the population model: biotic, abiotic, and pesticide induced mortalities. Biotic mortality factors include both predators and parasitoids. The relationships between these mortality sub-components and necessary system inputs are shown in Figure 8.7.

This flowchart actually protrays two independent groups of mortality calculations. The simplied of these two lines determines the number of parasitized aphids that will be removed from the distributed delays for large nymphs and adults. System inputs into this function are accumulated degree days (TDD), and the level of parasitism (high, medium, low). The more complicated sequence of calculations includes mortality caused by predation, rainfall, and pesticide applications. The last two factors are affected by the vertical within bush distribution of aphids. The proportion of the aphid population killed by each of these two processes is first summed. This result is then multiplied by the total number of aphids present and by the proportion of those aphids in a given third of the bush.

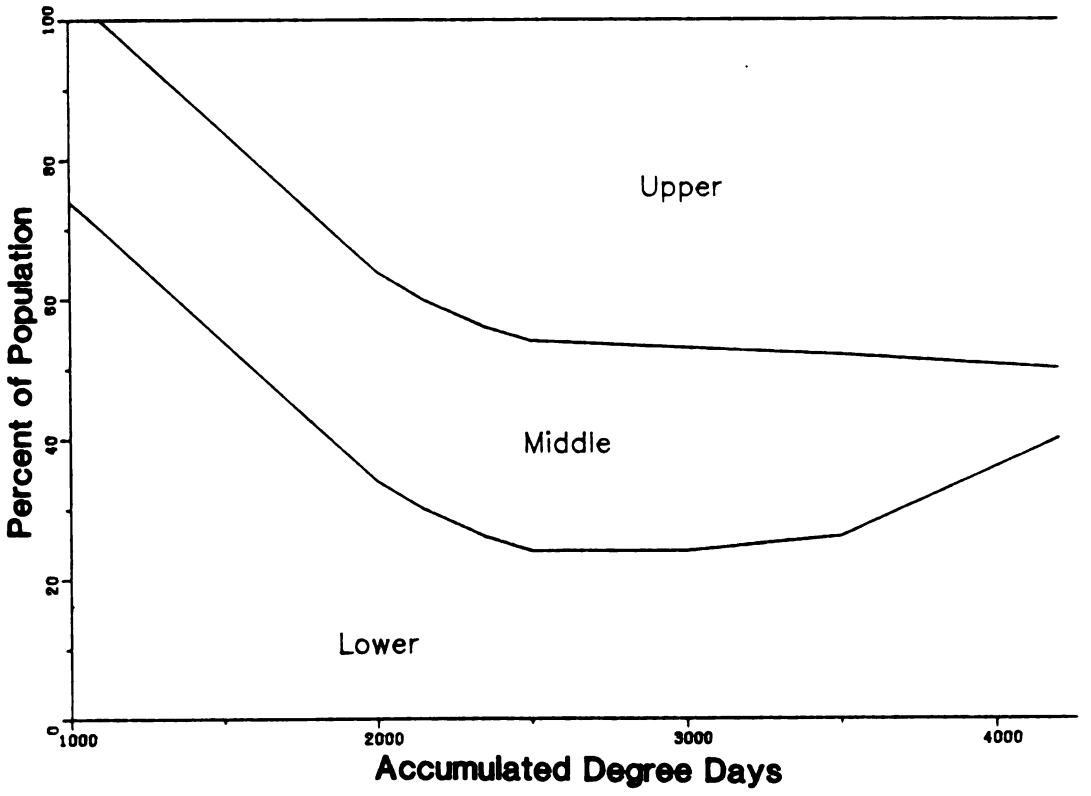


Figure 8.6 Table look-up function used to simulate the vertical within bush distribution of aphids through the growing season.

Table 8.2 Table look-up values for the percentage of the aphid population in each third of the bush versus degree days.

