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BIOLOGY OF ILLINOIA PEPPERI (MACG.), THE BLUEBERRY APHID, AND ITS RELATION TO BLUEBERRY SHOESTRING VIRUS DISEASE IN WESTERN MICHIGAN

presented by

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has been accepted towards fulfillment
of the requirements for

Masters degree in Entomology

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Date 12 February 1982

BIOLOGY OF *ILLINOIA PEPPERI* (MACG.), THE BLUEBERRY APHID, AND ITS RELATION TO BLUEBERRY SHOESTRING VIRUS DISEASE IN WESTERN MICHIGAN

By

Erwin Albert Elsner

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1982

ABSTRACT

BIOLOGY OF ILLINOIA PEPPERI (MACG.), THE BLUEBERRY APHID, AND ITS RELATION TO BLUEBERRY SHOESTRING VIRUS DISEASE IN WESTERN MICHIGAN

By

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The biology of *Illinoia pepperi* (MacGillivray) on cultivated highbush blueberry (*Vaccinium corymbosum* Linn.) in Michigan is examined. This aphid is a vector of Blueberry Shoestring Virus (BBSSV) disease, and its relation to this disease in Western Michigan is studied. An analysis of disease control economics is included. Symptomatology and details of the occurrance and spread of BBSSV within blueberry plantings are given. Field biological studies on *I. pepperi* include an analysis of yellow pan trap catches of alatae, aphid life cycle and seasonal history, and a brief discussion of the predators, parasitoids and other mortality agents of this aphid. The results of a 3 year search for alternate host plants for *I. pepperi* in Michigan are given. The development of an optimal sampling scheme for aphid density estimation is outlined and the results presented. Results of laboratory experiments to determine the lower developmental threshold temperature, developmental rate, generation time and fecundity of apterous viviparous *I. pepperi* are presented and discussed.

Dedicated to my parents in appreciation
for their 25 years of dedication to me.

ACKNOWLEDGEMENTS

I wish to thank Dr. Mark Whalon, my graduate advisor, for giving me the chance to work on this project; he guided my efforts, saved me from pitfalls and gave the necessary pushes when I slowed down.

I thank the members of my graduate committee, Drs. Jim Miller, Frederick Stehr and Donald Ramsdell for their ample support, openness to opinions and ideas, and their swift review of this manuscript.

I deeply appreciated the support of the Michigan Blueberry Growers Association, Grand Junction, MI. Their financial assistance made this project possible, and their administrators, employees and member growers helped carry it to completion. Their Director of Research, John Nelson, provided a great deal of information to me and often assisted with field projects, along with their field scouts, George Jaeger and Harold Huizenga. Member growers were extremely cooperative.

Terry Davis gave me many days of field assistance on every part of this project, rain or shine. His help with Laboratory experiments made it possible for me to get away when I needed a break.

The department of Entomology Graphics Laboratory produced many of the figures in this work. My special thanks to Lana Tackett for the excellent aphid illustrations.

I thank Kerry Hulliberger for her fine typing service in the preparation of this manuscript.

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INTRODUCTION

The blueberry aphid, *Illinoia* (= *Masonaphis*) *pepperi* (MacGillivray) can be found in most areas in which highbush blueberry (*Vaccinium corymbosum* Linn.) is grown in Michigan. It was a suspected vector of Blueberry Shoestring Virus (BBSSV) disease for many years[1], but not until 1979 was there substantial evidence for the association of *I. pepperi* and the spread of BBSSV (Ramsdell 1980a). In recent years, much attention has been directed toward the control of this aphid. BBSSV disease causes extensive economic loss to highbush blueberry plantings by the slow decline and eventual death of infected bushes. Berry production drops dramatically within a few years of the onset of symptoms. This reduction in productivity plus the eventual stand decrease (from removing bushes) was estimated to cause a $16,000,000 dollar loss to the blueberry growers and the associated industry (Ramsdell et. al. 1980) in the United States.

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[1]J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, Mi. Personal Communication, 1979.

Systematics of Illinoia (= Masonaphis) pepperi (MacGillivray)

The Classification of the group of aphids to which *I. pepperi* belongs has been revised many times in efforts to clear confusion due to synonomy. Wilson (1910) divided the subfamily Aphidinae into three tribes, the Trichosiphini, Aphidini and Macrosiphini. He erected the genus *Illinoia* in the Macrosiphini based partly on the length of cornicles. The genera *Amphorophora*, *Macrosiphum*, and *Myzus* were also placed in this tribe.

Hille Ris Lambers (1939) while discussing *Macrosiphum*, writes:

> "This genus (*Illinoia*) of Wilson was meant for those species of *Macrosiphum*. . . which have the cauda without a basal constriction. In this sense the genus *Illinoia* is senseless, because the closest allied species may show difference in this regard. . . and variation within species is quite common."

He then identified *Illinoia* on the basis of the complete absense of rhinaria on the 3rd antennal segment of apterous viviparous forms of this group.

In this same study the genus *Masonaphis* was erected based on the type species *Illinoia rhododendri* Wilson, an European species found on Ericaceae. The genus possesses rhinaria on the 3rd antennal segment, distinct reticulation of the apex of the cornicles and 5 hairs on the 1st tarsal joint. The last two characters separated *Masonaphis* from *Amphorophora*. He then placed *Amphorophora azaleae*, *A. borealis*, *A. rhododendronia* and *A. vaccinii* in the genus

Masonaphis, and suggested that these were likely all synonyms of A. rhododendri.

MacGillivray (1958) arranged the genus Masonaphis[2] into four morphologically and biologically homogeneous subgenera; Masonaphis "sensu stricto" containing species on Ericaceae; Oestlundia containing species from Rubus, Amphorinophora containing species associated with Lonicera and the subgenus Ericobium which was associated mainly with the compositae and Ericaceae. Masonaphis pepperi was then described as a new species in the subgenus Ericobium.

Her key to this subgenus uses many difficult and variable characters. Relative lengths, pigmentation (difficult with cleared and slide mounted specimens), number of tarsal hairs (admitted to be quite variable in the same work) and whether or not certain tubercles are conspicuous. Many judgements must be made to key a specimen. To add to the problem, she states:

> "Mention should be made to the very frequent occurrence in this subgenus of apterous viviparous morphs that in their higher number of rhinaria and presence of vestigial occeli resemble alatae; such alatiform apterae occur simultaneously with normal apterae viviparae."

Five morphological forms of M. pepperi were described; an apterous fundatrix, an apterous viviparous female,

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[2]She considered aphids of the "Amphorophora group" with swollen and reticulated cornicles to be in the genus Masonaphis.

an alate viviparous female, an apterous oviparous female, and an alate male which she doubted was of the same species (MacGillivray 1958).

The nature of the key characters and the frequent morphological variation may be the cause of the taxonomic difficulties experienced with the determination of aphids samples taken in recent years (see page 5 for discussion).

Smith and Parron (1978) stated that the genus _Masonaphis_ was synonymous with _Illinoia_ thus placing _pepperi_ in _Illinoia_ since it was the first of the two genera to be established. No mention was made concerning the morphological characters that were originally used to separate the genera, such as the rhinaria of the IIIrd antennal segment (present in _Masonaphis_, none in _Illinoia_ as originally described). The reason for this change of classification was not given.

Historically, the aphids found on cultivated highbush blueberry in Michigan have been determined as _I_. _pepperi_. Aphids collected from blueberry near Fennville, Michigan in 1964 were determined to be _I_. _azaleae_[3]. Surveys in the mid-1960's made by Giles (1966) reported _I_. _pepperi_ and _Myzus_ _scammelli_ colonizing highbush blueberry. Specimens

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[3]J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, MI. Personal Communication of Nov. 9, 1964, from E.H. Barnes, Assistant Professor of Plant Pathology, Michigan State University, East Lansing, MI.

were collected with a D-VAC[R] sampler and determined by that author with the assistance of Louise Russel[4].

Marucci[5] reported that similar aphids determined by systematists at the National Museum were identified differently in successive years, i.e. Amphorophora vaccinii, Masonaphis azaleae, Fimbriaphis sp. and Masonaphis pepperi. Pepper[6] has supplied this author with slide mounted specimens of I. pepperi and I. azaleae, and has never collected the latter on blueberry in Pennsylvania. Aphids collected from cultivated highbush blueberry (Vaccinium corymbosum L.) and caught in plant traps in western Michigan in July of 1979 were determined as I. azaleae by Dr. Monya Stoetzel[7], but these specimens were not slide mounted for identification, and the characters for keying the species are very difficult to discern on unmounted specimens.
In an effort to clear the taxonomic problems, specimens

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[4]L. Russel, Aphid Systematist, (Retired), USDA Insect Identification Laboratory, Beltsville, MD.

[5]P. E. Marucci, Research Professor in Entomology, Rutgers University, Chatsworth, N.J. Personal Communication, 1979.

[6]J. O. Pepper, Eremitus Professor of Entomology, Pennsylvania State University, University Park, PA. Personal Communication, 1980.

[7]M. Stoetzel, Systematist, USDA Insect Identification Laboratory, Beltsville, MD.

have been sent to M. Stoetzel, M. E. MacGillivray, J. O. Pepper and V. F. Eastop[8]. Specimens have been returned by J. O. Pepper and M. E. MacGillivray, determined as Illinoia pepperi. Specimens sent to M. Stoetzel were determined only as Illinoia sp.

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[8] V. F. Eastop, Insect Systematist, British National Museum, London, England.

Biology of Genus Illinoia (= Masonaphis)

MacGillivray (1958) listed the following host plant families for the subgenus Ericobium; Cupressaceae, Abietaceae, Liliaceae, Caprifuliaceae, Compositae, Corylaceae, Ericaceae, Hydrophyllaceae, Myricaceae, Ronuculaceae, Rosaceae and Violaceae. A preference was noted for the Compositae and Ericaceae. She also stated that the species for which biological data were available were monophagous or oligaphagous. Host alternation was not noted. Sexual forms were found only in autumn, no association with ants existed, and these aphids did not deform the host plant tissues, i.e. cause galls.

Extensive biological data are available for I. maxima (Mason) (Subgenus Oestlundia), the thimbleberry aphid. This aphid is holocyclic with all morpholical forms occurring on a single host species, Rubus parviflorus Nutt; plant-aphid-parasitoid relationships have been studied and modeled (Gilbert and Gutierrez 1973; Gilbert et. al. 1976)

The following description of the biology of I. maxima is taken from Gilbert and Gutierrez (1973). Eggs are laid in leaf litter during the spring and summer, and diapause until the following spring. After hatching, 1st instar nymphs walk into the bushes to the tips of the canes, where they develop into parthenogenic females (fundatrix). These have two types of progeny, termed gynoparae and virginoparae. Gynoparae eventually give birth to sexual females; virginoparae give rise to further parthenogenic females and sexual males, as outlined in Figure 1. Sexual forms first appear in the second generation, and continue throughout the growing season. Males and gynoparae forms are winged, sexual females apterous, and the virginoparae may or may not have wings. Adult *I. maxima* move away from the terminals on which they matured. Sexual females move to the base of the thimbleberry plants, before laying a maximum of 8 overwintering eggs in the leaf litter. Color differences make morph identification easy for *I. maxima*; males are red, sexual females white, and the parthenogenic forms are green. Gynoparae and winged virginoparae are indistinguishable unless their progeny are observed. The base temperature for development of this aphid is 3.3^{o}C (38^{o}F).

Few studies have dealt directly with *I. pepperi*. Earlier studies have indicated that this aphid is monophagous on highbush blueberry (even limited to certain cultivars) or rarely oligophagous, with no alternation of hosts; winged viviparous forms were generated throughout the growing season, and the overwintering strategy remained under investigation (Elsner and Whalon 1980). Both green and red colored morphs of *I. pepperi* were found in the study, but the red forms were a color phase of apterous or alate viviparous females, not males as in the case of *I. maxima*.

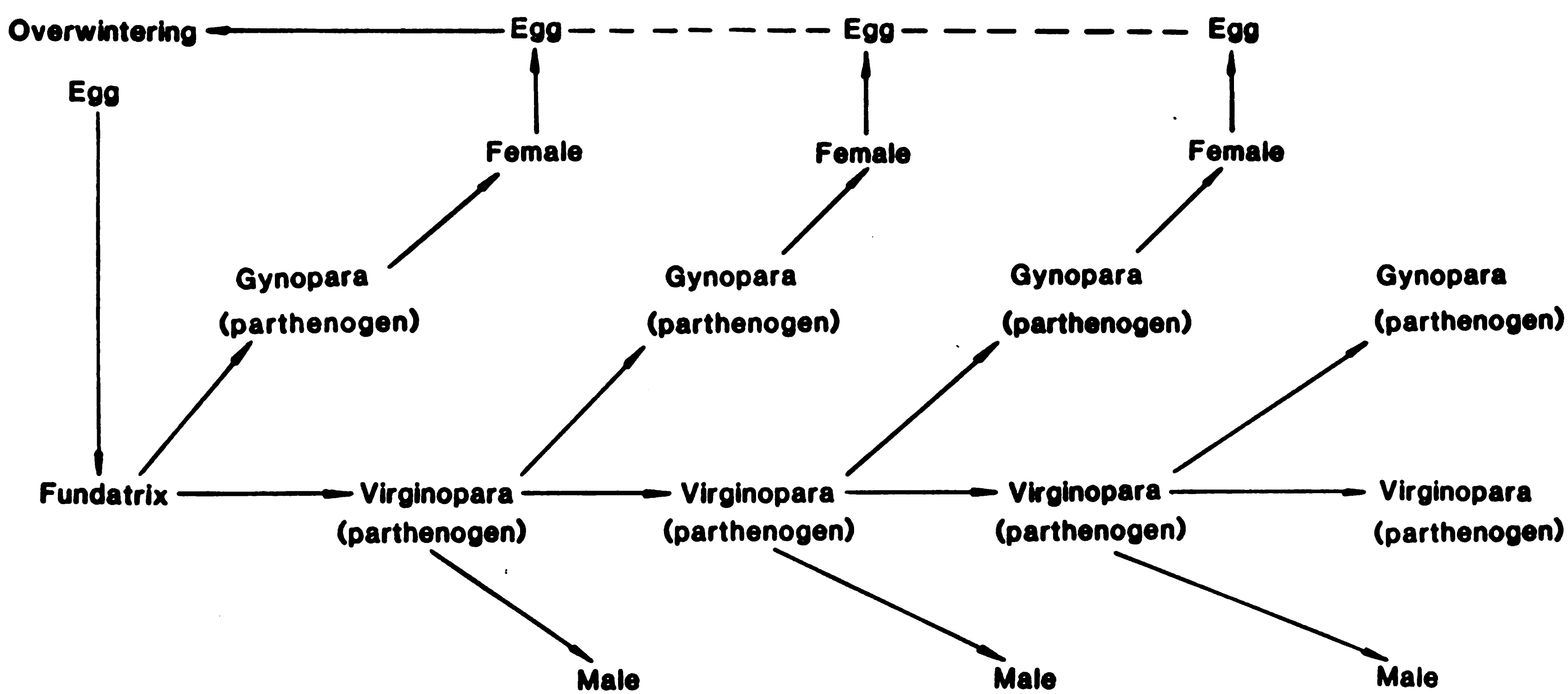


FIG. 1.--Life cycle of Illinoia maxima (Mason) on Rubus parviflorus (Gilbert and Guterrez 1973).

Giles (1966) gave the distribution of blueberry aphids in Michigan (Figure 2) and partially described the biology and behavior of _I_. _pepperi_. Table 1 gives the relative incidence of the species collected in his study by sampling with a D-VAC[R] unit.

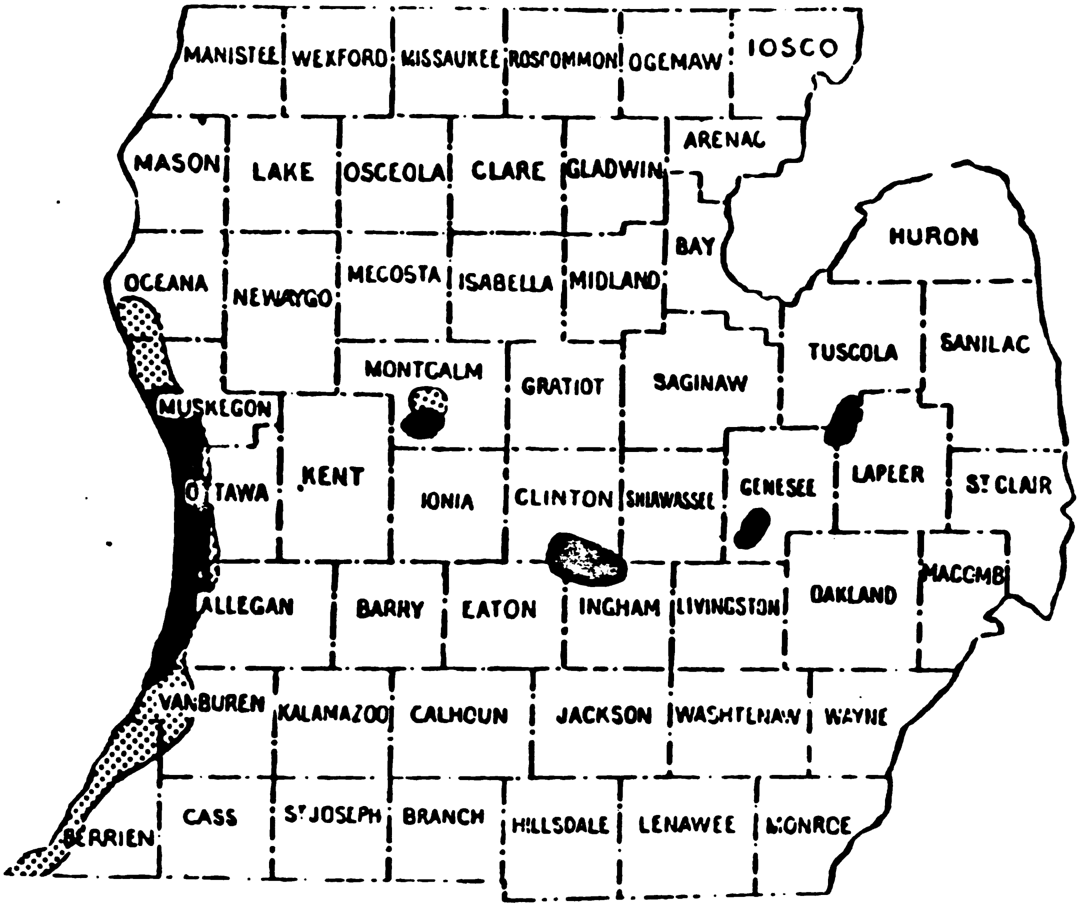
Table 1. Percent of Commercial Blueberry Plantations Infested with _Illinoia pepperi_ and _Ericaphis scammelli_ from 1961-1964 (Giles 1966).

Year	Relative Abundance of Species	
	I. pepperi	_E. scammelli_
1961	13.0%	6.7%
1962	34.2%	10.5%
1963	20.0%	3.3%
1964	28.0%	12.0%

He reported that the preferred feeding site for both of these aphids was the upper surface of leaves at the base of the bush. He found no aphids on the roots of blueberry.

Blueberry Shoestring Virus Disease

Blueberry Shoestring Virus (BBSSV) disease was first described in highbush Blueberry (_V_. _corymbosum_, 'Jersey' cultivar) in New Jersey (Varney 1957) which is considered to be its point of origin. Since that time, the most probable mode of dispersal to many other states has been




<u>Ericaphis</u> <u>scammelli</u> (Mason)


<u>Illinoia</u> <u>pepperi</u> (MacGillivray)

FIG. 2.-- Geographical distribution of blueberry infesting aphids in southern Michigan (Giles 1966).

through diseased propagation stock. Lockhart and Hall (1962) reported apparent visual and symptomless infection in lowbush blueberry, V. angustifolium, in Canada. Hartman et. al. (1973) visualized the virus-like particles in plant tissue using electron microscopy. The small spherical (27mm in diameter) virus has been purified and shown to cause the disease (Lesney et. al. 1978). Ramsdell (1980b) has characterized the virus and adapted the Enzyme Linked Immunosorbent Assay (ELISA) techniques of Clark and Adams (1977) for use in the detection of BBSSV infections in blueberry.

The ability of I. pepperi to be a vector of BBSSV was demonstrated in 1978. Successful transmission of the disease occurred only with 2 minute aquisition times and 100 hour inoculation periods only (Ramsdell, unpublished data). No other vectors have been determined.

ECONOMIC JUSTIFICATION

Michigan ranks first worldwide in highbush blueberry production. The annual yield exceeds 35 million pounds, constituting over 30% of the North American crop. In Michigan, blueberries are grown on organic soils with a pH from 4.0 - 5.5 and a high water table. Few other crops grow well in sites suitable for blueberries. The demand for good blueberry sites has raised the land values of what was previously unused areas.

Based on an estimated 1980 crop of 37 million pounds and an average sale price of $0.35 per pound (1980 prices ranged from $0.75 per lb. for roadside sales to $0.35 per lb. for processing grade fruit), a conservative estimate of the value of last year's crop is nearly 13 million dollars. Current highbush blueberry acreage production in Michigan is approximately 10,000 acres. It is estimated that another 1,000 acres have been planted but have not yet reached bearing age (8-10 years)[9]. Highbush blueberries will continue to be productive for well over 30 years if properly managed. Some fields in New Jersey which were planted in the early 1900's are still in production.

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[9]J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, MI. Personal Communication, 1981.

Many varieties of highbush blueberry are grown in Michigan. All have been bred from natural strains of *V. corymbosum*. The most popular cultivar is Jersey, which accounts for well over 50% of the acreage. Other common cultivars include Bluecrop (14%) and Rubel (12%)[10]. Bluecrop is apparently resistant to BBSSV but it is very difficult to propagate. Each cultivar has certain favorable characteristics which make it more applicable to the varied utilizations of blueberries. Blueberries are sold as U-Pick, or harvested by hand or machine for fresh pack and processing grades. Table 2 gives the typical utilization breakdown of a year's crop and the prices received for selected years.

Table 2. Crop Utilization and Average Market Prices for Michigan Blueberries[a].

Utilization (Grade)	% of Crop 1980	Average Price/lb. 1970	1972	1975	1980
Fresh Pack	20				$0.50
Process	75	$0.20[b]	$0.30[b]	$0.25[b]	$0.35
U-Pick	5				$0.50 - 0.60

[a]Source = J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, MI.