Degree days	Upper	Middle	Lower
1000	0	26	74
1100	0	30	70
1500	16	30	54
2000	36	30	34
2150	40	30	30
2350	44	30	26
2500	46	30	24
3000	47	29	24
3500	48	26	26
4200	50	10	40

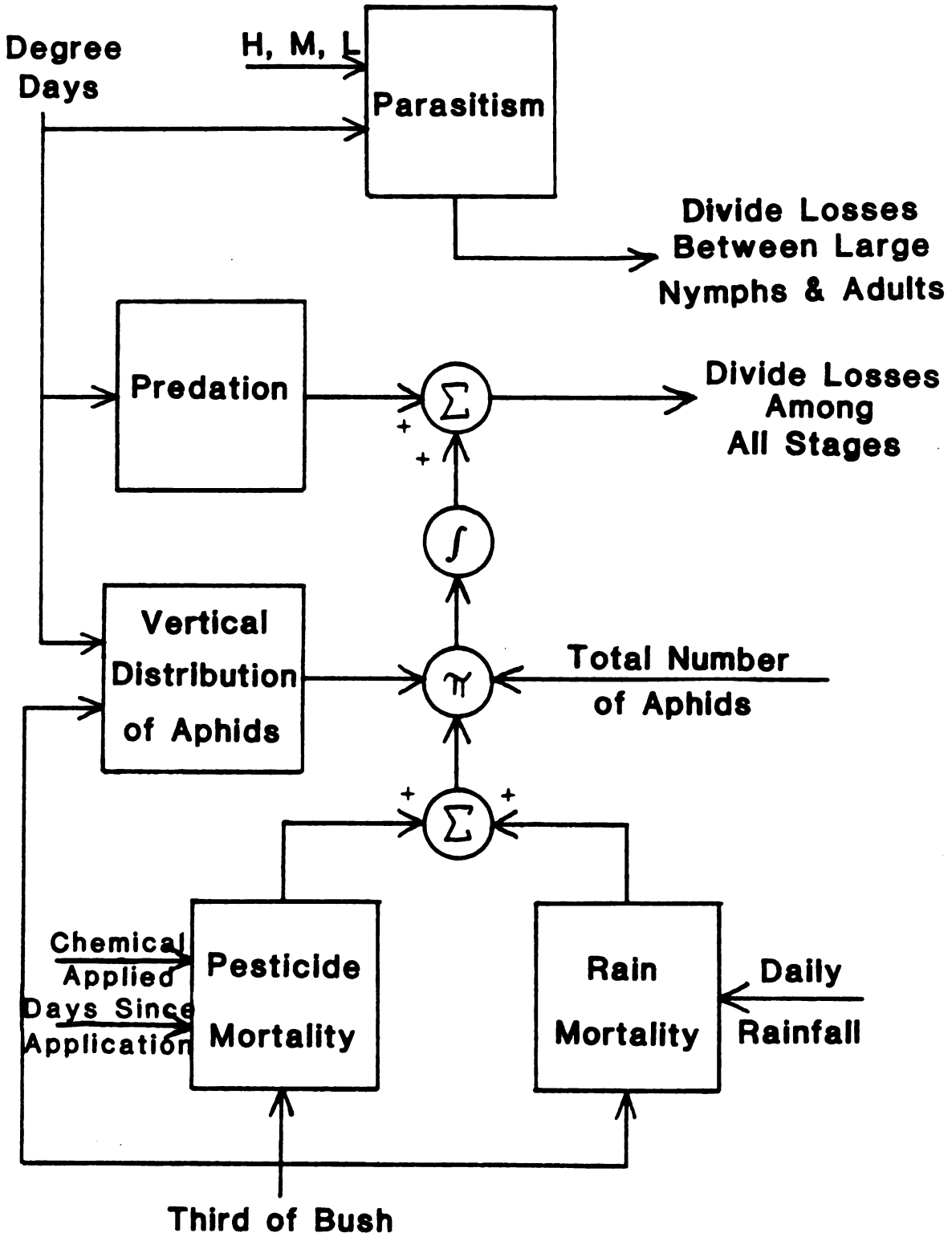


Figure 8.7 Flowchart for the mortality section of the aphid population dynamics model.

The number of aphids lost is then integrated over the three regions of the bush and added to predation losses. Aphid losses from this second group of calculations are removed from the distributed delays for all life stages.

Parasitoid mortality is modeled using one of three levels of parasitism. The level to be used (high, medium, or low) is selected by the user during the initialization portion of the program. The function describing each level of parasitism is generated using a table look-up function. The input table for this function contains an estimate of percent parasitism every 100 degree days from 1000 to 4500 degree days. These tables are reproduced graphically in Figure 8.8. The lowest level of parasitism represents a site subject to regular pesticide applications (site 2). On the other hand, the high level of parasitism was estimated from 1982 data at site 1 where chemicals were not applied regularly and where a substantial early season aphid population was observed. A third level of parasitism was provided as an intermediate between these two extremes.

Modeling aphid losses due to predation would be a very complicated process if any attempt was made to realistically simulate predator prey interactions for even the two most important aphid predators, chrysopids and syrphids. That process would necessitate an understanding of (1) predator phenologies, (2) predator abundance as a function of aphid density, and (3) predator avoidance of or mortality due to

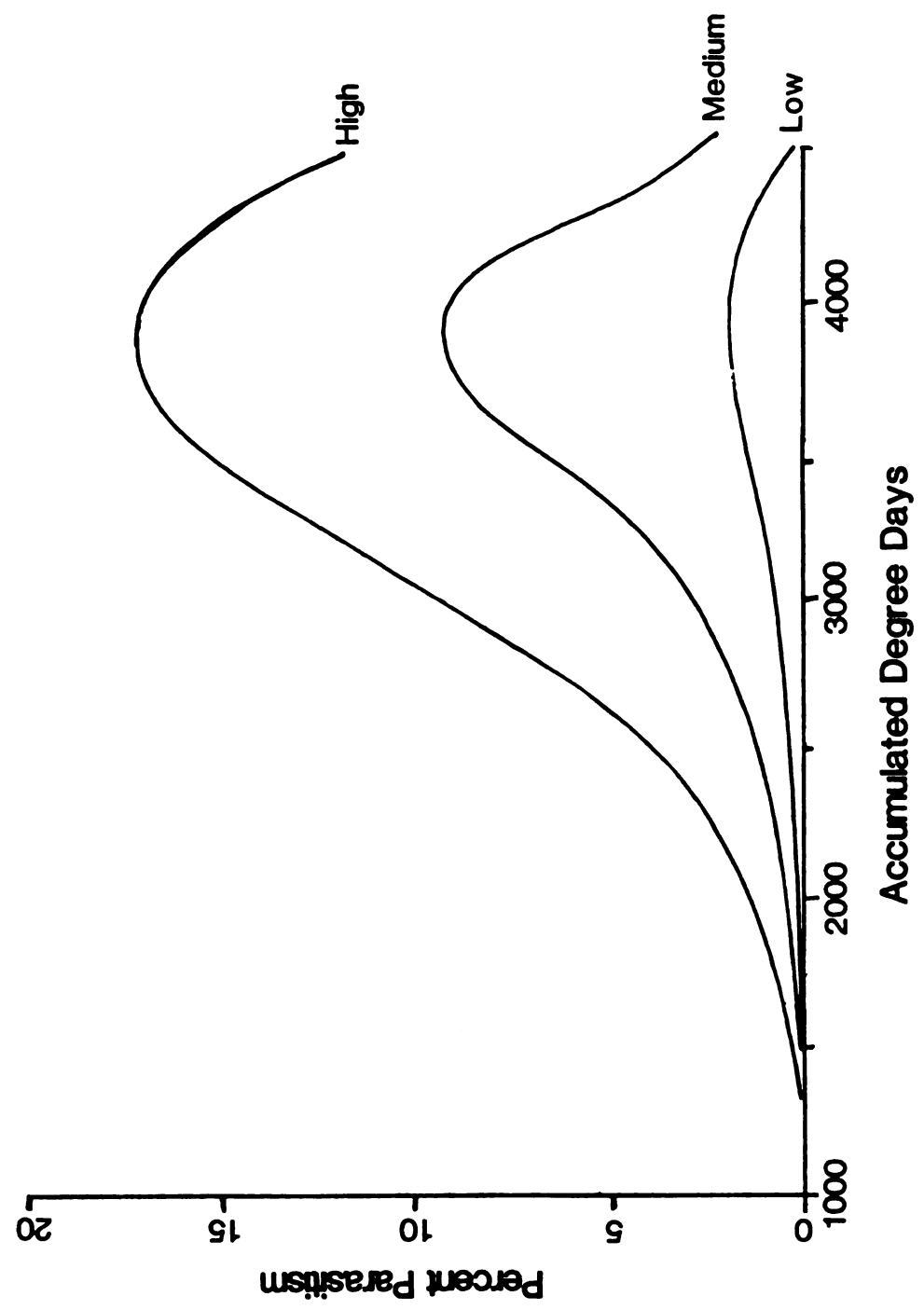


Figure 8.8 Table look-up functions used to simulate high, medium, and low levels of parasitism.

pesticides. Such detail is obviously beyond the scope of the present project. Instead, predation will be allowed to remain the one unknown process in the model. During model testing, predation will be estimated as the difference between field samples and model output. Once all other model variables have been fitted to field data, predation estimates will be calculated and stored in a table look-up. The applicability of these estimates can then be tested using an independent data set.