[b]Average price received, all grades.

[10]J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, MI. Personal Communication, 1981.

Prices are influenced by the size of the crop, environmental conditions (frosts, hail, excessive moisture, etc.), market competition with other fruits, and consumer demand. The 1972 crop illustrates the influence of weather and subsequent price variation; the crop was greatly reduced by spring frosts. Prices rose accordingly and demand for quality berries was high. Yield per acre varies due to soil conditions, variety and condition of plants, but averages nearly 4000 lb per acre in well kept plantings. At the average 1980 price of $0.35 per pound, an acre of blueberries would produce $1400 worth of fruit each year.

Energy inputs into blueberry production include petroleum products (fuels, fertilizers and pesticides). Cultural techniques contribute to the intensity of energy inputs as does the level of weed or pest control utilized. A good deal of human energy is also needed for successful blueberry production, due to manual labor inputs necessary for pruning, hand harvesting and packaging of the product.

Table 3 presents a breakdown of the estimated fixed costs per acre per year for blueberry production in Michigan.

Table 3. Highbush blueberry production costs. 1981 estimates.

Operation[a]	Cost/Acre/Year[b]
Fertilizer	$45.00
Herbicide	25.00
Phomopsis Canker control	55.00
Mummyberry control (funginex by airplane)	75.00
Pruning and brush chopping	180.00
Mowing or cultivation	30.00
Bee rental	25.00
Depreciation on plants	200.00
Taxes	50.00
Gasoline	15.00
Pesticide applications (by air)	60.00
Estimated Total	$760.00

[a]Typical operations. Individual grower situations or decisions may increase or decrease the number of production operations.

[b]Source: J. Nelson, Director of research, Michigan Blueberry Growers Association, Grand Junction, MI.

This table does not include the costs of harvest, so this total is underestimated. A grower with a large operation (70+ acres) may pay up to $30,000 per year to employees, mostly during harvest. Custom machine harvesting is available for $0.10 - $0.12 per lb.

Extent of BBSSV in Michigan

Yearly surveys have been made for plant diseases (mostly BBSSV, and Stunt, a mycoplasma disease) in blueberry since 1957. In 1976, 5,724 BBSSV infested bushes were found on 1576 acres surveyed. If this acreage was representative of the 10,000 acres in production, there were approximately 36,600 infected bushes in Michigan in 1976. Figure 3 shows the increase in visibly infected bushes for the last 25 years (figures were estimated in the same manner as the example above). From Figure 3 it is apparent that by 1985 there could be over 100,000 plants with visual BBSSV symptoms in Michigan.

BBSSV may have up to a 4 year latency period before visual symptoms are expressed. Because of this the actual number of infected bushes at any time is much greater than the number of plants showing visual symptoms. It has been proposed that there could actually have been over 145,000 infected bushes in 1976, compared to the visually based estimate of 36,000 (Ramsdell et. al. 1980).

Losses Due to BBSSV

Infection by BBSSV reduces a bush's production. At some point this declining yield renders a field an economic loss, making removal of diseased bushes and replacement with new plants necessary. Even before production drops significantly, the infected bushes serve as an inoculum source for the infection of other bushes, and should be

FIG. 3.--Observed [*] and extrapolated [■] plants with visual symptoms of Blueberry Shoestring Virus disease in Michigan from 1957 - 1985 (Ramsdell et.al. 1980). Y = number of infected plants; X = year.

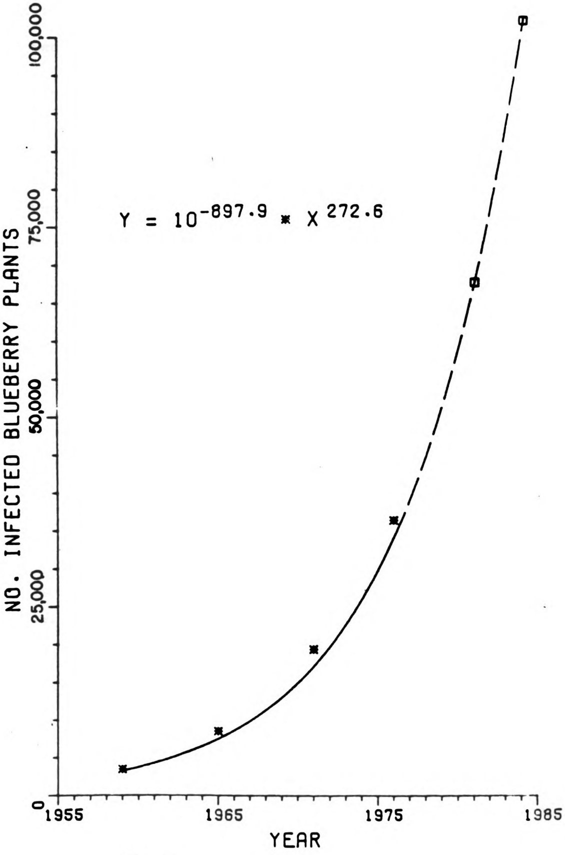

NO. INFECTED BLUEBERRY PLANTS
100,000
75,000
50,000
25,000
0
$Y = 10^{-897.9} * X^{272.6}$
1955
1965
1975
1985
YEAR

FIG. 3.

removed for this reason. Currently, removal of infected bushes is the only effective solution to BBSSV problems. The problem of latent infection renders bush removal practices less than perfect for complete removal of diseased bushes from field. Individual diseased bushes are often removed and replaced if a field is lightly infected. The practice is favored because the entire field does not have to be removed from production.

Severe infections call for the rouging out of entire fields and starting over. Costs for removal of diseased bushes is approximately $1,000 per acre. A two-year waiting period is recommended before replanting. The decision must then be made to plant a potentially resistant cultivar such as Bluecrop or one which is more suitable for other reasons. Site preparation starts with the complete removal of plant material when the old bushes are removed, leaving no stumps or roots. Before replanting, soil modifications may be made to favor the new planting and adjust the pH. Two year old plants certified free of disease should be used to replant the field. A typical planting scheme (4 x 10 ft. spacing) takes 1089 plants per acre. Typical costs of replanting with the resistant cultivar Bluecrop are given in Table 4.

Table 4. Approximate Costs Per Acre for a Removal-Replant Operation as a solution to BBSSV disease in Western Michigan, 1981.

Year	Operations	Main Inputs	Extra Costs	Fixed Costs[b]	Totals
1	removal, sanitation	energy labor	$1000	$200	$1200
2	soil management	energy labor	-----	$200	$ 200
3	replant	energy plants labor	$2000	$300	$2300
4+	management	energy labor	-----	$760 x 7	$5320
				10 year total	$9020

[a]Source: J. Nelson, Michigan Blueberry Growers Association, Grand Junction, MI

[b]Figures given are modified values from Table 3, as explained in text.

Figures given for fixed costs in Table 4 have been adjusted downward from those found in Table 3, since during the first 3 years of the replant procedure, certain operations, i.e., pruning, bush chopping, mowing, cultivation, bee rental and pest control are reduced or eliminated, thereby lowering costs.

Besides the direct costs due to the removal-replant operation itself, revenues are lost for the years that pass before the new bushes become productive (roughly 8 years to full production). On the average, the yield from an acre of blueberry plants is worth \$1400 per year. This revenue is lost completely for the first few years, and can be slowly regained as the planting matures. Considering this lost revenue as another cost of the removal-replant operation, the total cost over a 10 year period could approach \$14,000 per acre. It has been estimated that if all the known BBSSV infected acreage in Michigan were renovated, the total cost over 10 years would exceed \$3,000,000. This would of course be accompanied by a significant loss of production and allied reductions in support industries, labor, etc.

BLUEBERRY SHOESTRING VIRUS DISEASE

Symptomatology and Host Range

Blueberry is the only known host of BBSSV. The disease has been observed in the cultivars Burlington, Coville, Earliblue, Jersey, June, Rancocas, Rubel and Weymouth (Ramsdell 1980a). The cultivars Bluecrop, Northland and Bluejay appear to be resistant to the disease. Visual symptoms of BBSSV are as follows:

1) Narrow or strap like leaves: hence, the name shoestring; leaves may also be crescent shaped or curled,
2) Elongate red streaks: on current years stems; sometimes visible on older wood,
3) Red vein banding: on young tender leaves; along midrib or in oak leaf patterns,
4) Immature berries with purplish cast: apparently normal when ripe; no quality loss,
5) Twisted appearance to stem growth: also weakened and spindly wood; easily broken in wind or under fruit loading.

Symptoms on leaves and stems are most pronounced on vigorously growing tissues, especially near the base of the bush. Environmental conditions enhance or repress the expression of symptoms, even on bushes which were quite obviously infected the year before. Such was the case in 1980 when many infected bushes did not express symptoms, or visual symptoms were repressed.

True symptomless infections are quite common due to the latency period. Various immunological techniques are available for the detection of symptomless BBSSV infection. ELISA has proved to be reliable and accurate. Several new techniques are currently being tested for use in BBSSV detection in both blueberry tissue and the aphid vector (Ramsdell, unpublished data).

Aphid Transmission

Transmission studies by Ramsdell (Unpublished data 1978) produced successful inoculation under very specific conditions; only aphids which had a 2 minute acquisition period and a 100 hour inoculation time transmitted the disease. Table 5 presents the results of these transmission trials. Much work remains to be done to verify these results. From the existing information, the virus appears to be semi-persistant in *I. pepperi*. It may be circulative but is probably not propagative in the vector, as virus titre is quite low in aphids.

Illinoia pepperi appears to be an inefficient vector in the field. Infection rates are low and the disease spreads slowly through a planting. From 1959-1960, a 0.9% increase in infected bushes was found in one field. Lesney et. al. (1978) calculated a "compound interest rate (r)" for observed field spread in 1958 to 1959; the value

Table 5. Tests of Blueberry Shoestring Virus transmission by Illinoia pepperi[a] (Ramsdell, unpublished data 1978).

Acquisition access time[b]	Inoculation feeding time[c] 10 min	1 hour	24 hour	100 hour[d]	9 days
2 minutes	0/5	0/5	0/5	2/5	0/5
1 hour	0/5	0/5	0/5	0/5	0/5
24 hours	0/5	0/5	0/5	0/5	0/5
aphid control	0/5	0/5	0/5	0/5	0/5
non aphid control	0/5	0/5	0/5	0/5	0/5

[a] Ten aphids per test plant used. Aphids were starved 1 hour before acquistion period.

[b] Diseased rooted cuttings of 'Jersey' blueberry used as source plants.

[c] Five rooted cuttings of healthy 'Jersey' blueberry used per set inoculation feeding times. Aphids were transferred serially from one inoculation feeding set of plants to another.

[d] Experiment begun on October 27, 1977. On January 21, 1978 one plant showed shoestring symptoms. On July 26, 1978 two plants were ELISA positive for BBSSV, but only one showing symptoms.

was 0.269/unit/year. Other tests showed that infection occurred on a bush to bush basis along rows, and only occasionally across rows. Personal observations have confirmed this. Spread of the disease was determined not to be due to continuous re-introduction from sources outside a field (Lesney et. al. 1978).

Because of this pattern of spread, it can be suspected that apterous or immature aphids walking from stem to stem may be the most likely vectors of BBSSV. In most plantings, bushes within a row overlap somewhat so there is ample opportunity for aphids to move from one bush to another. Moving from row to row is significantly more dangerous to an aphid due to factors of distance, terrain, desiccation, starvation and ground dwelling predators. Infrequent transmission by winged forms or far ranging walking individuals may account for the spread of BBSSV to other rows. It would be worthwhile to study the spread of BBSSV in younger plantings, or closely trimmed fields where bushes do not touch along the rows. A different rate or pattern of spread under these conditions would be expected.

OCCURRANCE AND DISTRIBUTION OF BBSSV IN OTTAWA CO., MI

OBJECTIVES

Fields were surveyed for BBSSV infection in order to determine the seasonal and locational differences in symptom expression, spacial distribution and pattern of spread, and the relationship of field location, design and surroundings to the incidence of BBSSV disease.

METHODS AND MATERIALS

Five plantings of blueberry ('Jersey' cultivar) located in Ottawa County were chosen as the main study fields. Each was owned and operated by member of Michigan Blueberry Growers Association, Grand Junction, and were designated by their field numbers as listed by the Growers Association. The fields, from south to north were:

#393, Park Township, Wesley Waldron, owner;

#7, Port Sheldon Township, Allen Devries, owner;

#54A, Olive Township, Vern Brower, owner;

#54B, Olive Township, Vern Brower, owner;

#281, Polkton Township, Frank VenRoy, owner;

Historical maps of disease incidence were available for field #7. Field #54A and B are adjacent to each other, but have had different histories of disease incidence. Diagramatic maps of each field can be found in appendix 2.

Field #54B was examined for the effects of exposure to sunlight on symptom expression. Earlier workers suggested that symptoms were more vividly expressed on the sunny sides of bushes. Rows in #54B were east-west oriented, so there was a sunny (southern) and shady (northern) face of each row. Each row was surveyed for visual BBSSV symptoms from both sides, and diseased bushes recorded. This survey was made on July 23, 1979. Fields #393, #7, #54A and #281 were examined for visual BBSSV infection on June 28 and August 8, 1970. Infection was determined based on the observation of visible symptoms. Teams of two people examined a row (one on each side) and tagged diseased bushes with plastic ribbon. Tagged bushes were later recorded and mapped. Data was converted to a computer matrix form to be compared and analyzed for rate, direction and proximity of disease spread. It was planned to repeat this survey in 1980, but environmental conditions repressed the expression of symptoms on diseased bushes.

RESULTS

No significant difference in symptom expression was noted between sunny and shady sides of bushes or rows. As can be seen in Table 6, roughly equal numbers of bushes were expressing visual symptoms on the north side only, southside only, or both sides at once.

Table 6. Differences in BBSSV Symptom Expression on North and South Sides of Blueberry Bushes. July 23, 1979.

Bushes examined	Healthy	Symptoms		
		North only	South only	Both
382	310	23(31%)	25(34%)	24(32%)

These results imply that inspection of bushes from one side of a row only would not accurately determine the state of infection in a field.

On the average, a 1.9% greater number of visually infected plants were found on August 8 than on June 28 (Table 7).

Table 7. 1979 BBSSV Survey Results: Number of Bushes with Visual Symptoms on June 28 and August 8.

		June 28		August 8		
Field	Total Bushes	Infected	%	Infected	%	% Increase
7	1740	405	23%	431	24.7%	1.4%
54A	680	34	5.0%	47	6.9%	1.9%
54B	382	---	---	72[a]	19.0%[a]	---
281	3454	376	10.8%	458	13.2%	2.4%

[a]Fields 54B examined only once on July 23, 1979.

Fields #54A and B, although adjacent, show a quite different infection rate. This can be partially explained by a more extensive diseased plant removal program in #54A.

Computer matrices for all fields except #393 were generated with different symbols representing the bush conditions, i.e., normal, expressing symptoms on June 28, expressing symtoms on August 8, and removed. Field #393 had unequal bush spacing, allowing for different numbers of bushes in rows of the same length. It was therefore difficult to convert to a matrix form, and was analyzed by directly examining the field data. Maps generated for the fields were easily studied. A portion of the computer generated maps for fields #281 and #7 are shown in Figure 4.

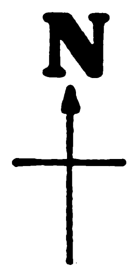
Direction effects on BBSSV infection were evident from these maps. Spread was mainly within rows and occasionally in other directions. These results supported the findings of Lesney et. al. (1978). Field #393 showed a greater number of infected bushes in the southern half of the field. Field #7 exhibited greater infection in the center and western portions. In #54A and B, greater infection was found in the northern end of the field. Field #281 had a rather even distribution of infected bushes, but increases could be seen in the west and south-east. Since there is no consistent compass direction in which greatest infection occurs, it is likely that field layout and surrounding areas have more relation to infection

SHOESTRING VIRUS FIELD MAP-- Field 281

```
. . . . . . . . . . . . . . . . . . . . . .
. . . . . . . . J . . . . . . . . . . . . .
. . . . . . . A A . . . . . . . . . . . . .
. . . . . . . . . . . . . . . J . . . . . .
. . . . . . . . . . . . . . . A . . . . . .
. . . . . . . . . . . . . . . . . . . . . .
. . . . . . . J . . J . . . . . . . . . . .
. . J . . . J . . . J . . . . . . . . . . .
. . . . . . . J . . . . . . . . . . . . . .
. J J . . . . . . . J J . . J . . . . . . .
. . . . . . . . J . J . . . . . . . . . J .
. . . . . . . . . . . . . . J . . . . . . .
```

SHOESTRING VIRUS FIELD MAP-- Field 7

```
J . . . J . .   . J . . . . . . .
. . . . . . J J . J . . . . . . .
J J . . . . J J . J . . . . . J J
J . J J J . J   . J . . .   . . .
J . A J J . J   . . . . . . . J J
  . J J J J   J . .   .   * . . .
  . . . J J J     . . . . . . . .
    . J .   J . . . . . . . . . .
    J . J J J   . . . . J . . . J
    J J   J J   . . . . .   . . .
  J . .   J . . . . . . .   . . .
. J J . J J .   J . J . . . . . .
```



Rows run north-south

Key to symbols:

. = bush without visual symptoms
J = bush with visual symptoms on June 28
A = additional bushes with symptoms on Aug. 8
* = stump of removed bush with infected shoots
space( ) = removed bush

FIG. 4.-- Sections of two computer generated BBSSV infection maps from 1979 survey, Ottawa Co., MI.

rate, probably due to the influence of these factors on aphid populations.

Field #393 is a relatively old field, with a long history of BBSSV problems. Along the western half of the northern border is a small deciduous woodlot with a few coniferous trees. To the east there is a drainage ditch lined with deciduous trees, with field crops beyond this. Until recently, there were more blueberries just to the south, but this planting was heavily infected and removed. It was replanted in 1980. Farther south are more blueberry plantings. To the west is a roadway, and a coniferous woodlot; beyond this lie more blueberries. The greater infection rate in the southern half of field #393 is probably related to the former heavily infected planting to the south.

Field #7 is also an older planting. Records of disease incidence for this field are available as far back as 1957.[11] To the north of the block is another blueberry planting, part of which is very recent (3-4 years old). To the east, west and south are blueberries of similar age. A woodlot is visible toward the west. There appears to be no obvious reason for the distribution of infected bushes in this field.

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[11] J. Nelson, Director of Research, Michigan Blueberry Growers Association, Grand Junction, MI. Original materials and mimeographed reports. 1979.

Field #54A is long and narrow, with the long axis running north-south. To the east is an open lot, followed by another blueberry planting. The open lot was once a planting as well, but was removed due to disease problems several years earlier. South of this field is a residence, and a small field of blueberry. West of #54A is field #54B, and some young pines. U.S. 31 lies farther to the west. The north end of field #54A is adjacent to a small pine woodlot, which partially surrounds this end of the field. Beyond the woodlot are more blueberry plantings. Greatest infection was noted in the northern portion of this field, and may somehow be related to the woodlot. The easternmost row was also quite infected, probably due to the former field with disease problems.

Field #54B, immediately west of field #54A, has similar surroundings. A pine woodlot is northeast of this field, and it is bordered on the west by U.S. 31. Once again, increased infection seems to be in the area nearest the woodlot. Many open spaces are present in this portion of the field, due to removal of diseased bushes.

Field #281 is a relatively younger planting, and is managed as a clean culture system; all other fields had herbaceous ground cover throughout the year. To the north of the field lies another planting of blueberry, the infection status of which is not known. A small deciduous woodlot lies to the northeast. Raspberries and strawberries are grown to the east of this field, and farther east lies a residence. The south border of the field is a gravel road, across which lies an open field where some livestock are grazed. A large mixed woodlot lies to the southeast. The west side of the field is bordered by a gravel road, ditch and fence row with trees and bushes. Beyond this is a pasture and dense woods. Although not greatly different in infection rate, the areas closest to the southeast and western woods are more diseased than other parts of this field.

DISCUSSION

It appears that certain features of the surrounding areas influence the incidence of BBSSV disease within fields; this can be referred to as an "edge-effect". An outside source of inoculum or vectors often account for such a phenomenon. However, past works have shown that there is likely not to be a significant outside source of inoculum (Lesney et. al. 1978) and personal observations have not revealed hosts of *I. pepperi* in areas surrounding the fields, except where more blueberry is present. I suggest that surrounding terrain and vegetation favor aphid populations in the blueberry fields, and therefore BBSSV spread, by providing protection in the fields from severe weather and other climatic effects. This shall be discussed in greater detail in the section on aphid biology.

SEASONAL HISTORY OF *ILLINOIA PEPPERI* ON HIGHBUSH BLUEBERRY

OBJECTIVES

Very little information on the lifecycle, seasonal history or behavior of *Illinoia pepperi* is available from the literature. Because of this, rather than concentrate on any specific aspects of the life of this aphid, a general biological study was initiated. It was assumed that through the course of such a project, the areas of key interest in future research would be identified.

METHODS AND MATERIALS

The majority of this work was conducted in fields #393, #7, #54A and B, and #281. Other western Michigan fields were also visited frequently. One central Michigan field[12] was of particular interest and often visited since no insecticides are used in the management of this planting. A very natural state exists in this field, with effective biological control of many insect pests.

Yellow pan traps were used to monitor the flight of alate aphids in fields #393, #7, #54A, and #281. Plastic dishpans (30 cm x 38 cm x 16 cm) were used for pan traps.

---

[12]Eaton Co., MI. 3.5 miles southwest of Charlotte, Lowel Cook, owner.

These were placed on wood or plastic stands (approximately 30 cm in height) to provide visibility above the herbaceous ground cover. Traps were filled with water to within 3 cm of the brim. Trap color differed in 1979 and 1980; samples of each are given in figure 5. A rather bright yellow trap was used in 1979; low trap catch and difficulty in obtaining the same brand of dishpan led to the use of a darker color (closer to goldenrod yellow) dishpan for traps in 1980. Five pan traps were used in each field; one at each corner (NW, NE, SW, SE) and one at the approximate center of each planting.

These traps were visited every 2-4 days during the activity period of aphids. Captured aphids were frozen in distilled water or a saline solution (.85%NaCl), or preserved in 70% EtOH. Data pertaining to numbers of aphids, location within fields, and date were recorded.

Large screen cages were used to enclose entire blueberry bushes in field #54B in 1980. Cages were erected on June 1. Bases of the cages were buried to prevent walking aphids from entering or leaving the cages. The screen mesh was sufficiently small (8 strands/cm) to exclude alate aphids from bushes. Aphid populations on these bushes were observed to study the effects of reduced predator populations and climate changes.

Numerical data were analyzed using Chi-Square contingency tables where appropriate (Gill 1978).

1979 material:

Rubbermaid Inc.
Wooster, OH.

2970 yellow

1980 material:

Fesco Operations of
Cities Services Co.

2412 gold

FIG. 5.--Samples of pan trap material for 1979 and 1980.

Soil, root, basal stem and leaf litter samples were taken in 1979-1981 to locate the possible overwintering sites of this aphid. Soil and root samples were made using a commercial bulb coring tool in September of 1979 and April 1980. Samples were examined in the laboratory or greenhouse. Samples of soil, roots, basal stems and under bush litter were taken in January and April 1981. These were first examined for the presence of overwintering forms of I. pepperi, and then placed in a greenhouse and observed frequently for the emergence of aphids. On April 2, 1981, halves of 2 bushes were removed from field #54B and transplanted into an isolated bin in a greenhouse courtyard on the M.S.U. campus. The soil around the roots and base of the bush was kept in place; leaf litter was removed, except that which was lodged between the branches at the base of the half bush. These bushes were examined for the presence of aphids as the season progressed. The movements of late season aphids were closely examined in 1981 to determine their overwintering strategies and forms.

In the field, observations on aphid biology, life history, populations and behavior were recorded during each visit to the study fields. Field weather data was obtained from Environmental Data and Information Service Monthly Summaries of the National Oceanic and Atmospheric Administration. Rainfall amounts were obtained from the stations closest to the study fields. The Holland station rainfall records were used for fields #393, #7 and #54A and B. Rainfall recorded at Nunica, MI was used for field #281. Due to the very scattered nature of summer storms in western Michigan, the amounts reported may be significantly different from actual rainfall at the field site. Only one local station recorded wind speeds. This was in Muskegon, MI which is 22, 27, 30 and 32 km away from fields #281, #54A, #7 and #393, respectively. Hygrothermographs were used to record temperature data for fields #281, #7 and #54A.

Greenhouse cultures of I. pepperi were maintained at 20-25^{o}C on 2-3 year old potted blueberry plants ('Jersey' cultivar). Aphids were transferred regularly to fresh plants to eliminate crowding and preserve plant quality.

RESULTS AND DISCUSSION

Pan trap catches of alate I. pepperi were quite low. A total of 46 specimens were collected from all 4 fields in 1979. In 1980, only 12 alate aphids were captured in pan traps. Results suggest that further work is necessary to determine a more effective trap to monitor winged I. pepperi. Competition as attractive stimuli between the blueberry leaves and traps may influence trap catch. Analysis of the spectral reflectance pattern of blueberry leaves may prove useful in the selection of trap colors. Refer to Table 8 for the dates of first and last alate aphid captures in study fields.

Table 8. Dates of first and last captured alate *Illinoia pepperi* in yellow pan traps in Western Michigan, 1979-1980.

		1979		1980	
Field		Date	Degree Days[a]	Date	Degree Days
#393	First	4 June	526	30 June	974
	Last	6 August	1515	31 July	1554
#7	First	10 July[b]	1055	3 July	1020
	Last	25 August	1796	5 August	1651
#54A	First	15 June	716	14 July	1090
	Last	23 July	1296	24 July	1262
#281	First	15 June	714	3 July	978
	Last	30 July	1481	21 July	1311

[a] Accumulated degree days since March 1, base temperature of 3.4°C.

[b] Traps were not placed in field #7 until June 30, 1979.

Dates on which alate I. *pepperi* were found in pan traps for each field are shown graphically in Figures 6 and 7. Rainfall greater than 0.4 inch per day and dates of pesticide applications are also shown in the figures. The following is a key to the pesticide application symbols used in Figures 6 and 7:

First letter:

G = Guthion (Azinphosmethyl) SC (2lbs. ai per gallon), 1 quart/acre.

M = Aqua Malathion (8lbs. ai gallon), 1 quart/acre by air, 1 pt/acre by ground.

U = Cythion U.L.V. 95% Tech. Malathion, 10 oz. ai/acre.

S = Sevin (Carbaryl), 80W if by air, at 2.5lbs/acre; Sevin 50% WP at 4lbs/acre if by ground.

Second letter:

G = ground application (air blast sprayer)

A = aerial application

Attempts to relate trap catch to the effects of windspeed, rainfall and pesticide applications proved to be difficult and inconclusive due to the very low numbers of aphids caught, and the lack of site specific weather information. It is likely that aphid catches occurred only at the peaks of flight activity; during the rest of the season there could have been significant numbers of winged aphids in the population, but these were not detected due to low trap efficiency.

FIG. 6.--Alate *Illinoia pepperi* caught in yellow pan traps in Ottawa Co., Mi., 1979. Arrows indicate the dates of significant rainfalls and pesticide applications.

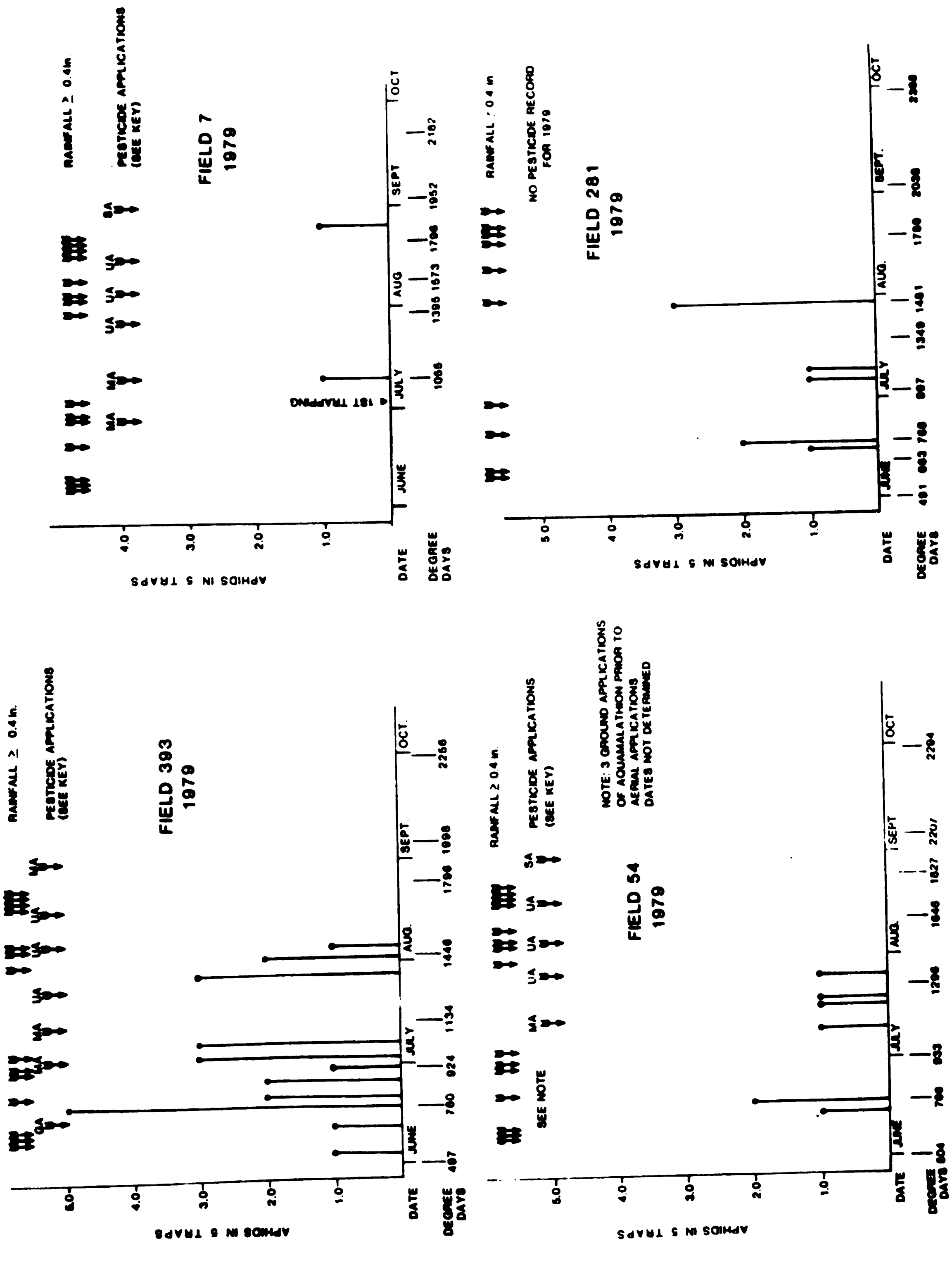
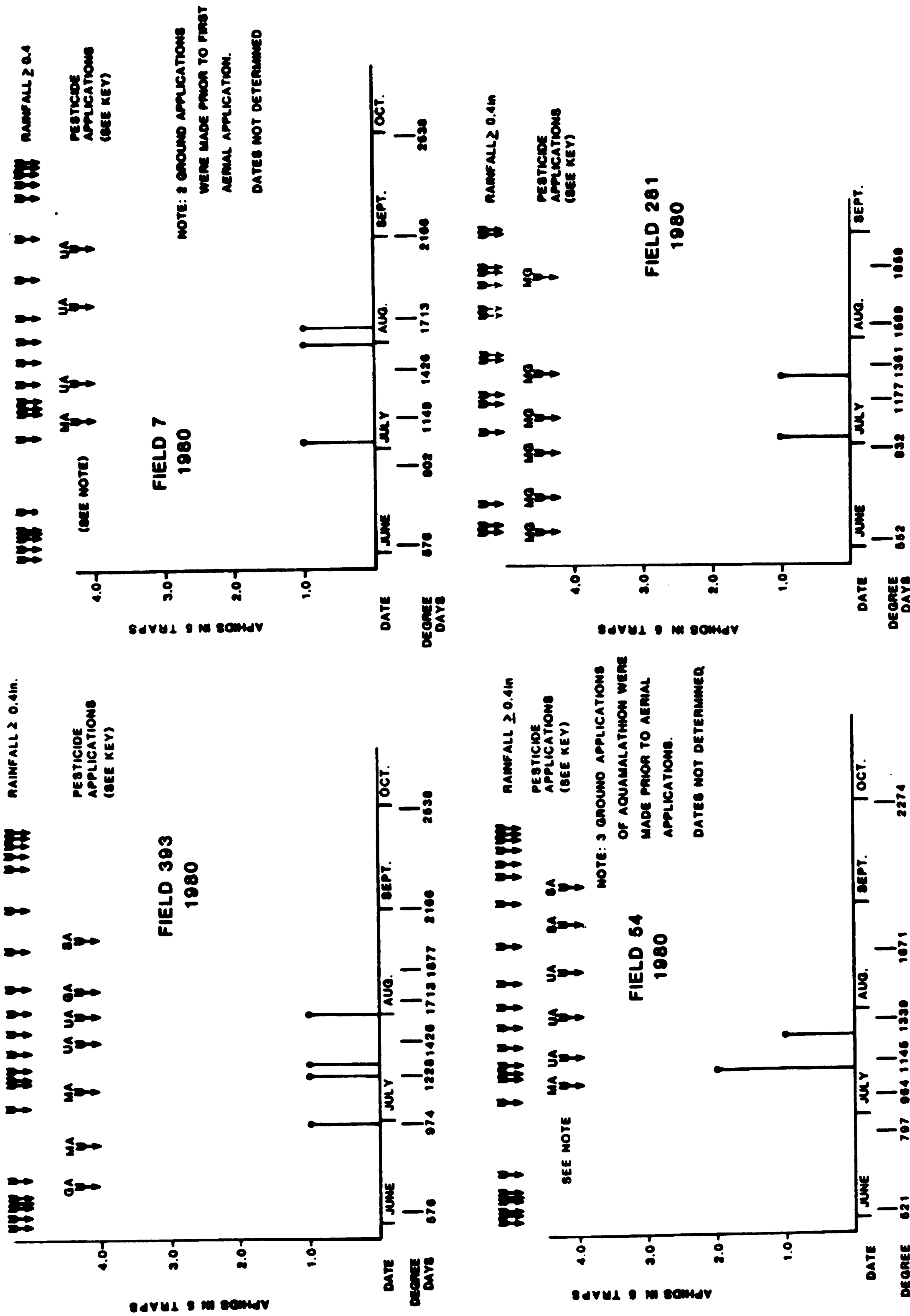

FIELD 7
1979
RAINFALL ≥ 0.4 in
PESTICIDE APPLICATIONS
(SEE KEY)
1ST TRAPPING
APHIDS IN 5 TRAPS
DATE
DEGREE DAYS
JUNE
JULY
AUG
SEPT
OCT
1066
1395
1573
1796
1952
2182
FIELD 281
1979
RAINFALL ≥ 0.4 in
NO PESTICIDE RECORD
FOR 1979
FIELD 393
1979
FIELD 54
1979
SEE NOTE
NOTE: 3 GROUND APPLICATIONS
OF AQUAMALATHION PRIOR TO
AERIAL APPLICATIONS
DATES NOT DETERMINED

FIG. 6.

FIG. 7.--Alate *Illinoia pepperi* caught in yellow pan traps in Ottawa Co., Mi., 1980. Arrows indicate the dates of significant rainfalls and pesticide applications.



FIELD 7
1980
RAINFALL ≥ 0.4
PESTICIDE APPLICATIONS (SEE KEY)
(SEE NOTE)
NOTE: 2 GROUND APPLICATIONS WERE MADE PRIOR TO FIRST AERIAL APPLICATION.
DATES NOT DETERMINED
APHIDS IN 5 TRAPS
DATE
DEGREE DAYS
FIELD 261
1980
RAINFALL ≥ 0.4in
FIELD 393
1980
RAINFALL ≥ 0.4in.
FIELD 54
1980
SEE NOTE
NOTE: 3 GROUND APPLICATIONS OF AQUAMALATHION WERE MADE PRIOR TO AERIAL APPLICATIONS.
JUNE
JULY
AUG.
SEPT.
OCT.

FIG. 7.

The trap catch for field #393 in 1979 suggests two periods of peak flight activity; one in mid June to early July and another in late July to early August. This pattern was not demonstrated in other fields.

Directional differences in the numbers of alate _I. pepperi_ caught were noted. Table 9 presents the directional breakdown of the 1979 trap catches.

Table 9. Directional analysis of alate _Illinoia pepperi_ caught in Yellow pan traps in blueberry plantings, Ottawa Co., MI. 1979.

Trap Location	Field			
	#393	#7[a]	#54A	#281
NW	2	1	4	1
NE	17	1	2	0
SW	9	0	1	1
SE	0	0	0	6
C	1	0	0	0
Totals	29	2	7	8

[a]No traps placed in field #7 until July 3.

This analysis showed a significant ($P \leq 0.01$) relationship between pan trap locations and the numbers of alate aphids caught in 1979.

The areas surrounding the fields were examined to develop possible explanations of directional effects, even though the small number of aphids caught may not represent the field situation accurately. Of the traps in field #393, the southwest and northwest had the greatest visibility range, and was also exposed to a greater amount of wind. The northeast trap was in an area protected from most winds, and closest to a dense woodlot north of the field. Immediately to the east of this trap was a drainage ditch with heavy shrubs and deciduous tree growth. No other plantings of blueberry were close to this corner of field #393. No conclusion was reached as to the reason(s) for the high catch in this trap. Due to the later starting date of trapping in field #7 and the very low number of aphids caught there, a meaningful analysis of the areas surrounding this field is not possible. In field #54A, the majority of aphids were caught in the northern traps. These had less line of sight visibility than the traps at the south end of the field, but the pine woodlot to the north of the field, probably reduced wind speeds thus improving the aphids ability to land in the trap. Aphid populations were also greater in the northern portion of this field. This combination of greater numbers and more favorable flight conditions may have led to the greater trap catches in these locations. It is interesting to note that the northern portion of field #54A has a greater BBSSV infection problem as well. In field #281, the southeast trap produced the most aphids in 1979. This trap was visible from great distances, but was notin an area sheltered from winds. The trap was closest to the large mixed woodlot southeast of the field. Once again, the same region of the field also had significant BBSSV disease incidence.

No single factor, i.e. shelter from wind, BBSSV infection, visibility or nearby vegetation, seemed to be correlated with the greatest trap catch in all fields. These relationships may not be determined until a more efficient trapping technique for alate I. pepperi is discovered.

Two other visually similar species of aphids were commonly caught in greater numbers than I. pepperi, making it necessary for close examination of specimens removed from pan traps. These species were Acyrthosiphon pisum (Harris), the pea aphid and Macrosiphon euphorbiae (Thos), the potato aphid. Cornicle morphology can be used as a "quick" field separation of these species using a hand lens. Cornicles of I. pepperi appear swollen while those of A. pisum and M. euphorbiae are cylindrical or tapering.

Overwintering Site Determination -- No forms of Illinoia pepperi were found in soil and root samples taken in 1979 or 1980. Caged bush examinations in 1980 showed the presence of both immatures and adults inside cages at the same time as the rest of the field. This led to the conclusion that I. pepperi did not necessarily overwinter outside the field and re-infest blueberry in the spring;

overwintering occurred somewhere on the bush or in the leaf litter below the bushes.

No forms of I. pepperi were found in the leaf litter or on the stems collected in December 1980 through April 1981. However, aphids did appear on the succulent basal growth of the half-bushes in the greenhouse courtyard by May 20, 1981. This information suggested that the overwintering form must be closely associated with the basal area of the blueberry bush, as it seemed not to be in the leaf litter or on stems.

Close observations in the fall of 1981 led to the discovery of oviparous females and overwintering eggs on the smallest basal shoots. These shoots are usually destroyed by freezing temperatures. 1980 and 1981 stem samples were apparently taken to late in the season for these shoots to be found. The eggs probably fall into the crevices and sheltered areas in the crown of the bush. The oviparous females and eggs are discussed in greater detail in the following section.

Biology of Illinoia pepperi -- A life history of I. pepperi is shown in Figure 8, based on greenhouse cultures, field observations and the literature (MacGillivray 1958; Gilbert and Gutierrez 1973). The first generation apterous female (fundatrix) develops from an overwintering egg in or near the base of a bush. Adults of this morph could be found from May 19th to June 4, 1981, in the Charlotte field

FIG. 8.--Life cycle of *Illinoia pepperi* (MacG.) on highbush blueberry (Vaccinium corymbosum) in Michigan.

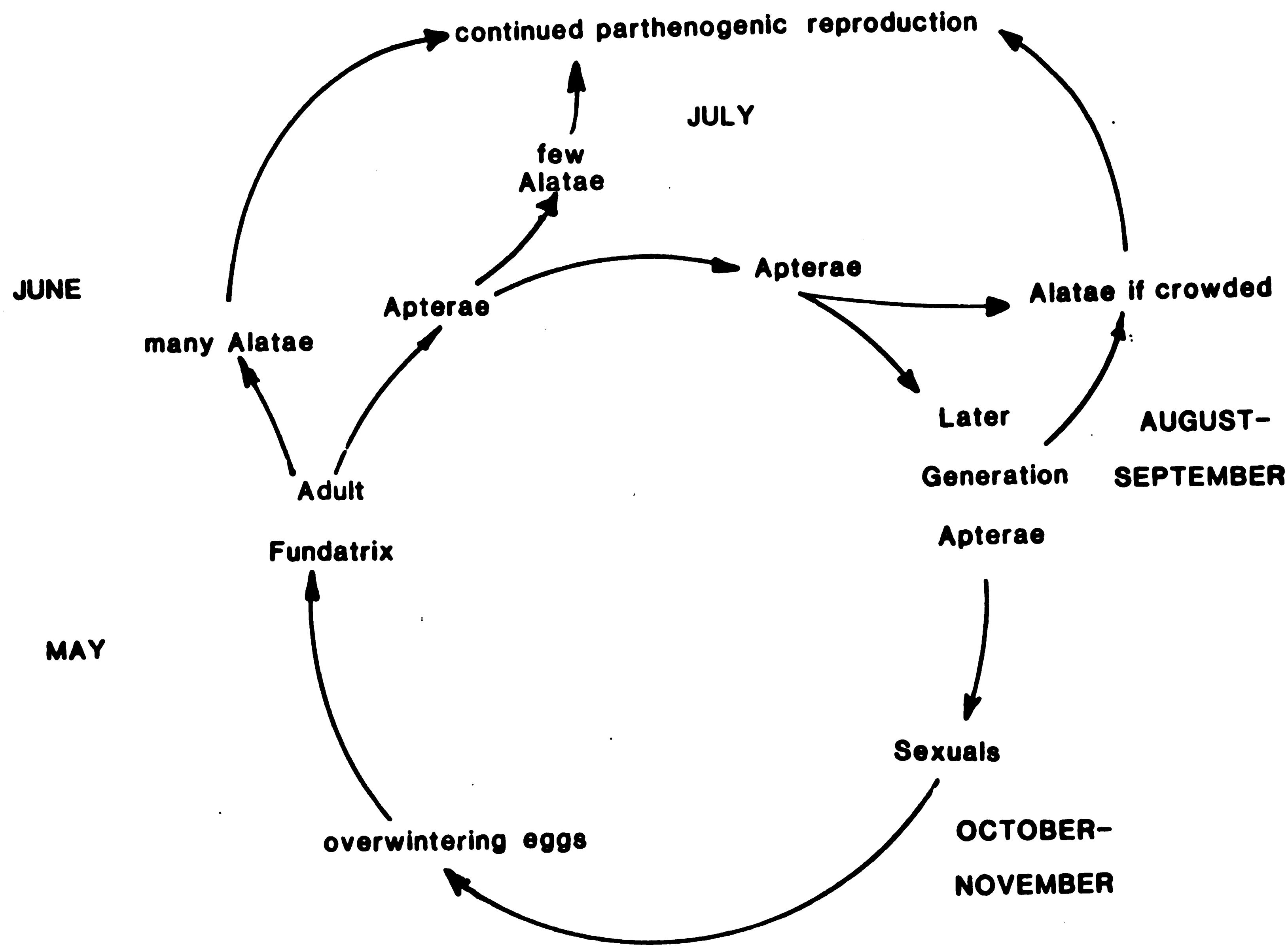

continued parthenogenic reproduction
JULY
few Alatae
JUNE
Apterae
Apterae
Alatae if crowded
many Alatae
Later Generation Apterae
AUGUST-SEPTEMBER
Adult Fundatrix
MAY
Sexuals
overwintering eggs
OCTOBER-NOVEMBER

FIG. 8.