Rain mortality is estimated using the regression statistics from Table 7.1. These equations estimate daily survivorship, Y_i, as a function of rainfall for three regions in the blueberry bush.

$$Y_u = 0.9905 - 0.4674 * X \quad (8.7)$$
$$Y_m = 0.8894 - 0.3907 * X \quad (8.8)$$
$$Y_l = 0.9901 - 0.4061 * X \quad (8.9)$$

where,
X = rainfall, in inches
u = upper, m = middle, l = lower third of bush

Simulating the effects of pesticide applications on the aphid population is also beyond the scope of the present work. After the model has been fitted to field data and predation has been estimated, pesticide mortality can be incorporated into the model. Pesticide mortality will be calculated using existing results from dosage mortality experiments with I. pepperi (Ramsdell et al. 1983, 1984), and published decay curves of residuals for these chemicals.

8.4 Discussion

The design and parameterization phases of building the model are now complete. However, the model has yet to be fully tested and validated against an independent data set. Until these steps have been completed, only limited trust should be placed in the model. The process of model testing is itself a time consuming endeavor involving running the model under a variety of conditions, sensitivity testing, and trial and error adjustments. But testing will also have a very tangible result. This result will be an estimate of predation losses across time.

A few words must be said regarding the differences between 'natural' sites and chemically intensive site management. Many of the model's parameters were determined from field results for a site where pesticides were not used. This site provided an opportunity to view the system without the perturbations that would result from regular pesticide use. The relative stability of this system made it much easier to identify the ecological relationships affecting the aphid population. However, the addition of pesticides to a system does not merely kill a few insects; it changes the structure of that system. As pesticide use increases, the levels of predation and parasitism are drastically curtailed. The biological feedback mechanisms that keep the aphid population in check are short-circuited. That is why three levels of parasitism were incorporated into the model. The different levels reflect changes in the

structure of the ecosystem. Likewise, it may be necessary to provide multiple predation estimates to reflect changes in predator adundance caused by regular chemical suppression strategies.

One shortcoming of this simulation is that model output represents expectations for samples conducted using the 'standard sample' technique. Since this method has not been calibrated against an absolute sample, model results cannot be transformed into absolute population estimates. This means that, at present, the model cannot provide estimates of aphids on a per bush or per acre basis.

CHAPTER 9. CONCLUSION

This thesis has explored many aspects of aphid ecosystems. It has also attempted to structure our knowledge of the I. pepperi agro-ecosystem into a predictive population model. The thesis stresses model design and parameterization. Model testing and validation are equally important; but, being beyond the scope of the present work, have been relegated to future efforts.

At this point it seems appropriate to review what has been learned about the I. pepperi system during the course of this research. Discussion revolves around four general topics: (1) natural enemies, (2) vertical within bush distribution, (3) aphid fecundity, and (4) aphid mortality.

Conclusions involving this aphid's natural enemies are several. First, as one would expect, natural enemies were much more common at a site where insecticides were not applied, than at a site subject to regular chemical suppression strategies. Second, although fungal pathogens in the genus Entomophthora are an important mortality agent in several other aphid ecosystems, they do not appear to play a significant role in the present system unless bushes are caged. Third, syrphids and chrysopids appear to be the most important predators in this ecosystem. Of the two, syrphids are the best candidate for the title 'most important predator' because they are more tolerant to insecticides, they consume about twice as many aphids during

their lifetime, and they occur as a large complex of species. Fourth, at least two species of primary parasitoids and one hyperparasitoid species are present in blueberry fields. Both primary parasitoids are members of the braconid family Aphidiidae. The first of the two species is present in the field from about 1500 degree days (base 38F) until the end of the growing season. The second species does not appear before 2500 degree days. Primary parasitoid species are easily distinguishable in the field by the appearance of their pupae. Although parasitoids were a significant mortality factor (10-18%) at an unsprayed site, the rate of parasitism remained below 2% at a chemically treated site.