(approximately 330 to 560 degree days, base 3.4°C); (see lower development threshold determination, page 81). Young produced by a fundatrix develop into second generation viviparous females. Many of these appear to develop into alatae, based on the examination of colonies in the Charlotte field. Winged adults were commonly found with younger aphids of the same colony on June 4, 1981. Fourth instar aphids in these colonies showed developing wing pads. In most cases the fundatrix was no longer present at this time. Most colonies consisted of 5-15 individuals. The second generation alatae viviparous females disperse to other stems or blueberry bushes and begin to produce young. A small percentage of the winged females had made such a flight by June 4th (560 degree days). Based on field observations in western Michigan and greenhouse cultures, the third and later generations of I. pepperi produce a very limited number of alate aphids. The factors inducing the development of winged forms is not known. Based on aphid life span and temperature requirements 7 or more of these parthenogenic generations may occur each year.

The most common morphological forms of I. pepperi are illustrated in Figure 9. The red colored forms of this aphid are normally found in low numbers compared to the green morphs. On August 11, 1981, counts taken on the "Bluecrop" variety showed that approximately 9% of the

FIG. 9.—Common morphological forms of Illinoia pepperi: (A) green viviparous apterae; (B) green viviparous alate; (C) red viviparous apterate.

population were red morphs. All forms of this aphid (immatures, adult apterous or adult alatae) can be found in either color. The red morphs arise within colonies of green aphids when a green viviparous female gives birth to a red first instar nymph. The mechanism determining this is not understood. Red nymphs appear to develop normally, and have the same behavior as the green forms. Adult red forms apparently give birth only to further red nymphs; I have not observed red morphs giving rise to green progeny, in field conditions or in greenhouse cultures.

The Charlotte population of I. pepperi has not been observed to contain red morphs. It is possible that biotypes of this aphid exist, and the "Charlotte biotype" is genetically incapable of producing red forms.

Early season colonies of I. pepperi are usually found within the lowest third of the bushes. Later in the season dispersal by winged forms or walking individuals distribute colonies more evenly within bushes.

During July, aphid populations steadily increase on cultivated blueberry bushes, with their numbers being moderated by weather conditions and natural control agents. There are apparent cultivar differences in host plant suitability to I. pepperi. The cultivars Jersey, Rubel and Blueray are most susceptible or suitable for aphids. Bluejay, Earliblue and Elliot appear most resistant to aphid infestation (Hancock et. al., unpublished data 1980).

On mature blueberry (cultivar 'Jersey'), aphid populations may exceed 800 individuals per bush. The time of peak populations varies in each field and each year and is affected by plant vigor, diseases, crop load, water stress, weather and the impact of biological control agents. In 1979 and 1980 peak populations occurred in most fields in mid to late July. In 1981 however, aphid populations remained quite low through the end of July, and increased in early August.

A large mid season colony may contain over 100 aphids and cover the top 7-10 cm of a terminal. Such crowded conditions gives rise to walking aphids and winged forms which disperse to other leaves and stems. Illinoia pepperi are rather long-legged aphids, and move quickly. Adult apterous viviparous aphids have been observed to walk 30 cm per minute when disturbed. All instars actively walk when crowding occurs, and can be found on the soil or ground cover between bushes in search of a new feeding site. On several occasions many apterous aphids were found walking on the brims of the yellow pan traps.
As the season progresses, the blueberry bushes begin to direct more resources towards fruit development and ripening; this lowers the food quality of stem and leaf tissue.

Aphid populations begin to decline during this period (early August onward depending on environmental conditions). Blueberry bushes will often put forth new succulent shoots after harvest when the stress of fruiting is removed. Aphid populations may also increase if this occurs. The natural senescense of blueberry leaves begins in late August and early September. The leaves and stems become tough and less nourishing due to the build-up of biochemical products such as tannins. Aphid populations decline quickly as this process takes place. At this time, colonies of I. pepperi can conly be found on the most succulent growth remaining, generally at the base of bushes or on young plants. Viviparous females were found in the field through early November in 1981.

Oviparous females develop from some of the young of the late season viviparous females. These closely resemble the apterous viviparous females, but are wider and have distinctly swollen hind tibia with sensoria. Their development is cued by environmental factors of temperature and photoperiod combined with the condition of the blueberry foliage. Very few oviparous females are generated, since there are few viviparous females remaining late in the fall; lack of acceptable foliage and freezing temperatures also would reduce their numbers.

Oviparous females of *I. pepperi* were not observed during the first two years of this study. Increased effort in the fall of 1981 finally led to their discovery in Ottawa Co., Michigan. Three oviparous adults were found in field #54B on November 3rd, two of which layed eggs (2 each) in captivity. On December 5th, two oviparous adults were found in field #281. These produced no eggs while kept in a controlled environment chamber set for 3 - 12°C and a 10L:14D photoperiod and died within 3 weeks.

Oviparous females and eggs of *I. pepperi* were found only on the small sucker shoots which grow from the base of bushes in the fall. Such shoots often appear after harvest when the fruiting stress is relieved; they are much more common in fields which have been pruned heavily within the last year. Only the latest and shortest of these shoots (1-10cm) appear to be acceptable to *I. pepperi* in October through December, as these are the youngest and have not matured or hardened off. Those aphids on taller shoots may be subject to greater mortality during frosts. Oviparous females lay eggs on the stem or leaves of the short shoots. Based on very limited observations, each female lays 2 eggs. In many fields these sucker shoots are rare and difficult to find, yet aphids consistantly infest these fields.

It therefore seems likely that the oviparous females also lay eggs in other locations not yet determined.

As the season progresses and freezing temperatures destroy the sucker shoots the eggs apparently fall into the crown or to the ground where they overwinter. An oviparous female and eggs of I. pepperi are shown in Figure 10.

The preferred feeding sites of I. pepperi are the undersides of tender leaves, succulent growing shoots and swelling buds. Aphids were rarely seen on the upper surfaces of leaves; this is in complete opposition to the work of Giles (1966), who reported that the preferred feeding site was the upper surface of the leaves. When feeding on leaves, they place their stylets in or close to the vascular tissues. Feeding I. pepperi are very sessile unless poor food quality or crowded conditions induce them to move. No particular preference was noted for specific locations within the bush. The location of the most succulent tissues and weather conditions determine the distribution of aphids within bushes, as well as the use of insecticides.

The phenology of the host plant is closely associated with the life history of I. pepperi. The immature fundatrix emerges shortly after the first leaves have expanded. At the time the second generation winged aphids mature, the blueberry bushes have a high number of suitable feeding

FIG.10.--Oviparous female and eggs of Illinoia pepperi found on December 5, 1981, Ottawa Co., Mi.

sites available for colonization. This assures a high probability of suitable sites for flying aphids. Late in the season, although the total number of terminals or leaves is greater, few are vigorously growing, and therefore, the probability of an aphid arriving at a suitable site is reduced.

No evidence of an alarm pheromone or specific behavior for communication between colony members has been observed in populations of I. pepperi. In aphid species that utilize alarm pheromones (as in Myzus persicae Sulz.), when an individual is disturbed by a predator, parasitoid or other stimulus, colony members are immediately "warned" of a threatening situation by the release of a volatile chemical by the disturbed aphid (Matthew and Matthews 1978). The nearby aphids then move away or drop from the plant to avoid the danger. Alarm pheromones are emitted from the cornicles. It is interesting that I. pepperi, which posses well developed cornicles, may not have evolved, of may have lost (atavism) an alarm pheromone system. One possible explanation for this could be the very limited host range of this aphid; blueberry is its only common host. Myzus persicae feeds on numerous plants, and chances are good that aphids dropping from one host will land on or near another host. If individuals of I. pepperi were to drop from a bush when alarmed, these aphids would then be some distance from a source of food.

The chances of aphids being killed before reaching blueberry leaves again may be as significant a threat as predators and parasitoids.

Populations of _I. pepperi_ are naturally moderated by the effects of predators, parasitoids, and pathogens. Table 10 lists the families of insects observed to attach this aphid in Michigan during 1979-1981.

Table 10. Predator and parasitoid families attacking _Illinoia pepperi_ in Michigan, 1979-1981.

Order	Family	Mode	Predominate period
Hemiptera	Anthocoridae	predator	general
Coleoptera	Coccinellidae	predator	May - June
Neuroptera	Chrysopidae	predator	mid June - August
	Hemerobiidae	predator	mid June - August
Diptera	Syrphidae	predator	June - September
	Cecidomyiidae	predator	July - August
Hymenoptera	Eulophidae	parasitoid	July - August

The most common coccinellids were _Coccinella novemnotata_ Herbst, _Coleomegilla maculata lengi_ Timberlake and _Hippodomia convergens_ Guérin-Meneville. Adults of these species and others were found searching blueberry bushes before leaves were present. Adults or larvae were present throughout the summer, usually in low numbers in sprayed fields. Ladybird beetles appear to be a significant population control only in June. Eggs of chrysopids are first found in early June. The larvae are quite effective predators on all instars of I. pepperi, but their impact does not appear to be great. Normal chemical control practices probably limit their numbers, reducing them as population control agents. The most significant predators during mid to late summer are in the dipteran families Syrphidae and Cecidomyiidae. Adult female syrphid flies lay eggs near colonies of aphids starting in early June. The slug-like larvae feed on great numbers of aphids before completing development. Later generations of syrphid fly larvae cause significant mortality to mid and late season populations of I. pepperi. The small orange larvae of the cecidomyiid fly, Aphidoletes aphidomyza Rhondoni, have been observed to be effective predators in some fields. Adult females search for aphid colonies, and lay eggs near them. Many larvae were found in late July and August in 1980. The most common parasitoid of I. pepperi is an eulophid wasp in the genus Aphelinus. Parasitized aphids develop a pearly appearance, and secured to the under surface of the leaf by the parasitoid larvae before it pupates within the skin of the host aphid. Adult wasps cut a hole in the dorsal surface of the abdomen and emerge to lay eggs in other aphids. Parasitized aphids were observed frequently from mid July to early September.

A fungal pathogen infects and kills I. pepperi. Most infected aphids become shiny black as the fungal spores fill the body cavity. Fungal disease was more common during periods of high humidity or in fields that had a dense canopy of leaves and reduced air flow. Fungal disease was a significant mortality factor in aphid populations on the caged bushes in 1980 since the screening reduced ventilation and raised the humidity and temperature.

Weather conditions have a great deal of influence on populations of I. pepperi. A rain drop carries sufficient force to knock an aphid off a stem if it is hit directly. Many summer rains in western Michigan are accompanied by strong winds, resulting in violent storms. Such storms aggitate the branches of the blueberry bushes and kill or dislodge aphids mechanically. Up to 50% of aphid populations may be killed during a day of severe weather. Rainy conditions also promote the infection of aphids by fungal pathogens. Very dry weather causes some aphid mortality due to desiccation. The combination of weather factors and biological controls kept the 1980 populations well below those of 1979 in the same locations. In 1981, the combination of abiotic weather-related mortality and biological controls maintained extremely low populations of I. pepperi until early August.

Weather conditions also affect the distribution of aphids within the bushes, and the field. Aphid colonies in more sheltered areas of the bush, such as the center or basal areas, survive severe weather better than those on the outer perimeter of the bush. In 1980, severe weather conditions contributed to the uneven distribution of aphids within bushes in this manner. Counts at Grand Junction, Michigan showed that 50% of the aphids were in the bottom third of the bushes (Hancock et. al., unpublished data). Similarly, aphid populations that are in parts of fields which receive some sort of protection from severe weather (as from nearby woods, fence rows, etc.) may benefit through reduced mortality from adverse weather.

The effects of shelter from weather conditions in combination with reduced predator pressures were demonstrated by the aphid populations on the caged bushes in 1980. Populations on these bushes and nearby bushes are presented in Table 11.

Table 11. Populations of *Illinoia pepperi* on caged and uncaged blueberry bushes, Ottawa Co., Mi. Counts made on August 8, 1980.

Caged bush	Nearby uncaged bush
1376	89
824	185

The populations on caged bushes were greater (2 x 2 Chi-Square contingency table analysis; $P \leq 0.001$ (corrected)). Apparently, the increased mortality from fungal disease in cages was more than offset by the lack of predators and protection from severe weather. The intensities of wind and rain within fields and how it is affected by field surroundings should be examined for possible relation to BBSSV incidence through reduced aphid mortality in sheltered areas.

ALTERNATE HOST SURVEY

OBJECTIVES

Knowledge of the alternate plant hosts of *I. pepperi* would be beneficial to efforts towards determining its life history, overwintering sites, and to develop control procedures. It would also be desirable to find a herbaceous and an easily grown plant host for greenhouse culture purposes. Continuous efforts were made to determine the non-*Vaccinum* host range of this species. A survey of wild blueberry (*Vaccinium*) hosts in Michigan was started in 1981. Part of this study will focus on the natural susceptibility or resistance of wild blueberry strains to aphid infestations. The information gained through this effort may be used in future blueberry breeding efforts to produce resistant cultivars.

METHODS AND MATERIALS

Alternate hosts of *I. pepperi* were sought in the field and under greenhouse or laboratory conditions. On every field day, possible alternate host species were examined for aphids. Plants within the fields and the surrounding area were included, as well as occasional plants at various locations within Ottawa Co., Michigan. Plants with vigorous or succulent growth were given greatest attention as these would be more likely to be infested with aphids. Plants adapted to acid soils, as are blueberries, were given extra attention. Specimens of aphids were preserved in KAA or 70% EtOH for later identification. Samples of the host plant were taken if identification was not possible in the field.

In a greenhouse, individuals from colonies of I. pepperi grown on potted blueberry were transferred or allowed to move to various test species of plants in efforts to determine alternate hosts. Aphids were not starved before introduction to new species of plants; this was to avoid "false" determination of alternate hosts, as aphids may probe or begin to feed on many plants under conditions of induced starvation.

RESULTS

Individual I. pepperi, being quite mobile, could often be found away from the primary host, blueberry. This aphid was observed to feed on alternate plant species only occasionally; few of these plants appeared to be acceptable hosts. Table 12 presents the field observations of I. pepperi on plant species other than blueberry in 1979-1981.

I. pepperi was more frequently found on other plant species in 1979. Populations were much higher that year than in 1980; apparently crowding and plant resource depletion drive individuals to these other hosts. Illinoia pepperi was never observed to feed actively or reproduce on an herbaceous host in the field. Red Oak, Black Gum,

Table 12. Observations of Illinoia pepperi on alternate host plants in Ottawa Co., Michigan 1979-1981.

Date	Plant	Field	Feed	Reproducing
7-13-79	Wood Fern, Dryopteris sp.	393	no	no
7-30-79	Red Oak, Quercus rubra	393	yes	yes
8-2-79	Prunus sp.	7,393	yes	yes
	Black Gum, Nyssa sylvatica	393	yes	yes
8-19-79	Red Oak, Q. rubra	393	yes	yes
	Ladysthumb, Polygonum persicaria	54	no	no
8-25-79	Red Maple, Acer rubrum	393	yes	no
	Black Gum, N. sylvatica	393	yes	yes
8-30-79	Knotweed, P. pennsylvanicum	54	no	no
7-14-80	Black Gum, N. sylvatica	393	yes	yes
8-12-81	Common Winterberry Holly, Ilex verticillata	54B	yes	yes
8-21-81	Virginia Creeper, Parthenocissus quinuefolia	54	yes	no
8-25-81	Virginia Creeper, Parthenocissus quinuefolia	54	yes	no
10-6-81	Prickly Dewberry, Rubus flagellaris	54B	no	no

Winterberry Holly and _Prunus_ sp. appeared to be acceptable alternate host species. Small colonies of _I_. _pepperi_ developed on these hosts. Aphids fed and reproduced to a limited extent on Red Maple, but no lasting populations occurred on this host. Under field conditions, colonies or individuals never remained on any alternate host for perids of time greater than 2 continuous weeks; the longest surviving colonies occurred on Black Gum and Common Winterberry Holly. All the observations of _I_. _pepperi_ on other plant species occurred on plants within the blueberry fields. Plants of the same species and similar growth conditions found outside of the field boundaries were never observed with blueberry aphids.

In a greenhouse, _I_. _pepperi_ were observed to move away from a heavily infested potted blueberry and walk to other plants. Amongst plants tested for suitability to _I_. _pepperi_ under greenhouse conditions were cabbage, pea, chickweed, Mouse-ear chickweed, hibiscus and hybrid rose. Chickweed species were tested because of frequent observation of aphids on small seedlings of these plants which grew in the pots under the blueberry plants. _Illinoia pepperi_ could not survive for more than 3-4 days on pea, cabbage, or the chickweed species.

Individuals were observed to feed for a week or more on hibiscus; very young leaves and flower buds were preferred sites. Very little reproduction was noted. Hybrid rose apparently is a very acceptable host for _I. pepperi_. Individuals moved to it from blueberry, and situated on developing flower buds. Significant reproduction occurred, covering the surface of the flower bud with aphids.

DISCUSSION

No acceptable herbaceous host plants were found. Red Oak, Black Gum, Red Maple, Winterberry Holly and _Prunus_ sp. do not appear to be very significant alternate hosts of _I. pepperi_ in the field. Wild rose can be found in hedgerows and woodlots near many blueberry plantings in western Michigan. Although no _I. pepperi_ have yet been observed on wild rose in this study, the laboratory observations with hybrid roses indicate the possibility of wild rose as a significant alternate host.

OPTIMUM SAMPLE DETERMINATION

OBJECTIVES

One of the most important questions facing the development of controls for BBSSV spread is what population levels of *I. pepperi* result in significant disease transmission. To answer this question, spread of the disease must be related to aphid populations, in order for an economic injury level to be established. A method was needed to effectively estimate the aphid populations on blueberry bushes. Direct counting of aphids over large areas is time-consuming and difficult. Therefore, an implementable technique by which total populations or densities can be estimated was developed.

Two important criteria were considered in the determination of the optimal sample procedure:

Accuracy: which sample technique has the highest correlation between sample means and true aphid populations?

Precision: which sample technique will yield the smallest variation of sample means?

METHODS AND MATERIALS

Four 8.2 meter randomly selected portions of rows were chosen in each of 2 study fields. In a 3rd field, four 16.4 m sections were randomly chosen. Plant density, age, size, cultivar ('Jersey') and vigor were comparable in all locations. All counts and subsamples in 1979 were made on August 30; the degree day total was approximately 1900 (base 3.4°C). For determination of actual densities all *I. pepperi* were counted in each row section. The following systematic counting procedure was used on heavily infested terminals:

1) leaves were divided into 4 equal parts subdivided by midvein and an arbitrary line drawn midway between the base and tip of the leaf;

2) one section was selected for counting;

3) aphids in that section were counted and this number was multiplied by4 to arrive at the approximate total number of aphids/leaf.

Samples were taken immediately after the actual density counts were made, in the same selected row sections. Sampling crews rotated row sections to avoid any subconsious selection of leaf or stem samples with known infestations. The following samples were made, non-destructively:

1) aphids per leaf; aphids found on samples of 5, 10, 15 and 20 leaves were counted and recorded;

2) aphids per terminal shoot (10-20 cm stem); aphids found on samples of 1, 5, 10 and 15 stems were counted and recorded.

Leaf samples and stem samples were made by randomly selecting the appropriate number of sample units from the bush canopy over the 8.2 meter section. Data was submitted to graphical and statistical analysis for comparison of sample unit efficiency, using the criteria stated earlier.

RESULTS

Actual aphid density counts for the 12 row section counted in 1979 are presented in Table 13.

Table 13. Actual density counts of Illinoia pepperi on blueberry ('Jersey' cultivar) in Ottawa Co., Mi. All counts made on August 30, 1979.

Field	Row Section[a]	Section Length	Total Count	Mean Density per 8.2 meter
7	1	8.2 m	1010	
	2	"	3375	1349.8
	3	"	411	
	4	"	603	
54A	1	"	398	
	2	"	285	272.0
	3	"	289	
	4	"	116	
281	1	16.4 m	947	
	2	"	474	223.9
	3	"	151	
	4	"	219	

[a]Randomly selected and assigned numbers 1-4 for each field.

Significant variation in aphid density within fields can be seen. Some of this difference can be explained by varying bush size within fields, but other factors are apparently involved. Field #7 had a denser canopy of leaves than did fields #54A or #281. This could provide greater protection from severe weather and pesticide applications and therefore allow for greater populations of aphids.

Actual densities for each row section were arranged into naturally apparent classes:

1) 0 < density $\leq$ 125 per 8.2 meters,

2) 126 < density $\leq$ 400 per 8.2 meters,

3) 401 < density $\leq$ 600 per 8.2 meters,

4) 601 < density $\leq \infty$ per 8.2 meters.

Values for all sample means, average sample means, acutal densities and average actual densities are presented in Table 14.

Table 14. Actual densities, average densities, sample means and averaged sample means of Illinoia pepperi on 'Jersey' cultivar blueberry. Data are arranged by ascending order of actual densities and grouped into levels.

Actual Density/8.2m	Sample Means						
	Leaves				Stems		
	5	10	15	20	5	10	15
75.5	0.00	0.20	0.13	0.00	0.80	0.30	0.13
109.5	0.20	0.00	0.13	0.20	0.20	1.60	0.33
116.0	0.00	0.00	0.20	0.25	0.00	0.80	0.87
average - 100.33	0.07	0.07	0.16	0.15	0.33	0.90	0.44
237.0	0.00	1.50	0.07	0.40	0.60	1.40	1.87
285.0	0.80	0.10	0.07	0.40	0.00	1.00	2.50
289.0	0.60	0.00	0.67	0.15	0.20	0.30	2.00
average - 269.66	0.46	0.53	0.45	0.33	0.27	0.90	2.12
398.0	1.60	0.20	0.27	1.05	1.20	1.30	1.87
411.0	0.20	0.60	0.27	0.70	5.60	7.70	6.20
473.0	5.40	1.30	0.53	0.25	2.20	5.50	5.10
average - 427.33	2.40	0.70	0.36	0.67	3.00	4.83	4.39
603.0	0.60	1.70	0.20	0.35	0.60	0.90	7.50
1010.0	0.40	1.60	0.13	0.40	0.00	3.80	2.30
3375.0	4.00	0.20	6.60	4.35	21.40	29.70	12.90
average - 1662.66	1.67	1.17	2.31	1.17	7.33	11.47	7.42

Plots were made of actual density *vs* sample means, actual density *vs* averaged sample means, and averaged actual density *vs* averaged sample means. Straight line regression using the least squares method was used to fit a line through the data points of each plot. The regression values were compared using residual analysis. Plots of actual density *vs* averaged sample means produced the greatest correlation coefficients and lowest residual values. The regression equations and related statistics for these plots are given in Table 15.

Table 15. Regression equations and related statistics for each sample type tested.

Sample Type	Regression Equation[a] $Y = A + B\bar{X}$	Statistics[b]		
		r	R^2	s^d
STEMS				
5	$Y = 48.6 + 207.3\,\bar{X}$	.73	.54	6.40
10	$Y = -11.6 + 138.5\,\bar{X}$	.95	.91	8.30
15	$Y = -170.5 + 218.7\,\bar{x}$	.83	.68	3.61
LEAVES				
5	$Y = 249.8 + 317.6\,\bar{X}$	.55	.29	7.70
10	$Y = -251.8 + 1406.0\,\bar{X}$	.22	.15	9.96
15	$Y = 39.4 + 703.2\,\bar{x}$	.95	.91	1.81
20	$Y = -109.3 + 1017.0\,\bar{X}$	.95	.91	1.20

[a]Y=observed density; $\bar{X}$=average sample mean; A and B are parameters of the regression equation for the plot of Y vs. X.

[b]r=correlation coefficient; R^2=coefficient of determination; s^d= standard deviation.

Samples of 10 stems, 15 stems, 15 leaves and 20 leaves gave the greatest correlation between average sample means and actual densities (Figure 11). The sample technique producing the lowest standard deviations of sample means were 15 stem and 15 and 20 leaf samples. Based on the two criteria of accuracy and precision, the 20 leaf sample was chosen as the most effective sample unit and technique of those tested in 1979. The following method was proposed for blueberry aphid density determination:

1) take several 20 leaf samples over a distance of 8.2m (25 feet);

2) calculate the mean number of aphids per leaf of each sample, and average these means;

3) use the regression equation $Y = -109.3 + 1017.0(X)$ where X = average sample mean, to calculate Y, the estimate of the aphid population in that section.

On August 12 and 15, 1980, four more 8.2 meter sections were counted and sampled in the above manner in an attempt to evaluate this sample technique. Actual counts and calculated values for aphid density are presented in Table 16.

Calculated aphid populations averaged 171.2 aphids less (s.d. = 215.1) than the actual numbers present. This result does not support the 1979 findings.

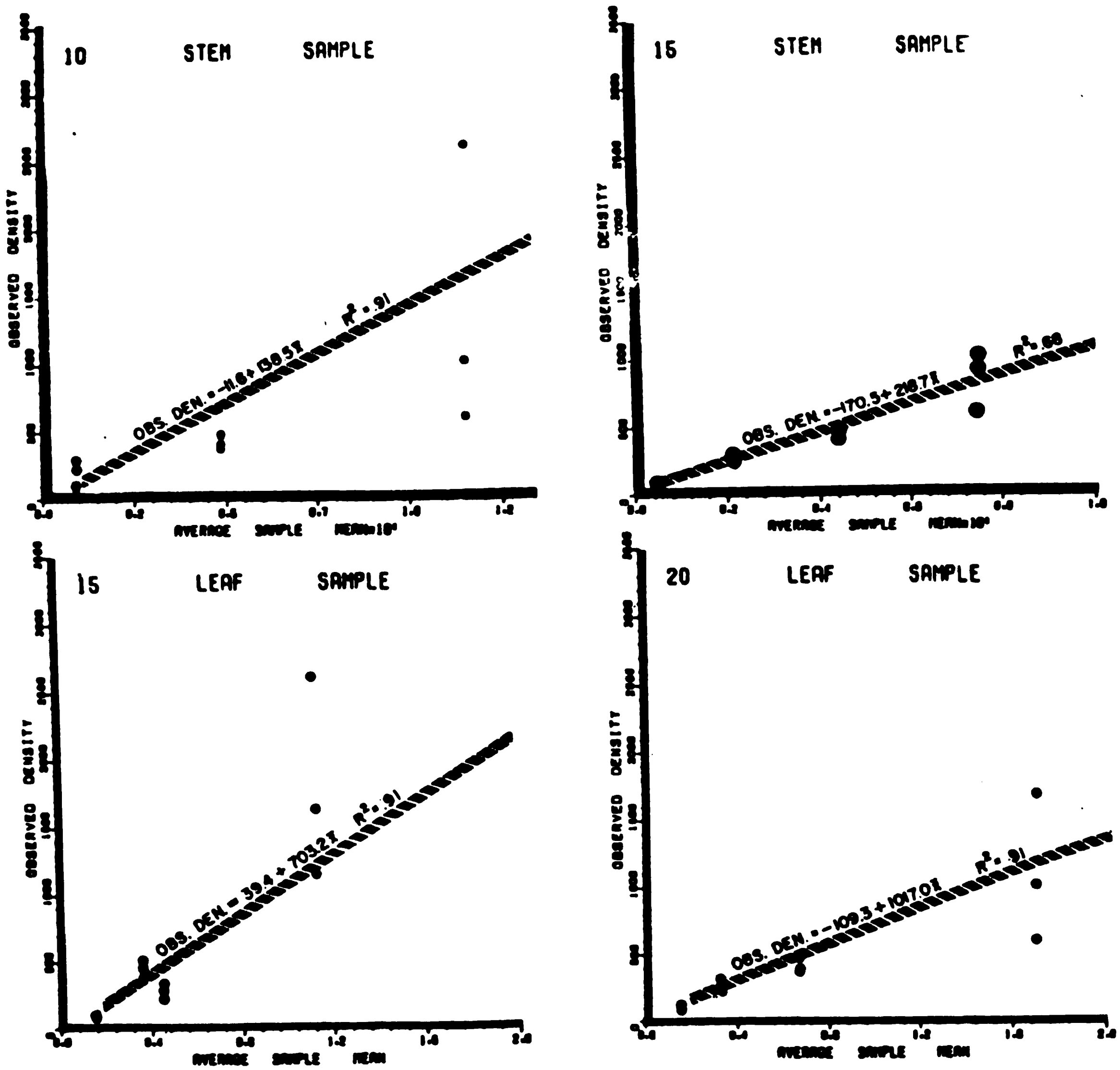


FIG.11.—Plots of observed (actual) density vs. average sample means for four sample types used for estimating densities of Illinoia pepperi on mature highbush blueberry ('Jersey' cultivar), Ottawa Co., Mi., 1979.

Table 16. 20 leaf sample means, predicted densities and actual counts of Illinoia pepperi, August 12-15, 1980.

Row section	20 leaf mean	predicted density	actual count	difference
1	0.15	43.3	210	-166.7
2	0.45	348.4	171	+177.4
3	0.35	246.7	620	-373.3
4	0.70	603.0	925	-322.0

DISCUSSION

Examination of the field conditions for each year showed that in 1979 favorable climatic conditions and bush growth allowed for a very even distribution of I. pepperi within the bushes. In 1980, harsh weather and fewer succulent terminals near the surface of the bush canopy created an uneven distribution of aphids within the bush; a greater proportion of the populations was in the lower 3rd and inside areas of the bushes. The random selection of terminals or leaves used in the estimation technique were made primarily from the periphery of the canopy. Because of this, most calculated populations were too low. Future attempts to refine the density estimation techniques may be improved by selecting sample units from assigned regions within the bushes; base, interior side of exterior and top of exterior. This change would probably assure a more accurate estimation of aphid populations regardless of their distributions within the bushes.

LABORATORY STUDIES

OBJECTIVES

The developmental rate, lower temperature threshold for development, generation time, fecundity and life span of _I. pepperi_ are needed to aid in further field studies and the construction of aphid population models. Laboratory experiments were initiated in late 1980 to determine values for these biological parameters of _I. pepperi_.

METHODS AND MATERIALS

Colonies of _I. pepperi_ were maintained at 20-24°C on 2 year old potted 'Jersey' blueberry in a greenhouse. All colonies were clones from a single individual, an apterous viviparous female taken in field #54A on July 3, 1980. Laboratory studies were carried out in Percival® environmental chambers[13]. The food source for experimental aphids was 14 mm circular leaf discs, cut from vigorously growing blueberry leaves on greenhouse plants. Leaf discs were floated upsidedown on a nutrient media (Coon 1959) in 15 x 60 mm plastic petri dishes. The dishes were kept covered to maintain a relatively constant humidity inside.

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[13]Percival[R] model 1-35L, Percival Mfg. Co., Boone, Iowa.

Mature apterous viviparous females were kept on potted blueberry in a growth chamber at 23°C. Young were removed daily or more frequently, and moved to a leaf disc with a camel hair brush. At this time they were given an identification number and were recorded as 0 days old. Treatment temperatures were 5, 10, 17, 23, 26 and 29°C. Photoperiod was held constant at 16L:8D. Aphids were moved to new leaf discs on a regular schedule to assure quality and uniformity of food source.

Observations were made every 24 hours and each aphid's development noted. The ages at which instar changes, first birth of young, and death occurred were recorded, along with notes on behavior and appearance. Progeny were counted and then removed to avoid possible influence of crowding on fecundity. Data obtained from this experiment were length and number of instars, generation time, fecundity and longevity.

RESULTS

Table 17 gives the mean days per developmental stage of apterous viviparous females of *I. pepperi* as determined in this study. For those treatments in which aphids completed development, instars per day were calculated and plotted against treatment temperature (Figure 12).

Instars per day were regressed on temperature using the least spuares method (Gill 1978). The resulting equation and line (Figure 12) can be used to calculate the development rate of *I. pepperi* at various temperatures.

Table 17. Mean days per developmental stage of *Illinoia pepperi* on excised leaf discs at six treatment temperatures (16L:8D photoperiod).

Treatment and Temperature	Number of days in stage INSTAR I			II			III			IV			ADULT			PRE-REPRODUCTIVE PERIOD		
	N[a]	x	sd	N	x	sd	N	x	sd	N	x	sd	N	x	sd	NB[c]	x	sd
1- 5C	28	17.2	6.6	28	15.0	4.7	23	16.5	3.5	19	19.8	3.8	17	b		6	32.7	13.2
2- 10C	44	6.1	1.9	43	6.6	1.8	42	7.8	1.3	41	9.5	1.1	40	20.1	6.4	36	11.6	1.1
3- 17C	45	2.8	1.1	44	2.4	0.8	43	2.8	0.7	42	3.6	0.9	42	14.2	8.8	39	3.3	1.2
4- 23C	33	1.6	0.5	33	1.9	0.3	33	2.0	0.6	33	2.7	0.7	32	14.0	5.6	29	2.3	0.6
5- 26C	45	2.1	0.7	45	2.5	0.7	39	3.5	1.1	27	4.3	2.0	10	7.0	5.8	0	b	
6- 29C	83	2.0	0.9	83	2.4	0.9	38	b		6	b		0	b		0	b	

[a]N = number of aphids entering stage
x = mean number of days in stage for aphids completing stage
sd= standard deviation of mean

[b]insufficient replication

[c]NB = number of aphids that produced young

FIG.12.—Relationship between developmental rate (instars/day) and treatment temperature for *Illinoia pepperi* on excised leaf discs.

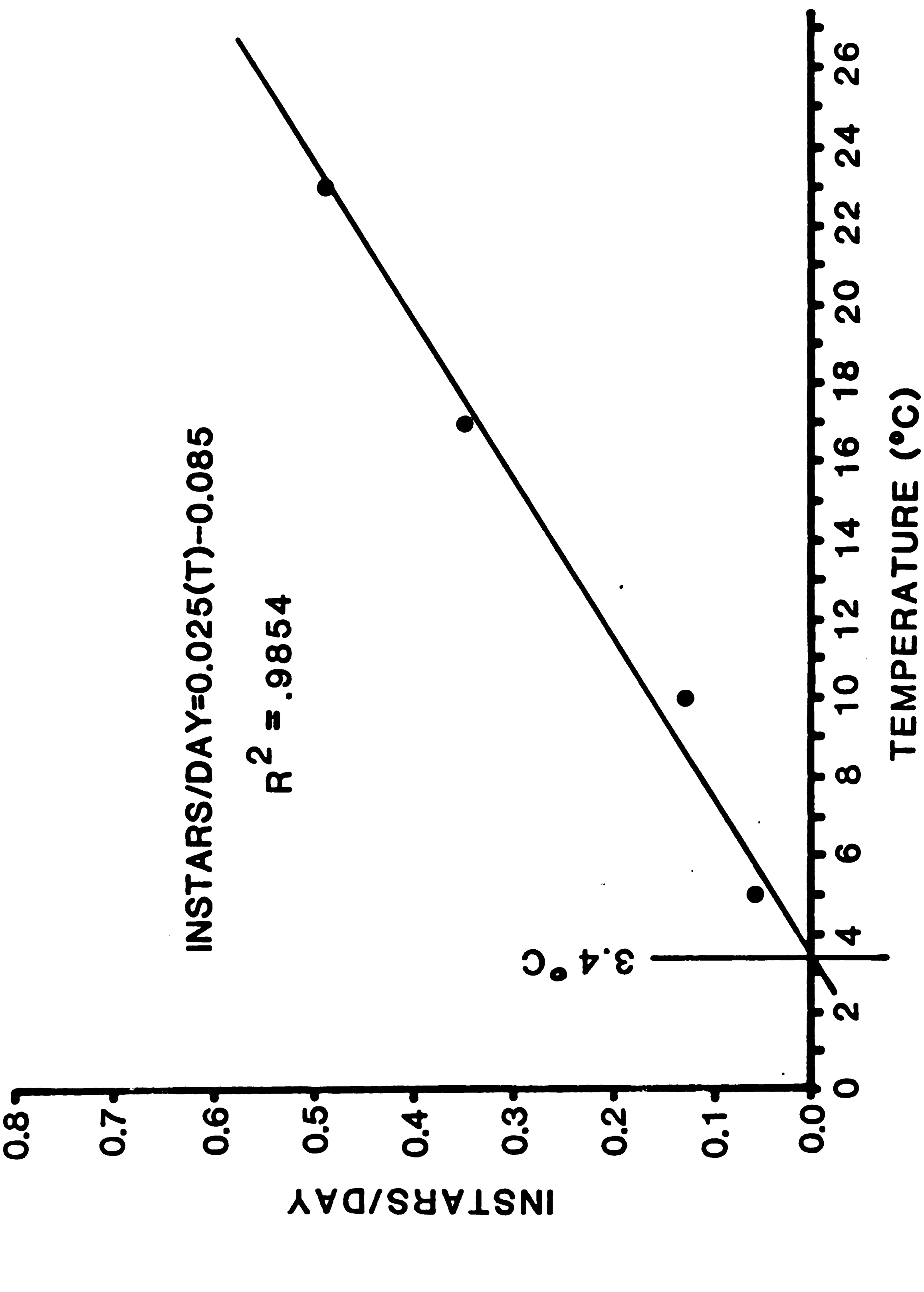

INSTARS/DAY=0.025(T)−0.085
R2 = .9854
3.4°C
INSTARS/DAY
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
2
4
6
8
10
12
14
16
18
20
22
24
26
TEMPERATURE (°C)

FIG.12.

The statistics relating to the regression line are presented in Table 18.

Table 18. Regression Statistics from *I. pepperi* Developmental Rate Studies in controlled environment chambers, 1980-81.

Y intercept = 0.085   STD error = 0.015

Slope = 0.025   STD error = 0.002

Variable	Mean	SS	St. Dev.
X	13.75	943.0	7,89
Y	0.2575	0.383	0.198

Coefficient of determination, R^2 = 0.9854

Coefficient of correlation, R = 0.9927

AVON:

Source	D^f	SS	Mean
Spuares			
Regression	1	0.1162	0.1162
Residual	2	0.0017	0.0009
Total	3	0.1179	

The Arnold's X intercept method was used to determine the lower threshold of development temperature. Solving

$$\text{Instars/Day} = 0.025\ (T^{o}C) - 0.085$$

by setting instars per day equal to zero, a base temperature of 3.4° is obtained. Theoretically, this is the temperature at which the developmental rate is zero; at any temperature above this some development may take place. 3.4°C is therefore the base temperature to be used in calculating accumulated heat, or degree days. This base temperature may not necessarily be correct; the developmental rate at very low temperatures may actually level off somewhat, so that a temperature slightly less than 3.4°C would be the base.

Using this base temperature, data were converted to degree day units, and are presented in Table 19.

Table 19. Mean degree days (base 3.4°C) per developmental stage of *Illinoia pepperi* on excised leaf discs at six treatment temperatures (16L:8D photoperiod).

Treatment and Temperature	Degree days per stage INSTARS					Pre-Reproductive Period
	I	II	III	IV	ADULT	
1- 5C	27.5	24.1	26.4	31.7	a	52.3
2- 10C	40.0	43.4	51.3	62.7	132.7	76.56
3- 17C	37.5	32.1	37.5	48.9	193.1	44.9
4- 23C	31.9	37.6	38.8	52.7	274.4	45.1
5- 26C	46.8	55.6	79.1	96.1	158.2	a
6- 29C	46.9	62.2	a	a	a	a

[a]Insufficient replications.

In all treatments, the number of degree days per instar increased with each successive instar. Further computations produced the information in Table 20.

Table 20. Mean ages and mean degree days (Base 3.4°C) for molt to adult stage, generation time, and age of death of Illinoia pepperi on excised leaf discs.

Treatment	Temp	Molt to Adult		Generation Time		Death		Oldest aphid
		Days	DD	Days	DD	Days	DD	Age
1	5°C	64.8	103.6	97.0	155.2	a		a
2	10°C	30.7	202.7	41.2	270.6	55.4	365.6	110
3	17°C	11.5	155.9	14.8	201.3	25.1	341.36	54
4	23°C	8.1	159.3	10.4	203.8	22.4	439.0	33
5	26°C	b	b	b		13.3	300.6	30
6	29°C	b	b	b		6.4	163.8	18[c]

[a]Many still alive at end of experiment

[b]Insufficient replications

[c]Oldest was in IIIrd instar

From these tables an interesting phenomenon was observed; the number of degree days per any given stage was much greater in treatment 2, at 10°C. This shall be addressed later (see page 88). Another interesting observation was the failure of test aphids to complete development at 26° or 29°C. This was probably due to increased water loss by aphids at higher temperatures. Aphids at higher temperatures also walked about their leaf discs more, and often fell into the growth media and drown. Both of the mortality factors can be seen in Tables 19 and 20 from the reduced life span of aphids in the highest temperature treatments. Figure 13 shows plots of mean degree days per developmental stage or event at the treatment temperatures. Figures 14 and 15 show the same information for the pre-reproductive period and generation time.

In each plot, the interesting result in the 2nd treatment group is plainly visible; for the instars III and IV, pre-reproductive period and generation time the degree day requirements were significantly different from other treatment temperatures.

Longevity of I. pepperi as reported in Tables 19 and 20 may not be very accurate in terms of real world field conditions. The majority of aphids died by drowning after walking off the the leaf disc. Their actual life span could be considerably longer where such a mortality factor does not exist. Actual field life spans, of course, could be shortened by many other factors, i.e., wind, rain, temperature extremes, and natural control. Further tests of aphid longevity need to be conducted, possibly using cuttings or potted plants as a food source.

FIG. 13.—Relationship of degree days per developmental period to temperature for *Illinoia pepperi* on excised leaf discs. Bars represent $\pm$ 1 standard deviation about the means.

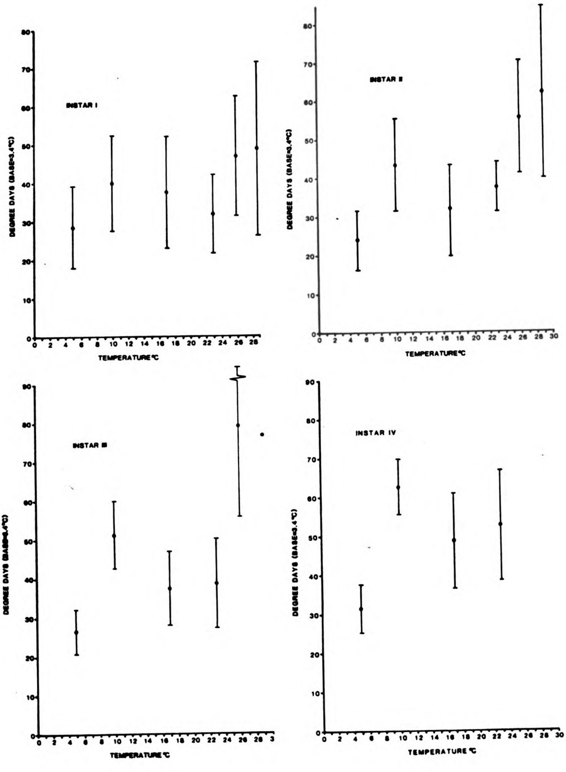

INSTAR I
INSTAR II
INSTAR III
INSTAR IV
DEGREE DAYS (BASE=3.4°C)
TEMPERATURE °C

FIG.13.

FIG.14.--Relationship of adult pre-reproductive period and generation time in degree days to temperature for *Illinoia pepperi* on excised leaf discs. Bars represent $\pm$ 1 standard deviation about the means.