Results regarding the vertical distribution of I. pepperi within highbush blueberry bushes agree well with what was previously known about this aphid's habits. Early in the growing season the bulk of the aphid population is located in the bottom third of the bush. As the season progresses the proportion of the population in the bottom third of the bush declines, with most of the aphids residing on new growth in the upper third of the bush. Late in the growing season this trend is reversed as aphids recolonize the base of the bush. By late August the majority of aphids are found on short, late season terminal shoots growing around the crown of the bush. The middle third of the bush consistently contains the smallest proportion of the population. I. pepperi's parasitoids do not exhibit similar

shifts in their vertical distribution. Instead, more than half of the parasitoid population is consistently found in the bottom third of the bush.

Two aspects of aphid fecundity were addressed in the thesis. First, results from a field experiment indicate that the aphid's fecundity declines seasonally from a high of 24 young per female early in the growing season to less than three young per female by late August. Although this function was determined using a linear model, future work may well reveal that it is in fact a polynomial relationship. Second, a re-analysis of Elsner's (1982) fixed temperature rearing experiment revealed the temporal distribution of births during a stem mother's reproductive period. Both of these relationships were taken into account when modeling I. pepperi's fecundity.

Four potential sources of aphid mortality were also designed into the population model: predation, parasitism, rainfall, and pesticide applications. Of these, parasitism and rain induced mortality were estimated experimentally during the course of this research. Results from field sampling were used to generate three equations describing percent parasitism as a function of degree days. The functions depicted high, medium, and low levels of parasitism. Rain mortality was described using a different linear function for each of three vertical regions in the bush. Rain induced mortality was greatest in the bottom third of the bush, and least in the middle of the bush.

Heavy rains were often responsible for more than 50% mortality to the aphid population. The impact of predators remains to be determined during model testing. Pesticide mortality will also be estimated at a later date using results from dosage mortality experiments with I. pepperi and published curves of chemical residues across time.

Before the aphid population model can be used with any confidence it will be necessary to test and validate it. Testing consists of fine tuning the model to reproduce results from systematic field samples used to generate its various state and rate functions. Validation involves comparing model results against an indeopendent data set, ie. one not used in the construction of the model.

One of the weakest links in the present model is the estimate of the length of the aphid's adult life stage. Due to unforeseeable problems in the fixed temperature experiment, the estimate for this variable was arrived at very subjectively. Another shortcoming of the model is that its results are only applicable when the system is sampled using the 'standard sample' method. Since this systematic sample has not been compared against any absolute sampling method, model results cannot be transformed into absolute units, ie. aphids/bush or aphids/acre.

To conclude, I should like to reflect for a moment on the uniqueness of aphids as the object of scientific scrutiny. Like many other insects their small size and short generation time makes them ideal experimental

subjects. But aphid ecosystems are also a complex web of interdependent relationships. Most aphid species are highly polymorphic, exhibiting a gradation of forms from completely wingless to functionally alate and combining both parthenogenic and sexual reproduction. They are also one of the most multivoltine insect families, with some species undergoing more than twenty generations per year. In addition, they serve as food for a wide range of predators and parasitoids. These complexities increase the difficulties associated with experimentation, particularly regarding proper experimental controls. The study of aphid morph determination provides a case history of some of these potential difficulties. Such difficulties are major challenges to those who desire to gain a better understanding of aphid ecosystems through modeling. Modeling is not merely a process of mathematizing an ecosystem. Of necessity, the process also results in an abstraction and simplification of the system in question. One of the most useful results of the modeling process may well be that errant model results help identify important relationships of the system that are either absent from the model or poorly understood. Hopefully, the research presented here has succeeded in spotlighting some of the more important relationships in the I. pepperi agro-ecosystem.

APPENDIX 1

Voucher Specimens

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1987-3

Title of thesis or dissertation (or other research projects):

A VARIABLE LIFE-TABLE FOR Illinoia pepperi (MacGillivray)

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Abbreviations:
OV oviparous female
AL viviparous, alate female
AP viviparous, apterous female

Investigator's Name (s) (typed)
Robert Delain Kriegel II

Date July 28, 1987

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 5 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Illinoia pepperi (MacG.)	MI: Ottawa Co., West Olive, MI, 31-NOV-1980 Col. E. Elsner	X							MSU
Illinoia pepperi (MacG.)	MI: Ottawa Co., West Olive, MI, 5-DEC-1980 Col. E. Elsner	X							MSU
Illinoia pepperi (MacG.)	MI: Ottawa Co. West Olive, MI, Field 54B 24-APR-1981, Col. F. Petit on V. corymbosum					OV			MSU
Illinoia pepperi (MacG.)	MI: Ottawa Co. West Olive, MI, Field 54B 3-NOV-1981, Col. E. Elsner on V. corymbosum cv 'Jersey'						X		MSU
Illinoia pepperi (MacG.) (2 specimens)	MI: Ottawa Co. West Olive, MI, Field 54B 24-APR-1981, Col. F. Petit on V. corymbosum					AL			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Robert Kriegel

Date 28-JUL-1987

Voucher No. 1987-7

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date

APPENDIX 1.1

Voucher Specimen Data

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Illinoia pepperi (MacG.) (2 specimens)	MI: Ottawa Co., West Olive, MI., Field 54B 24-APR-1981, Col. F. Petit on V. corymbosum					AP			MSU
Illinoia pepperi (MacG.) red morph	MI: Ottawa Co., West Olive, MI., Field 54B 20-JUL-1981, Col. E. Elsner on V. corymbosum cv. 'Jersey'					AP			MSU
Illinoia pepperi (MacG.)	MI: Ottawa Co. West Olive, MI 10-JUL-1980, Col. E. Elsner in pan trap near V. corymbosum					AL			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Robert Kriegel

Date 28-JUL-1987

Voucher No. 1987-7

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date

APPENDIX 1.1

Voucher Specimen Data

Page 3 of 5 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Illinoia pepperi (MacG.)	MI: Ingham Co., East Lansing, MSU, PRC Bldg., 4-APR-1982, Col. R. Kriegel aphid culture on V. corymbosum	MI				AL			MSU
Illinoia pepperi (MacG.)	MI: Eaton Co., Charlotte, MI Kalamo Hwy, T2N R5W Sec 22 13-JUN-1982, Col. R. Kriegel on V. corymbosum cv. 'Jersey'					AL			MSU
Illinoia pepperi (MacG.) (3 specimens)	MI: Van Buren Co., Grand Junction, MI T1S R15W Sec 9 24-JUN-1982, Col. R. Kriegel on V. corymbosum cv. 'Jersey'					AL			MSU
Illinoia pepperi (MacG.) (5 specimens)	MI: Van Buren Co. Grand Junction, MI, 54th St. T1S R15W Sec 9 24-JUN-1982, Col. R. Kriegel on V. corymbosum cv. 'Jersey'					AP			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Robert Kriegel

Date 28-JUL-1987

Voucher No. 1987-7

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Illinoia pepperi (MacG.)	MI: Van Buren Co., Grand Junction, MI, 54th St. T1S R15W Sec 9 24-JUN-1982, Col. R. Kriegel on V. corymbosum cv. 'Jersey'			x					MSU
Illinoia pepperi (MacG.) red morph	MI: Mackinac Co., Cut River rd., T45N R7W Sec 1 19-AUG-1982, Col. R. Kriegel on wild V. angustifolium Ait.					AP			MSU
Illinoia pepperi (MacG.) parasitized aphid mummy	MI: Eaton Co., Charlotte, MI Kalamo Hwy, T2N R5W Sec 22 20-JUL-1982, Col. R. Kriegel on V. corymbosum cv. 'Jersey'							X	MSU
Illinoia pepperi (MacG.) (3 specimens)	MI: Van Buren Co. Grand Junction, MI, 54th St. T1S R15W Sec 9 12-JUL-1982, Col. R. Kriegel					AP			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Robert Kriegel

Date 28-JUL-1987

Voucher No. 1987-7

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date

APPENDIX 1.1

Voucher Specimen Data

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Illinoia pepperi (MacG.) red morph (4 specimens)	MI: Ottawa Co., West Olive, MI, Field 54A&B 24-JUL-1981, Col. E. Elsner on V. corymbosum				AP				MSU
Illinoia pepperi (MacG.) (2 specimens)	MI: Van Buren Co., R. Bodke Farm, T1S R16W Sec 1 13-MAY-1983, Col. M. Whalon on V. corymbosum cv. 'Jersey'				AL				MSU
Illinoia pepperi (MacG.)	MI: Eaton Co., Charlotte, MI. Kalamo Hwy, T2N R5W Sec 22 23-NOV-1983, Col. R. Kriegel on V. corymbosum cv. 'Jersey'	X							MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)
Robert Kriegel

Voucher No. 1987-7

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

Date

Date 28-JUL-1987

APPENDIX 2

Distribution Map Data

APPENDIX 2.