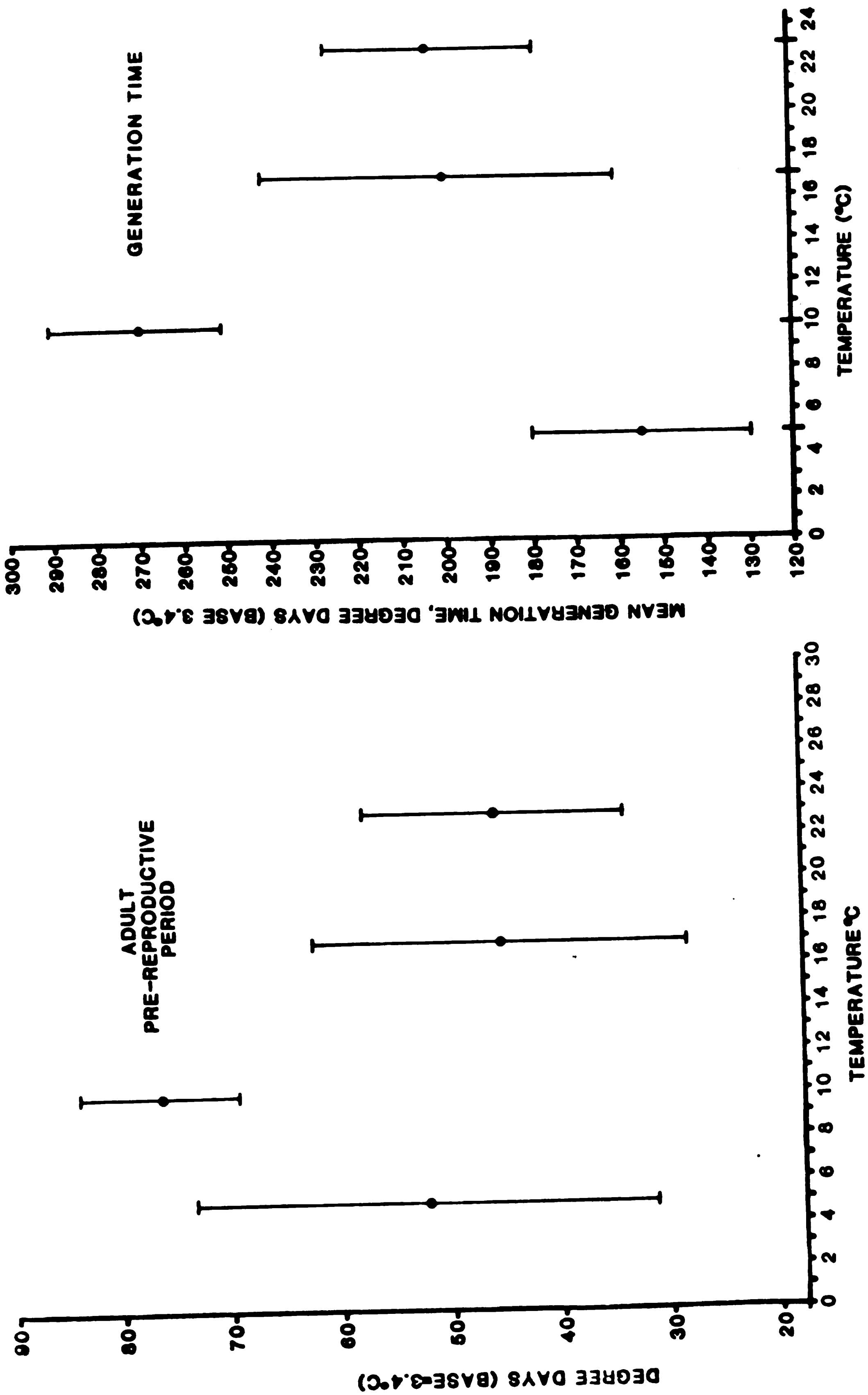

GENERATION TIME
MEAN GENERATION TIME, DEGREE DAYS (BASE 3.4°C)
TEMPERATURE (°C)
ADULT
PRE-REPRODUCTIVE
PERIOD
DEGREE DAYS (BASE=3.4°C)
TEMPERATURE °C

FIG.14.

Table 21 gives the fecunditv data collected in this experiment.

Table 21. Fecundity of apterous viviparous Illinoia pepperi at 6 treatment temperatures on excised blueberry leaf discs with a 16L:8D photoperiod.

Treatment	Temperature °C	Mean Fec.	Sd	Most per Female
1	5	2.33	1.21	4[a]
2	10	6.68	3.60	15
3	17	10.90	7.73	31
4	23	18.67	8.94	37
5	26	_[b]		
6	29	_[b]		

[a]aphid had not yet died

[b]no young produced

Total fecundity was also greatly affected by the drowning deaths of female aphids which were still producing young. A more useful value to examine was therefore the mean young per day, since this reduces the influenceof sudden deaths. A plot of the mean young per day vs days after reaching the adult stage is shown in Figure 15. Dashed lines indicate means for which less than 10 aphids were available for calculations. Production of young by individual aphids appeared to follow a pattern in which young were born at a fluctuating rate. The plots of mean young per day also show this trend. This may be an unnatural effect due to

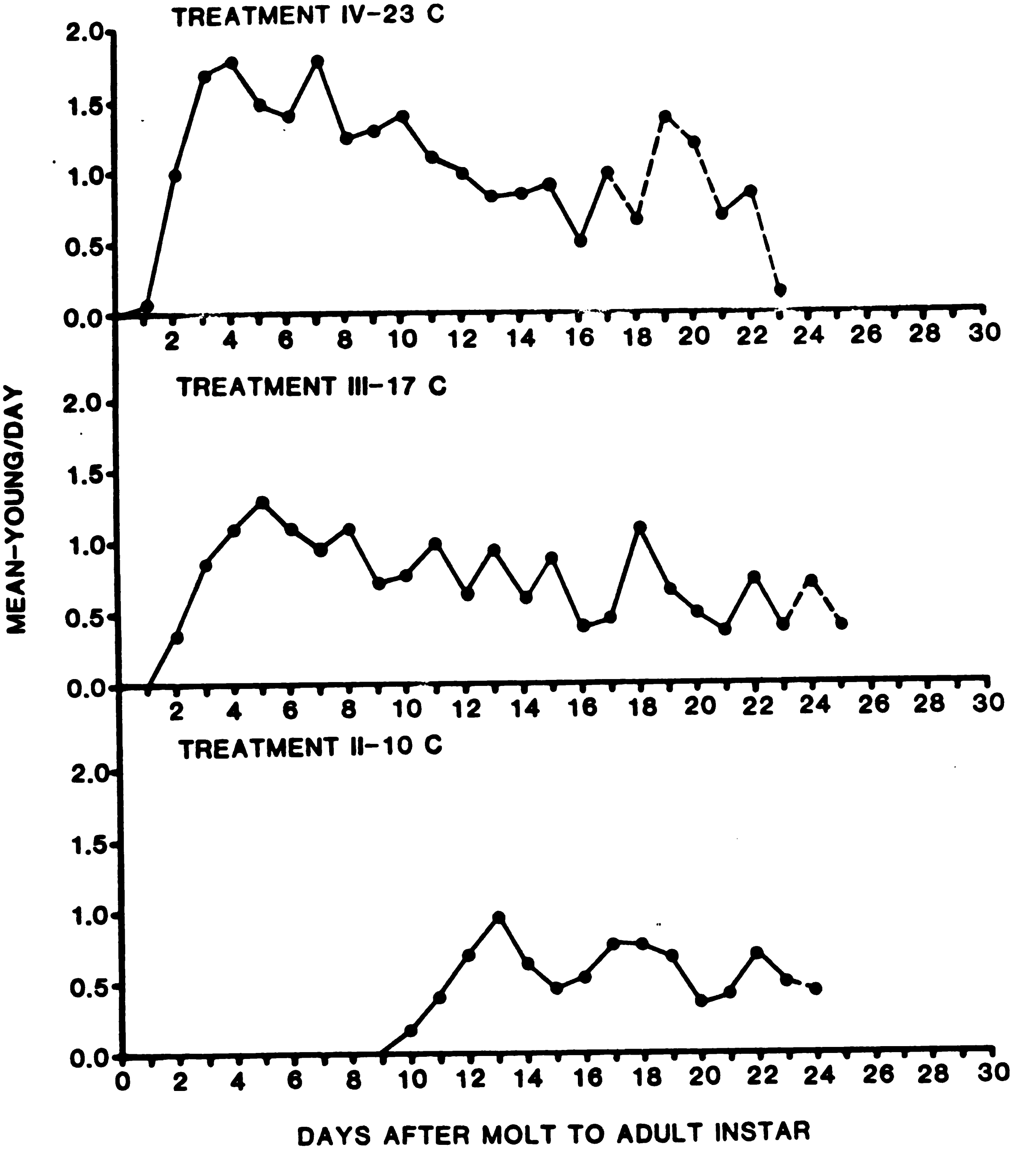


FIG.15.—Fecundity of apterous viviparous Illinoia pepperi on excised blueberry leaf discs at 3 temperatures.

the observation scheme, or possibly a physiological system involving timing of births according to light dark periods, and the temperature.

DISCUSSION

The most interesting biological feature discovered in this experiment was that I. pepperi raised at 10°C required the greatest number of degree days to complete a given amount of development, while aphids at 5°C required the fewest. Normally, it is expected that within a certain range, the amount of degree days needed to complete a fixed amount of development should be equal at any temperature. This relationship breaks down outside the acceptable range, where extreme temperatures adversely affect enzyme reaction and inactivate or denature proteins. Also, on the whole organism level, desiccation progressively increases at highers temperatures. Previous research indicates that treatments at the highest and lowest temperatures would exhibit lower developmental rates in aphids, thus requiring more degree days per stage or event. The experimental data for I. pepperi fit this scenario at the higher temperature treatments. Development was never completed at these temperatures. However, the lowest temperature treatment also did not show a lowered developmental rate: it was actually greater than all the other temperatures. Even more atypical was the very slow developmental rate found for the aphids kept at 10°C. These aphids required significantly more degree days to develop than aphids raised at the temperatures above or below 10°C. Figure 16 compares the developmental rates, in terms of degree days per stage, for the six treatments.

The physiology of the host plant may partially explain the effects observed in this experiment. Many different physiological processes are taking place within living blueberry leaf tissue. Plant tissues normally begin a "hardening off" process when triggered by environmental factors such as water stress, changing photoperiods, and changes in temperature. This process is normally gradual, and in blueberry the leaves become tough, leathery, and dark reddish or purple in color when the process is complete. There is a build up of tannins and other cell products, and such tissues are generally less suitable to insects, slowing their development.

Plant tissues kept above this temperature would continue to develop and produce photosynthetic products in a normal manner, and remain suitable for insect development. Normally growing plant tissues suddenly exposed to very low temperatures would be cued to start the hardening off process, but because of the extremely slow rates of enzymatic reaction at the low temperature, hardening off occurs <u>very</u> slowing; the tissue may actually remain very acceptable in terms of changes in texture, nutritional status, and suitability to insects

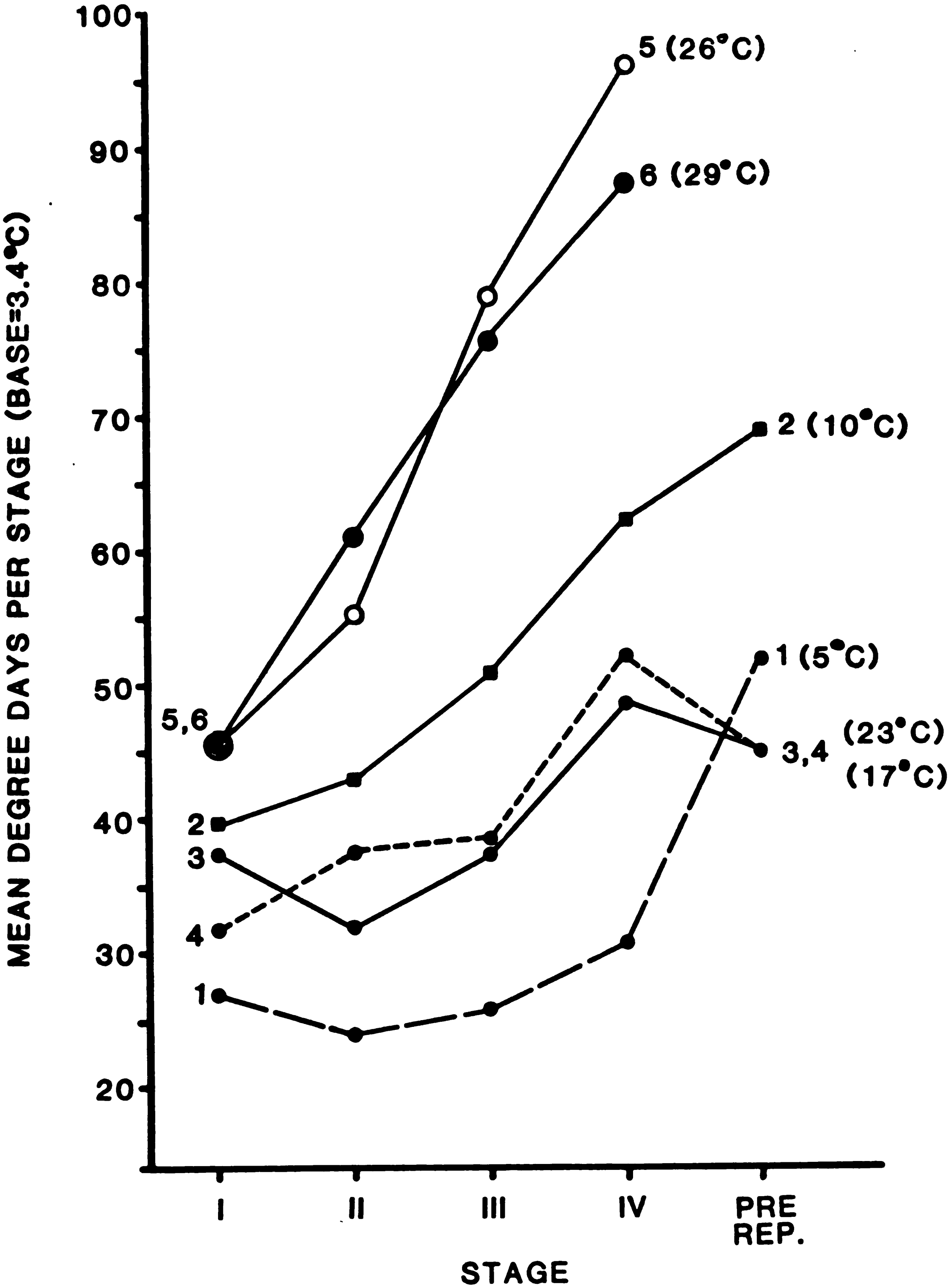


FIG.16.—Mean degree days per stage of Illinoia pepperi on excised leaf discs. Treatment temperatures: (1) 5°C; (2) 10°C; (3) 17°C; (4) 23°C; (5) 26°C; (6) 29°C.

feeding upon it. Degradation of cell components would also be very slow at the lower temperatures; at the warm temperatures the breakdown products within plant tissues may affect the food quality of the tissues.

The apparently abberant experimental results can be supported using the cell physiology explanations outlined above. At 5°C in treatment 1, the blueberry leaf tissue was at a sufficiently low temperature to eliminate degradation of cell contents, but too cold to allow normal hardening off processes to render the leaf less suitable to aphids. These 5°C leaf discs may represent the best in terms of aphid nutrition. Leaf discs at 10°C were actively hardening off and becoming unfit for aphid growth faster than the leaf discs at other temperatures. Leaf discs at 17° and 23°C were not hardening off; they actually grew in diameter while floating on the media. However, due to more waste products and degradation at the higher temperatures, they might actually have been slightly less suitable for growth of aphids.

There is a possibility that aphid physiology may have a significant relationship to the lower developmental rate at 10°C. Further experiments using artificial diets would eliminate the variability due to leaf disc quality and resolve this situation. Also similar experiments using leaf discs but changing discs at very short intervals may reveal the reason for the unexpected results at 10°C (more frequent handling of aphids may lead to other problems, if such an experiment were undertaken).

NOTES ON BEHAVIOR AND MORPHOLOGY OF I. PEPPERI

Behavior -- Through the course of the laboratory experiments constant observation of individual *I. pepperi* provided some information on the behavior and general appearance of the different stages. *I. pepperi* is a relatively fast aphid when walking, allowing them to travel significant distances. However, when feeding they are very sessile. This aphid prefers to place its stylets into or as close to leaf veins as possible. All instars remain for a long period of time in the feeding position unless provoked in some manner to move away. Repeated attempts to disturb them with a fine brush are often necessary to cause them to remove their stylets from a leaf. As noted in the section on field studies, there apparently is no alarm pheromone communication between colony members of *I. pepperi*.

Morphology -- All aphids in the laboratory studies were apterous viviparous females. The eyes of future progeny become pigmented days before they are born, and can be seen through the cuticle of adult females. Up to 3 embryos could be seen at one time in this manner. The adult stage can be separated from the earlier instars very easily by body size and shape. Adult apterous viviparous *I. pepperi* have a somewhat flattened dorsum, with depressions and a ridge towards the lateral edge of this surface (see Figure 17). The antennae of older individuals began to curl slightly at the tip. The entire body is covered with a whitish waxy coating, powdery in appearance. This is formed shortly after ecdysis, and slowly wears off or dissipates in some manner during the instar. In old adults this surface coating is completely absent, giving the aphid a very shiny cuticle.

GENERAL DISCUSSION

The biology of Illinoia pepperi and the spread of Blueberry Shoestring Virus disease can now be more easily related, and the information to be sought in future research identified. The slow in-row spread pattern of BBSSV is likely due to the rather sessile feeding behavior of all stages of this aphid, and the rather low percentage of winged aphids produced under normal conditions. Analysis of disease incidence has led to the conclusion that the source of inoculum for transmission was within field and not due to constant re-introduction from other sources (Lesney et. al. 1978). I. pepperi are found almost exclusively within blueberry fields, even when acceptable alternate hosts are present in surrounding areas; there

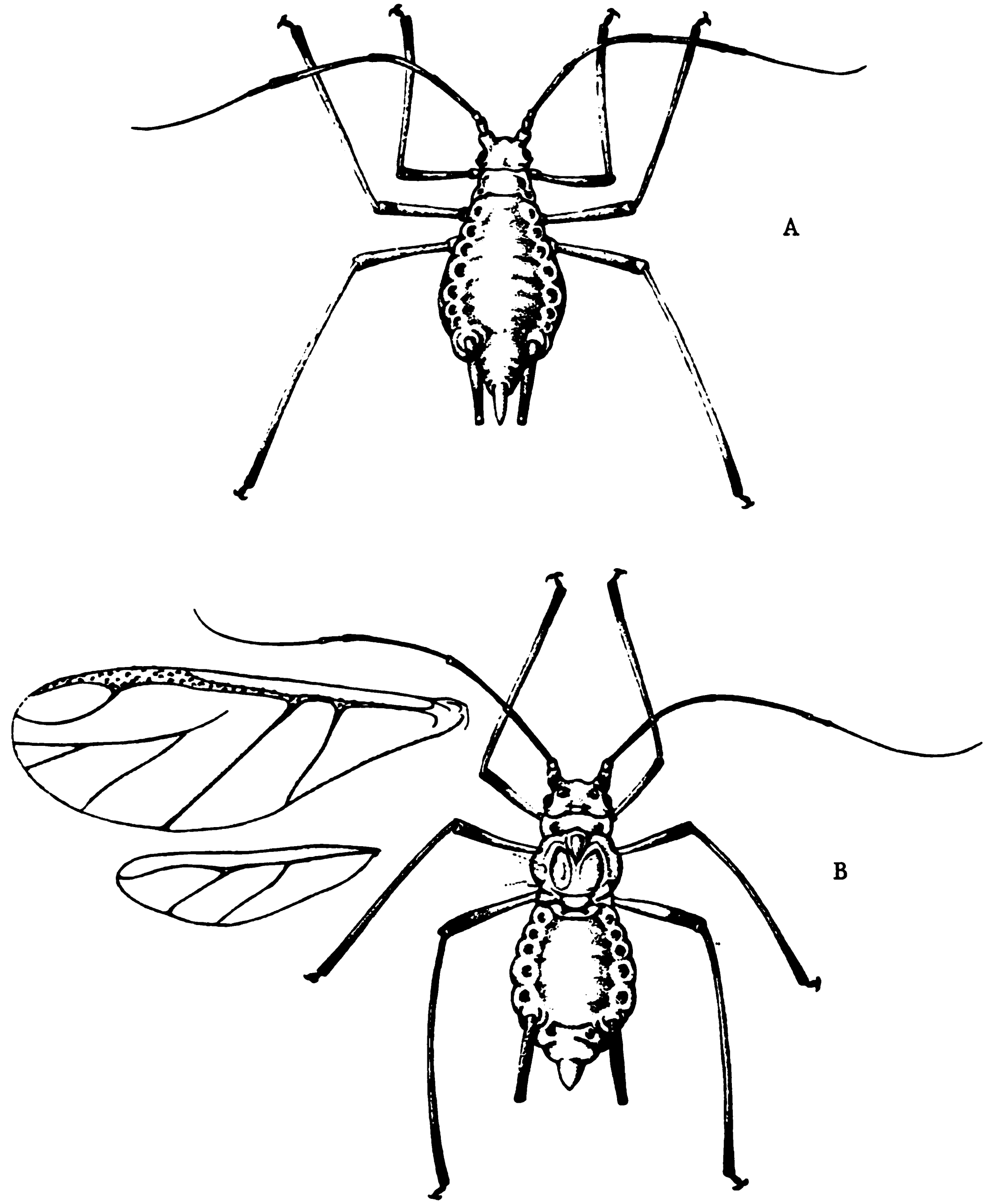


FIG.17.--Apterous viviparous (A) and alate viviparous (B) forms of Illinoia pepperi (MacG.). Approximately 20X.

is apparently little movement out of or into fields by aphids. These two findings support each other. It is interesting that both BBSSV and _I_. _pepperi_ have very limited host ranges. The disease is exclusive to blueberry, and the aphid has few alternate hosts. This suggests a very close ecological relationship between blueberry, BBSSV and _I_. _pepperi_. Control strategies involving the disruption of this relationship may only have to impact on one specific feature in order to be effective. Resistance of certain cultivars to BBSSV or aphids is known and may be sufficient to significantly reduce transmission of the disease.

Before the value of cultivar resistance or other control tactics can be accurately measured, the remaining details of aphid biology, behavior and disease transmission need to be determined. Further refinements of the aphid density estimation techniques are needed. Aphid behavior within bushes in fields needs to be analyzed to determine the factors which induce movement and the directions and distance traveled. Further transmission studies will be necessary to generate an accurate estimation of vector efficiency. With such a value for BBSSV and _I_. _pepperi_, aphid populations within fields could be related to a possibility of disease spread. From such information, and economic injury level for aphid populations could be established and used for careful planning of controls.

Much of the information generated in this study has potential use in the development of models or simulations of the blueberry-BBSSV-aphid relationship. A preliminary model dealing with aphid population dynamics and movement has been constructed by Cameron et. al. (unpublished report 1981). Future additions to this model may someday produce a management tool for the control of BBSSV disease, once other critical components are developed. The relationship between populations of I. pepperi, plant or field conditions and vector potential of the aphids at any moment would have to be generated and compared to an economic injury level. Plainly, much information remains to be found before such a model could be adequately constructed and verified.

APPENDIX 1

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.: 1982-2

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

BIOLOGY OF ILLINOIA PEPPERI (MacG.), THE
BLUEBERRY APHID, AND ITS RELATION TO BLUEBERRY
SHOESTRING VIRUS DISEASE IN WESTERN MICHIGAN

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

Entomology Museum, Michigan State University (MSU)

Other Museums: none

abbreviations:

AL = alate viviparous
AP = apterous viviparous
OV = oviparous

V. corymbosum = Vaccinium corymbosum Linn.
cult. = cultivar

Additional specimens are in the collection of M. Whalon, Dept. of Entomology, M.S.U.

Investigator's Name (s) (typed)

Erwin A. Elsner

Date February 8, 1982

*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 3 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.)	Ottawa CO., MI. Coopersville, field 281 5 December 1981 on V. corymbosum cult. 'Jersey' Col. E. Elsner	3							MSU
Illinoia pepperi (MacG.)	Ottawa Co., MI. Coopersville, field 281 5 December 1981 on V. corymbosum cult. 'Jersey' coll. E. Elsner					1 (OV)			MSU
Illinoia pepperi (MacG.)	Ingham Co., MI. M.S.U., East Lansing 8 September 1981 on V. corymbosum 'Jersey' in greenhouse ex 3 July '80, field 54					1 (AP)			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Erwin A. Elsner

Date 8 Feb. 1982

Voucher No. 1982-2

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

[illegible]
Curator

8 February 1982
Date

APPENDIX 1.1

Voucher Specimen Data

Page 2 of 3 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.)	Ottawa Co., MI. West Olive field 54 A 4 August 1981 on _V._ _corymbosum_ cult. 'Collins' coll. E. Elsner					1 (AP)			MSU
Illinoia _pepperi_ (MacG.)	Ottawa Co., MI. West Olive, field 54 A 12 August 1981 On _V._ _corymbosum_ cult. 'Jersey' coll. E. Elsner					1 (AP)			MSU
Illinoia _pepperi_ (MacG.)	Ottawa Co., MI. West Olive, field 54 A & B 24 July 1981 on _V._ _corymbosum_ cult. 'Jersey' coll. E. Elsner					1 (AP) 1 (AL)			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Erwin A. Elsner

Date 8 Feb. 1982

Voucher No. 1982-2

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

R. L. Fischer — Curator

8 February 1982 — Date

APPENDIX 1.1

Voucher Specimen Data

Page 3 of 3 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.)	Eaton Co., MI. Charlotte 4 June 1981 on V. corymbosum cult. 'Jersey' coll. Elsner/Petitt					1 (AL)			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Erwin A. Elsner

Date 8 Feb., 1982

Voucher No. 1982-2

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

[illegible] 8 February 1982

Curator Date

APPENDIX 2

APPENDIX 2

FIELD LOCATIONS AND LAYOUTS

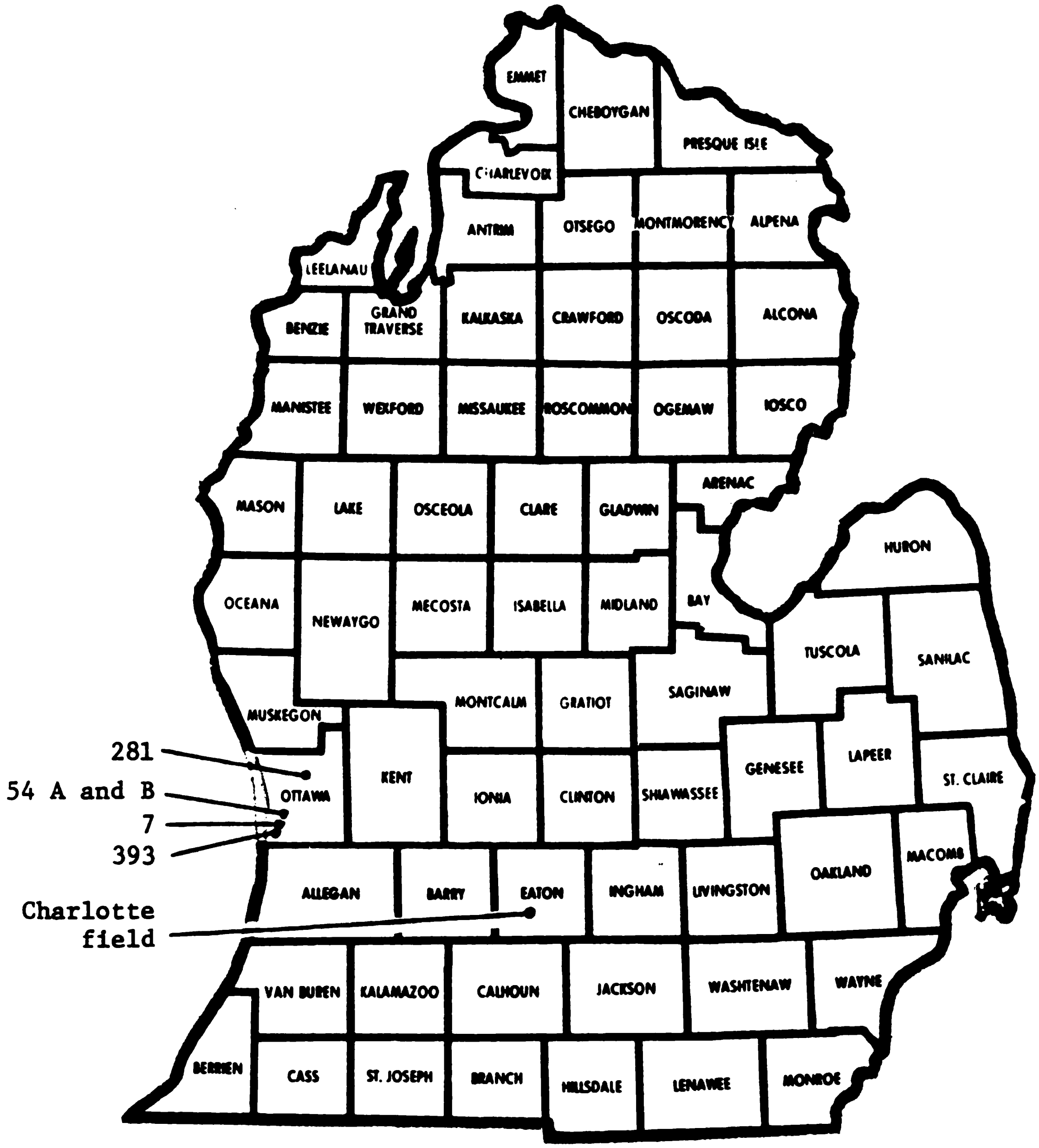


FIG.18.--Map of southern Michigan showing locations of principle study fields.

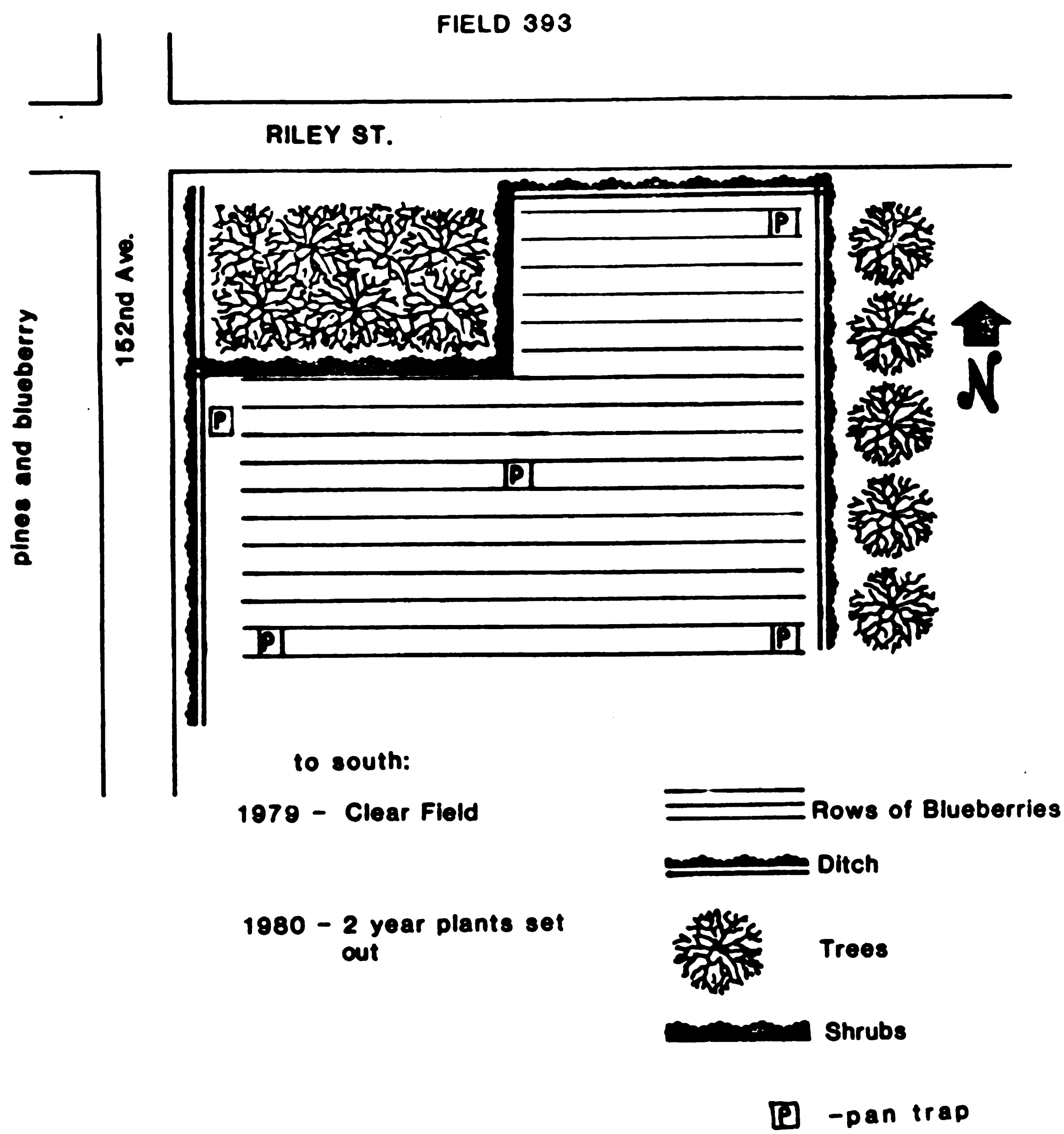
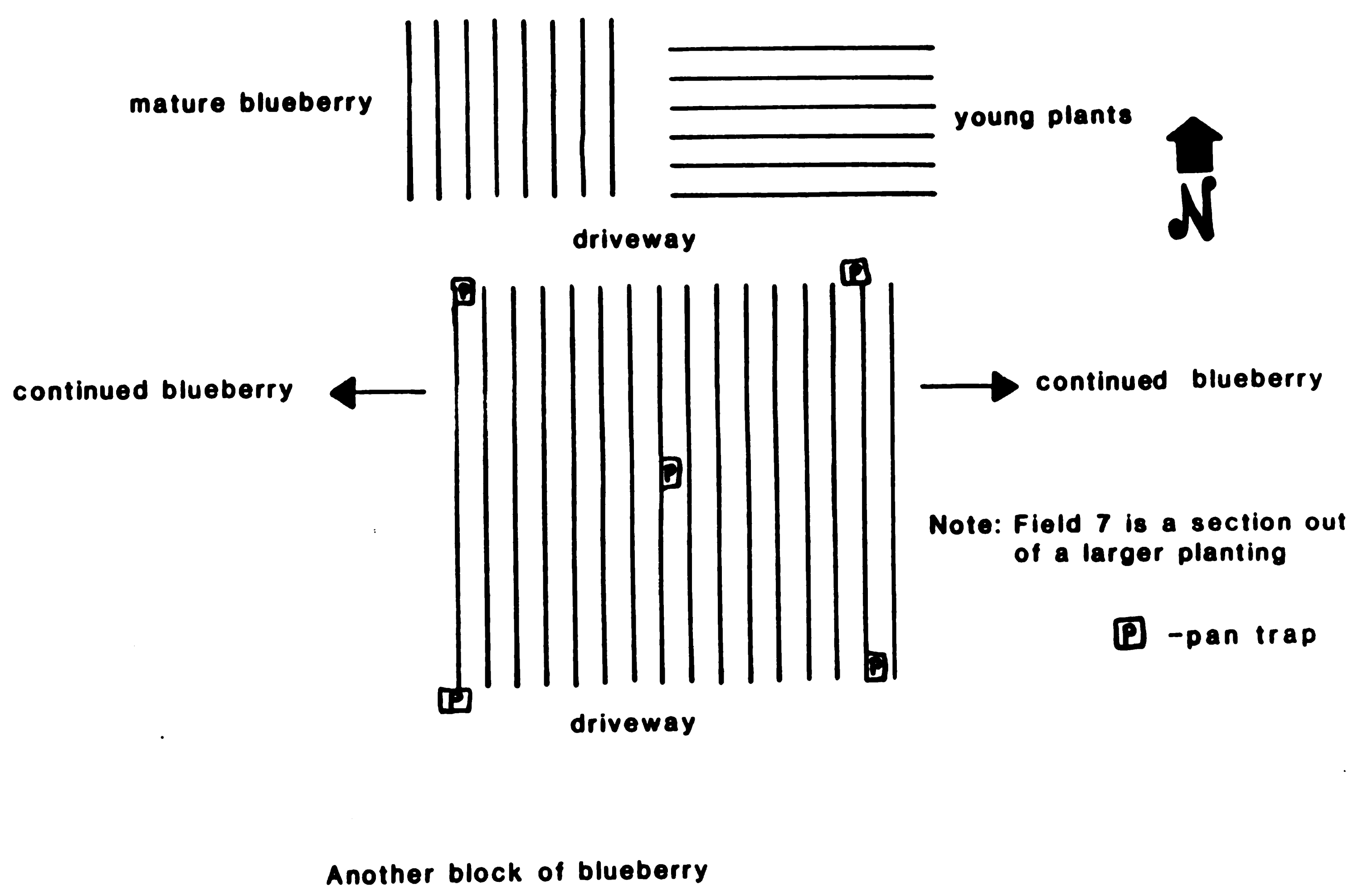


FIG.19.--Field # 393, Park Township, Ottawa Co., Mi. Wesley Waldron, owner.

FIG.20.--Field # 7, Port Sheldon Township, Ottawa Co., Mi. Allen DeVries, owner.

FIELD 7


mature blueberry
young plants
N
driveway
continued blueberry
continued blueberry
P
Note: Field 7 is a section out of a larger planting
P -pan trap
driveway
Another block of blueberry

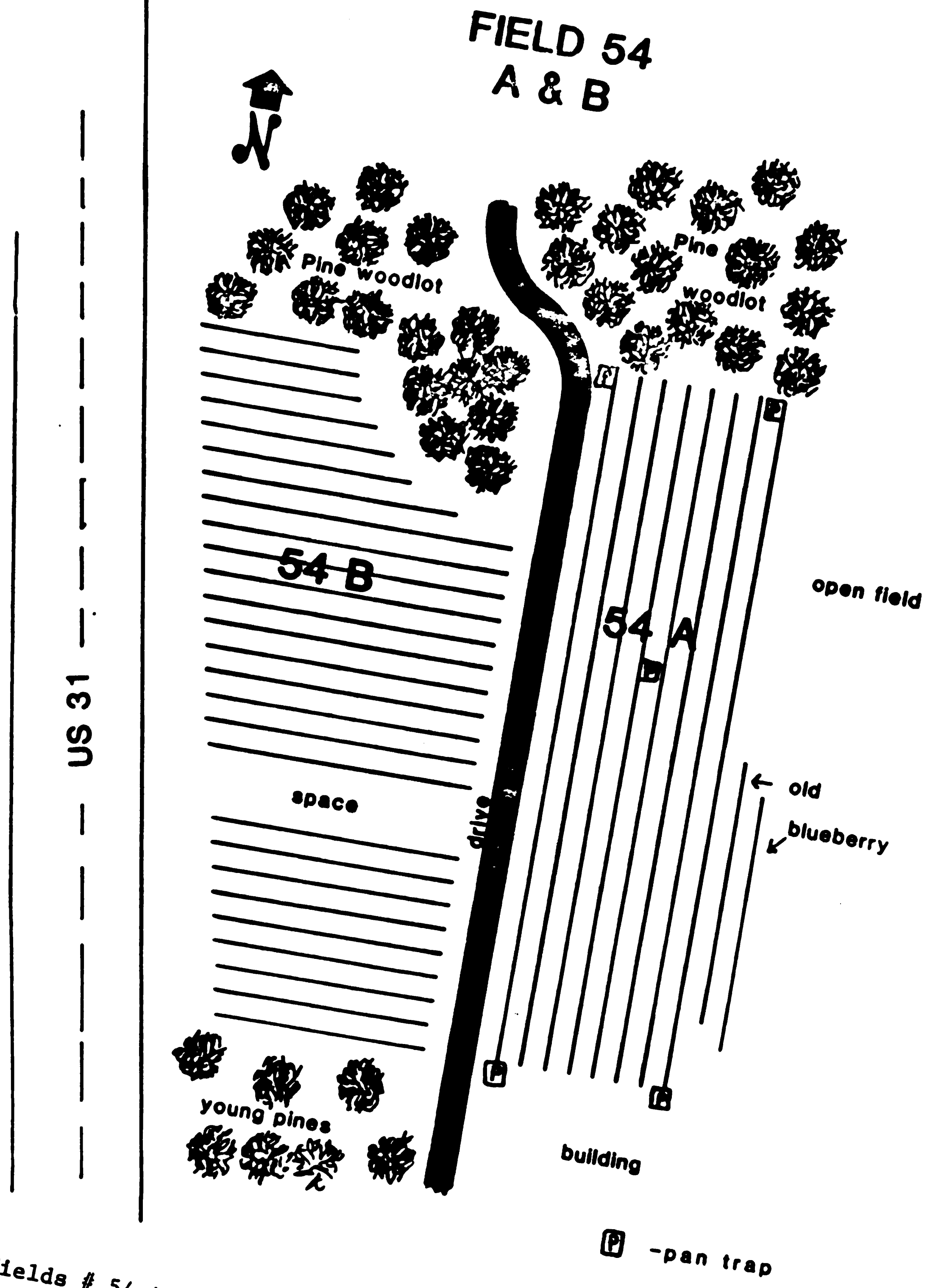


FIG.21.--Fields # 54 A and B, Olive Township, Ottawa Co., Mi.
Vern Brower, Owner.

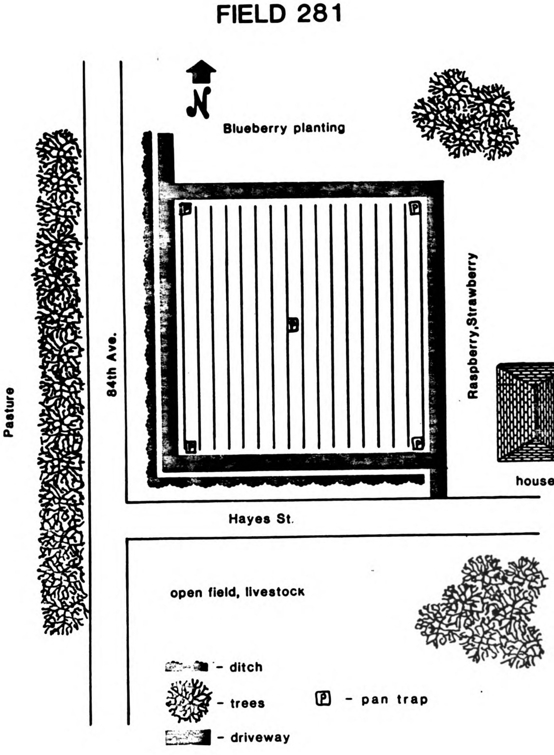


FIG. 22.--Field # 281, Polkton Township, Ottawa Co., Mi. Frank VenRoy, owner.

APPENDIX 3

APPENDIX 3

1979 PAN TRAP DATA AND WEATHER INFORMATION

weather data sources:

temperatures; in-field hygrothermographs for fields 7, 54 and 281. Field 393 temperatures obtained from NOAA Monthly Summaries, Holland MI. recording station.

rainfall; amounts for fields 393, 7 and 54 from Holland, MI. station. Amounts for field 281 taken from Nunica, MI. station.

wind speed and direction; data recorded at Muskegon, MI. station were used for all fields. This was the closest station recording such information.