Table A2.1 Localities in Michigan where *I. pepperi* has been collected.

County	Location	Year	Host[15]	Source[16]
Alger	Adams Trail (Co. 637) & Ausable Point rd., T48N, R16W, Sec 29 NW	1984	*angustifolium*	J.H.
Alger	Lk. Superior shoreline West of Beaver Lk., T48N, R17W, Sec 13	1984	*corymbosum*	J.H.
Allegan	T4N, R15W, Sec 30	1962	*corymbosum*	ENT
Allegan	Fennville, MI	1963	*corymbosum*	ENT
Berrian	Shawnee & Cleveland rds.	1962	*corymbosum*	ENT
Berrian	Hawthorne & Cleveland rds.	1964	*corymbosum*	ENT
Berrian	St. Joseph, MI	1964	*corymbosum*	ENT
Berrian	New Buffalo, MI	1965	*corymbosum*	ENT
Berrian	North Watervillet rd. & Indiana State line	1965	*corymbosum*	ENT
Berrian	Sawyer, MI	1965	*corymbosum*	ENT
Crawford	Hwy I-75 South rest stop	1981	*myrrtilloides*	E.E.
Eaton	Charlotte, MI, Kalamo Hwy, T2N, R5W, Sec 22 SW	1981	*corymbosum*	R.K.
Ingham	Dannsville St. Game Area, Potter rd., T2N, R1E, Sec 32 W	1981	*corymbosum*[17]	E.E.
Mackinaw	Cut River rd., T43N, R6W, Sec 5	1982	*angustifolium*	M.W.
Montcalm	Sidney, MI	1961	*corymbosum*	ENT
Muskegan	Quarterline & Pontaluma rds.	1962	*corymbosum*	ENT
Muskegan	Giles & Buys rds.	1962	*corymbosum*	ENT
Ogemaw	Mills Township, R3E, T21N, Sec 7 SW	1981	*angustifolium*	E.E.

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[15] All host plants are *Vaccinium* sp. Unless otherwise noted all specimens collected on *V. corymbosum* were captured on cultivated plants. All non *corymbosum* hosts represent captures from non-cultivated sites.

[16] Abbreviations for data sources are as follows: J.H. = Dr. Jim Hancock, ENT = Department of Entomology museum specimens, E.E. = Erwin Elsner, M.W. = Dr. Mark Whalon, K.M. = Kathy Morimoto, R.K. = Robert Kriegel.

[17] Collected on wild *V. corymbosum*.

Table A2.1, continued.

County	Location	Year	Host	Source
Oscoda	USFS rd. #4147 R3E, T25N, Sec 7 SE	1981	angustifolium	E.E.
Ottawa	Coopersville, MI	1981	corymbosum	E.E.
Ottawa	West Olive, MI	1981	corymbosum	E.E.
Ottawa	Barry rd. at 144th St., T6N, R16W, Sec 36	1983	corymbosum	K.M.
Ottawa	84th St. & Haynes rd., T8N, R14W, Sec 32	1983	corymbosum	K.M.
Schoolcraft	M77 at E. Branch Fox R. T46N, R13W, Sec 4 SW	1982	angustifolium	M.W.
Schoolcraft	Sable St. Forest, Stanley Lk. Campgrnd, on Little Fox River, T47N, R15W, Sec 11 [18]	1983	angustifolium	R.K.
Van Buren	0.3 mi. E. of 72nd St. and 36th Av.	1962	corymbosum	ENT
Van Buren	Hartford, MI	1964	corymbosum	ENT
Van Buren	Grand Junction, Mi., 54th St, T1S, R15W, Sec 9 SW	1982	corymbosum	R.K.
Van Buren	MI. Blueberry Grower's Association research plot Grand Junction, MI, 54th St., T1S, R15W, Sec 8	1982	corymbosum	R.K.
Van Buren	54th St., T1S, R15W, Sec 4 SW	1983	corymbosum	M.W.
Van Buren	56th St., T1S, R15W, Sec 8 NW	1983	corymbosum	M.W.
Van Buren	57th St., T1S, R16W, Sec 1 E	1983	corymbosum	M.W.
Van Buren	95th St. & Phoenix rd., T1S, R16W, Sec 1	1983	corymbosum	M.W.

[18] Wild demonstration site managed by the Michigan Department of Natural Resources.

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