Table 22. 1979 Pan Trap Catches of Alate *Illinoia pepperi* and associated weather statistics. Field 393.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
June	1	895	62	58		28	9.2	x	0	0	0	0	
	2	914	72	43		21	4.8						
	3	940	78	50		24	8.1						
	4	965	81	46		20	8.8	x	0	0	1	0	
	5	992	77	52		35	7.3						
	6	1022	81	57		13	8.5						
	7	1056	77	67		16	10.9	x	0	0	0	0	
	8	1089	81	60	1.24	22	6.2						
	9	1118	75	60	0.85	19	4.3						
	10	1151	75	67	0.71	25	15.7	x	0	0	0	0	
	11	1170	67	48	0.10	29	6.9						
	12	1187	70	40		35	7.5	x	0	0	1	0	
	13	1208	76	42		12	7.3						
	14	1235	82	49		18	12.8						
	15	1279	84	71		20	18.7	x	0	0	0	0	
	16	1312	85	68		20	15.2						
	17	1344	71	68		28	14.7						
	18	1368	71	54	T	08	11.1	x	1	3	2	0	
	19	1394	81	48		12	15.1						
	20	1430	81	67		15	16.8						
	21	1464	79	65	0.79	22	11.8	x	1	0	0	0	
	22	1486	67	54		33	11.7						
	23	1498	58	41		35	11.2	x	0	2	2	0	
	24	1512	64	42		35	7.8						

[a]Degree days (Base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 22, continued.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
June	25	1528	72	35		16	7.2						
	26	1549	78	41		19	11.9	x	0	2	0	0	
	27	1582	77	64		22	9.1						
	28	1610	83	50	0.02	11	7.3	x	0	0	0	0	
	29	1640	75	61	0.91	06	8.5						
	30	1664	67	58	1.33	33	11.8	x	0	0	1	0	
July	1	1686	68	53	T	33	16.5						
	2	1706	68	47	0.02	32	9.8						
	3	1730	81	45		10	6.0	x	0	3	0	0	0
	4	1757	71	58	0.87	01	12.4						
	5	1773	70	39		34	9.1						
	6	1791	73	39		28	5.0						
	7	1813	79	41		25	3.5	x	0	2	1	0	0
	8	1840	82	49		17	4.5						
	9	1872	80	60		29	5.3						
	10	1899	79	52		21	6.8	x	0	0	0	0	0
	11	1933	84	61		25	4.9						
	12	1969	88	60		22	5.0						
	13	2004	86	61		19	5.8						
	14	2041	82	67		22	9.5	x	0	0	0	0	0
	15	2079	82	66		24	6.5						
	16	2108	81	55		34	10.4						
	17	2134	71	56		33	9.1	x	0	0	0	0	0
	18	2153	73	42		30	6.0						
	19	2176	79	43		23	4.6	x	0	0	0	0	0
	20	2201	88	46		22	6.5						
	21	2228	83	49		22	5.9						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 22, continued.

Month	Day	Accumulated[a] Degree days	Temp Max	Temp Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
July	22	2258	84	51		23	3.6						
	23	2292	85	60	0.13	20	6.0	x	0	0	0	0	0
	24	2327	81	66		18	13.8						
	25	2363	76	72	0.15	22	13.2						
	26	2389	74	55	T	30	9.1	x	0	2	1	0	0
	27	2418	83	50		21	7.2						
	28	2451	79	65	0.18	32	8.3						
	29	2480	81	52		31	7.2						
	30	2511	82	56		17	9.6	x	0	0	0	0	0
	31	2545	76	70	0.48	30	10.4						
Aug.	1	2575	73	63		04	8.5						
	2	2603	76	57	0.09	25	9.1	x	0	2	0	0	0
	3	2633	79	56		22	9.6						
	4	2665	84	57		19	8.8						
	5	2696	79	60	0.47	26	7.6						
	6	2728	81	59	0.53	09	7.8	x	0	0	0	0	1
	7	2766	85	67		22	11.9						
	8	2797	78	61		29	5.9						
	9	2831	83	60	0.09	17	11.1	x	0	0	0	0	0
	10	2866	79	68	2.10	30	13.7						
	11	2889	73	49		01	9.8						
	12	2907	73	41		19	7.5	x	0	0	0	0	0
	13	2930	67	54		21	14.7						
	14	2952	63	58	0.14	32	14.2						
	15	2966	65	40		33	11.1						
	16	2985	78	34		24	4.8	x	0	0	0	0	0
	17	3008	66	58	0.11	16	11.1						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.
[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 22, continued.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
Aug.	18	3036	75	56	0.98	27	4.9						
	19	3066	82	55	T	11	4.3	x	0	0	0	0	0
	20	3091	69	58	1.32	10	7.8						
	21	3121	78	58	0.61	10	9.8	x	0	0	0	0	0
	22	3147	71	58		11	8.8						
	23	3181	79	64	1.13	19	9.4						
	24	3210	69	65	0.03	24	9.9						
	25	3233	70	54		26	8.2	x	0	0	0	0	0
	26	3258	78	47		15	4.9						
	27	3286	72	61		10	7.3						
	28	3316	73	64	0.31	19	5.8						
	29	3347	75	63	0.10	22	11.5	x	0	0	0	0	0
	30	3378	81	58	T	28	8.9						
	31	3412	85	59		16	7.6						
Sept.	1	3447	83	64		18	10.2						
	2	3483	78	70		22	10.9						
	3	3514	79	58		35	7.1	x	0	0	0	0	0
	4	3539	74	53		07	7.1						
	5	3567	80	52		19	4.9						
	6	3597	76	62		30	10.2	x	0	0	0	0	0
	7	3619	66	53		35	12.5						
	8	3633	64	40		01	6.6						
	9	3648	69	39		18	10.8						
	10	3670	74	46		18	13.7	x	0	0	1	0	0
	11	3701	84	55		12	10.4						
	12	3735	81	62		18	8.3						

[a] Degree days (base 38.2°F) accumulated from March 1, 1979.

[b] Resultant wind direction in tens of degrees clockwise from true north; average wind spee[illegible] in m.p.h.

Table 23. 1979 Pan Trap Catches of Alate *Illinoia pepperi* and associated weather statistics. Field 7.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
June	25	1528	72	35		16	7.2						
	26	1549	78	41		19	11.9						
	27	1582	77	64		22	9.1						
	28	1610	83	50	0.02	11	7.3	x					
	29	1640	75	61	0.91	06	8.5						
	30	1664	67	58	1.33	33	11.8	x					
July	1	1686	68	53	T	33	16.5						
	2	1706	68	47	0.02	32	9.8						
	3	1730	81	45		10	6.0	x	0	0	0	0	0
	4	1757	71	58	0.87	01	12.4						
	5	1773	70	39		34	9.1						
	6	1791	73	39		28	5.0						
	7	1813	79	41		25	3.5	x	0	0	0	0	0
	8	1840	82	49		17	4.5						
	9	1872	80	60		29	5.3						
	10	1899	79	52		21	6.8	x	1	0	0	0	0
	11	1933	90	59		25	4.9						
	12	1969	93	56		22	5.0						
	13	2004	90	57		19	5.8						
	14	2041	87	64		22	9.5	x	0	0	0	0	0
	15	2079	93	65		24	6.5						
	16	2108	83	50		34	10.4						
	17	2134	79	74		33	9.1	x	0	0	0	0	0
	18	2153	86	35		30	6.0						
	19	2176	86	38		23	4.6	x	0	0	0	0	0
	20	2201	85	40		22	6.5						
	21	2228	89	44		22	5.9						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 23, continued.

Month	Day	Accumulated[a] Degree days	Temp Max	Temp Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
July	22	2258	89	46		23	3.6						
	23	2292	82	58	0.13	20	6.0	x	0	0	0	0	0
	24	2327	81	64		18	13.8						
	25	2363	78	65	0.15	22	13.2						
	26	2389	82	54	T	30	9.1	x	0	0	0	0	0
	27	2418	86	46		21	7.2						
	28	2451	85	65	0.18	32	8.3						
	29	2480	88	46		31	7.2						
	30	2511	80	50		17	9.6	x	0	0	0	0	0
	31	2545	85	63	0.48	30	10.4						
Aug.	1	2575	72	62		04	8.5						
	2	2603	82	54	0.09	25	9.1	x	0	0	0	0	0
	3	2633	84	53		22	9.6						
	4	2665	86	53		19	8.8						
	5	2696	83	62	0.47	26	7.6						
	6	2728	84	56	0.53	09	7.8	x	0	0	0	0	0
	7	2766	89	62		22	11.9						
	8	2797	84	58		29	5.9						
	9	2831	84	60	0.09	17	11.1	x	0	0	0	0	0
	10	2866	83	67	2.10	30	13.7						
	11	2889	75	46		01	9.8						
	12	2907	78	36		19	7.5	x	0	0	0	0	0
	13	2930	67	53		21	14.7						
	14	2952	70	54	0.14	32	14.2						
	15	2966	73	35		33	11.1						
	16	2985	77	28		24	4.8	x	0	0	0	0	0
	17	3008	63	55	0.11	16	11.1						

[a] Degree days (base 38.2°F) accumulated from March 1, 1979.
[b] Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 23, continued.

		Accumulated[a]	Temp.		Inches	Wind[b]			Pan Location				
Month	Day	Degree days	Max	Min	Precip.	Dir.	Speed	Visit	NW	NE	SW	SE	C
Aug.	18	3036	77	63	0.98	27	4.9						
	19	3066	80	52	T	11	4.3	x	0	0	0	0	0
	20	3091	68	53	1.32	10	7.8						
	21	3121	81	54	0.61	10	9.8	x	0	0	0	0	0
	22	3147	71	54		11	8.8						
	23	3181	80	66	1.13	19	9.4						
	24	3210	74	50	0.03	24	9.9						
	25	3233	77	44		26	8.2	x	0	1	0	0	0
	26	3258	79	42		15	4.9						
	27	3286	72	60		10	7.3						
	28	3316	80	54	0.31	19	5.8						
	29	3347	80	63	0.10	22	11.5	x	0	0	0	0	0
	30	3378	88	55	T	28	8.9						
	31	3412	88	57		16	7.6						
Sept.	1	3447	84	60		18	10.2						
	2	3488	80	60		22	10.9						
	3	3514	83	55		35	7.1	x	0	0	0	0	0
	4	3539	79	51		07	7.1						
	5	3567	86	49		19	4.9						
	6	3597	78	61		30	10.2	x	0	0	0	0	0
	7	3619	66	49		35	12.5						
	8	3633	65	33		01	6.6						
	9	3648	72	34		18	10.8						
	10	3670	76	60		18	13.7	x	0	0	0	0	0
	11	3701	82	54		12	10.4						
	12	3735	84	60		18	8.3						

[a] Degree days (base 38.2°F) accumulated from March 1, 1979.

[b] Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 24. 1979 Pan Trap Catches of Alate *Illinoia pepperi* and associated weather statistics. Field 54 A.

		Accumulated[a]	Temp.		Inches	Wind[b]			Pan Location				
Month	Day	Degree days	Max	Min	Precip.	Dir.	Speed	Visit	NW	NE	SW	SE	C
June	1	907	66	45		28	9.2	x	0	0	0	0	
	2	927	76	40		21	4.8						
	3	953	80	48		24	8.1						
	4	982	82	54		20	8.8	x	0	0	0	0	
	5	1011	78	55		35	7.3						
	6	1044	86	57		13	8.5						
	7	1077	77	65		16	10.9	x	0	0	0	0	
	8	1109	81	60	1.24	22	6.2						
	9	1136	71	60	0.85	19	4.3						
	10	1161	72	54	0.71	25	15.7	x	0	0	0	0	
	11	1178	68	41	0.10	29	6.9						
	12	1199	70	50		35	7.5	x	0	0	0	0	
	13	1222	78	43		12	7.3						
	14	1249	82	50		18	12.8						
	15	1289	88	67		20	18.7	x	1	0	0	0	
	16	1327	88	65		20	15.2						
	17	1353	70	58		28	14.7						
	18	1379	74	55	T	08	11.1	x	0	2	0	0	
	19	1407	84	48		12	15.1						
	20	1441	81	63		15	16.8						
	21	1474	78	64	0.79	22	11.8	x	0	0	0	0	
	22	1496	68	54		33	11.7						
	23	1509	60	42		35	11.2	x	0	0	0	0	
	24	1523	62	43		35	7.8						

[a] Degree days (Base 38.2°F) accumulated from March 1, 1979.

[b] Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 24 , continued.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
June	25	1545	83	36		16	7.2						
	26	1576	79	60		19	11.9	x	0	0	0	0	
	27	1607	85	52		22	9.1						
	28	1632	70	58	0.02	11	7.3	x	0	0	0	0	
	29	1660	75	56	0.91	06	8.5						
	30	1680	65	52	1.33	33	11.8	x	0	0	0	0	
July	1	1699	67	47	T	33	16.5						
	2	1725	76	53	0.02	32	9.8						
	3	1755	84	52		10	6.0	x	0	0	0	0	0
	4	1780	70	56	0.87	01	12.4						
	5	1796	70	40		34	9.1						
	6	1815	73	40		28	5.0						
	7	1841	87	42		25	3.5	x	0	0	0	0	0
	8	1870	84	58		17	4.5						
	9	1898	77	56		29	5.3						
	10	1926	77	56		21	6.8	x	1	0	0	0	0
	11	1962	86	62		25	4.9						
	12	1999	87	62		22	5.0						
	13	2035	88	62		19	5.8						
	14	2073	84	68		22	9.5	x	0	0	0	0	0
	15	2110	86	64		24	6.5						
	16	2143	82	60		34	10.4						
	17	2167	72	53		33	9.1	x	0	0	1	0	0
	18	2188	75	44		30	6.0						
	19	2213	82	43		23	4.6	x	1	0	0	0	0
	20	2238	82	45		22	6.5						
	21	2267	84	50		22	5.9						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 24, continued.

Month	Day	Accumulated[a] Degree days	Temp Max	Temp Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
July	22	2296	85	50		23	3.6						
	23	2333	85	65	0.13	20	6.0	x	0	0	0	0	0
	24	2371	82	71		18	13.8						
	25	2401	74	63	0.15	22	13.2						
	26	2431	76	59	T	30	9.1	x	1	0	0	0	0
	27	2462	84	55		21	7.2						
	28	2498	82	66	0.18	32	8.3						
	29	2531	84	58		31	7.2						
	30	2570	82	73		17	9.6	x	0	0	0	0	0
	31	2601	74	63	0.48	30	10.4						
Aug.	1	2630	71	62		04	8.5						
	2	2660	80	58	0.09	25	9.1	x	0	0	0	0	0
	3	2691	80	58		22	9.6						
	4	2724	84	58		19	8.8						
	5	2757	78	64	0.47	26	7.6						
	6	2788	80	58	0.53	09	7.8	x	0	0	0	0	0
	7	2823	85	63		22	11.9						
	8	2855	78	62		29	5.9						
	9	2889	84	61	0.09	17	11.1	x	0	0	0	0	0
	10	2922	76	66	2.10	30	13.7						
	11	2944	70	44		01	9.8						
	12	2963	72	43		19	7.5	x	0	0	0	0	0
	13	2988	67	60		21	14.7						
	14	3008	65	52	0.14	32	14.2						
	15	3029	68	49		33	11.1						
	16	3043	69	36		24	4.8	x	0	0	0	0	0
	17	3062	61	52	0.11	16	11.1						

[a] Degree days (base 38.2°F) accumulated from March 1, 1979.
[b] Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 24, continued.

		Accumulated[a]	Temp.		Inches	Wind[b]			Pan Location				
Month	Day	Degree days	Max	Min	Precip.	Dir.	Speed	Visit	NW	NE	SW	SE	C
Aug.	18	3091	75	61	0.98	27	4.9						
	19	3118	75	55	T	11	4.3	x	0	0	0	0	0
	20	3146	72	61	1.32	10	7.8						
	21	3178	81	58	0.61	10	9.8	x	0	0	0	0	0
	22	3206	73	60		11	8.8						
	23	3240	78	66	1.13	19	9.4						
	24	3266	70	59	0.03	24	9.9						
	25	3288	69	52		26	8.2	x	0	0	0	0	0
	26	3313	76	49		15	4.9						
	27	3337	64	61		10	7.3						
	28	3366	72	62	0.31	19	5.8						
	29	3398	75	65	0.10	22	11.5	x	0	0	0	0	0
	30	3430	79	62	T	28	8.9						
	31	3465	84	63		16	7.6						
Sept.	1	3500	82	64		18	10.2						
	2	3534	79	66		22	10.9						
	3	3564	79	57		35	7.1	x	0	0	0	0	0
	4	3591	75	56		07	7.1						
	5	3619	77	55		19	4.9						
	6	3650	75	63		30	10.2	x	0	0	0	0	0
	7	3672	64	57		35	12.5						
	8	3686	61	42		01	6.6						
	9	3703	69	42		18	10.8						
	10	3731	72	60		18	13.7	x	0	0	0	0	0
	11	3759	78	55		12	10.4						
	12	3790	80	59		18	8.3						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 25. 1979 Pan Trap Catches of Alate *Illinoia pepperi* and associated weather statistics. Field 281.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	Pan Location NE	Pan Location SW	Pan Location SE	Pan Location C
June	1	883	68	58	0.06	28	9.2	x	0	0	0	0	
	2	905	78	42		21	4.8						
	3	932	82	50		24	8.1						
	4	962	85	51	T	20	8.8	x	0	0	0	0	
	5	991	78	56	0.05	35	7.3						
	6	1024	86	56		13	8.5						
	7	1058	78	67		16	10.9	x	0	0	0	0	
	8	1094	85	63	0.90	22	6.2						
	9	1125	74	64	0.13	19	4.3						
	10	1151	72	56	0.66	25	15.7	x	0	0	0	0	
	11	1171	68	47	0.08	29	6.9						
	12	1194	72	52		35	7.5	x	0	0	0	0	
	13	1217	78	46		12	7.3						
	14	1246	82	52		18	12.8						
	15	1286	86	69		20	18.7	x	1	0	0	0	
	16	1324	88	66		20	15.2						
	17	1357	76	66		28	14.7						
	18	1383	74	55	T	08	11.1	x	0	0	0	2	
	19	1411	84	47		12	15.1						
	20	1444	78	64	T	15	16.8						
	21	1478	82	64	0.66	22	11.8	x	0	0	0	0	
	22	1504	72	56		33	11.7						
	23	1521	68	43		35	11.2	x	0	0	0	0	
	24	1542	72	46		35	7.8						

[a]Degree days (Base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 25, continued.

Month	Day	Accumulated[a] Degree days	Temp. Max	Temp. Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
June	25	1566	80	43		16	7.2						
	26	1595	79	56		19	11.9	x	0	0	0	0	
	27	1625	84	52		22	9.1						
	28	1652	71	60	0.05	11	7.3	x	0	0	0	0	
	29	1680	75	58	0.30	06	8.5						
	30	1711	77	60	0.47	33	11.8	x	0	0	0	0	
July	1	1734	67	57	0.02	33	16.5						
	2	1762	78	54		32	9.8						
	3	1794	80	61	T	10	6.0	x	0	0	0	0	0
	4	1823	76	59	0.32	01	12.4						
	5	1844	76	42		34	9.1						
	6	1869	81	46		28	5.0						
	7	1896	82	48		25	3.5	x	0	0	1	0	0
	8	1927	84	55		17	4.5						
	9	1961	84	61		29	5.3						
	10	1990	77	56		21	6.8	x	0	0	0	1	0
	11	2026	88	62		25	4.9						
	12	2065	91	63		22	5.0						
	13	2103	88	64		19	5.8						
	14	2142	86	68		22	9.5	x	0	0	0	0	0
	15	2182	90	66	T	24	6.5						
	16	2214	82	60		34	10.4						
	17	2244	80	56		33	9.1	x	0	0	0	0	0
	18	2270	81	48		30	6.0						
	19	2299	85	48		23	4.6	x	0	0	0	0	0
	20	2328	86	49		22	6.5						
	21	2358	83	53		22	5.9						

[a]Degree days (base 38.2°F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 25, continued.

Month	Day	Accumulated[a] Degree days	Temp Max	Temp Min	Inches Precip.	Wind[b] Dir.	Wind[b] Speed	Visit	Pan Location NW	NE	SW	SE	C
July	22	2392	88	56		23	3.6						
	23	2430	91	62	0.05	20	6.0	x	0	0	0	0	0
	24	2464	78	67		18	13.8						
	25	2497	74	67		22	13.2						
	26	2529	84	57		30	9.1	x	0	0	0	0	0
	27	2562	88	55		21	7.2						
	28	2600	86	66	0.10	32	8.3						
	29	2634	89	55		31	7.2						
	30	2666	82	58		17	9.6	x	0	0	0	3	0
	31	2701	80	67	0.85	30	10.4						
Aug.	1	2730	72	62		04	8.5						
	2	2761	80	59	0.03	25	9.1	x	0	0	0	0	0
	3	2794	82	60	T	22	9.6						
	4	2828	84	61	T	19	8.8						
	5	2861	80	62	0.25	26	7.6						
	6	2891	80	57	0.23	09	7.8	x	0	0	0	0	0
	7	2927	84	64		22	11.9						
	8	2960	79	64		29	5.9						
	9	2994	82	62		17	11.1	x	0	0	0	0	0
	10	3025	80	58	1.01	30	13.7						
	11	3050	74	52		01	9.8						
	12	3070	72	45		19	7.5	x	0	0	0	0	0
	13	3092	64	57	T	21	14.7						
	14	3114	66	53	0.15	32	14.2						
	15	3130	65	45		33	11.1						
	16	3145	69	36		24	4.8	x	0	0	0	0	0
	17	3163	61	52	0.18	16	11.1						

[a] Degree days (base 38.2°F) accumulated from March 1, 1979.
[b] Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

Table 25, continued.

		Accumulated[a]	Temp.		Inches	Wind[b]			Pan Location				
Month	Day	Degree days	Max	Min	Precip.	Dir.	Speed	Visit	NW	NE	SW	SE	C
Aug.	18	3194	76	61	0.60	27	4.9						
	19	3220	75	54		11	4.3	x	0	0	0	0	0
	20	3248	72	61		10	7.8						
	21	3279	81	58	1.15	10	9.8	x	0	0	0	0	0
	22	3308	73	60		11	8.8						
	23	3342	78	66	0.70	19	9.4						
	24	3368	70	59	0.21	24	9.9						
	25	3390	69	52		26	8.2	x	0	0	0	0	0
	26	3414	76	49		15	4.9						
	27	3439	64	61		10	7.3						
	28	3468	72	62	0.83	19	5.8						
	29	3499	75	65	0.03	22	11.5						
	30	3534	82	63		28	8.9	x	0	0	0	0	0
	31	3568	84	61		16	7.6						
Sept.	1	3602	80	65		18	10.2						
	2	3639	82	68		22	10.9						
	3	3669	80	57		35	7.1	x	0	0	0	0	0
	4	3697	77	55		07	7.1						
	5	3727	81	56		19	4.9						
	6	3760	82	60	T	30	10.2	x	0	0	0	0	0
	7	3781	64	54		35	12.5						
	8	3797	66	42		01	6.6						
	9	3816	71	43		18	10.8						
	10	3842	72	60		18	13.7	x	0	0	0	0	0
	11	3872	78	55		12	10.4						
	12	3903	80	59		18	8.3						

[a]Degree days (base 38.2° F) accumulated from March 1, 1979.

[b]Resultant wind direction in tens of degrees clockwise from true north; average wind speed in m.p.h.

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