EXPLOITATION OF SEASONAL DEVELOPMENT AND SEMIOCHEMICALS FOR THE REFINEMENT OF PEST MANAGEMENT PROGRAMS INVOLVING THE MULLEIN BUG, *CAMPYLOMMA VERBASCI* (MEYER) AND PEAR PSYLLA, *PSYLLA PYRICOLA* FOERSTER.

BY

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ABSTRACT

Successful pest management is dependent on reliable methods of predicting pest populations above the economic threshold. Research designed to facilitate the improvement of predictive methodology was conducted on two pome fruit pests. The mullein bug, Campylomma verbasci (Meyer) (Heteroptera: Miridae) was established on eggplant in a laboratory colony. Females lived 17.4 ± 0.8 days (x ± S.E.), laid 50% of their eggs within the first 12 d and averaged 39 fertile eggs. Hatch first occurred after 9, 7, 6 and 5 d, at 20°, 22°, 25° and 27°C, respectively. Nymphal body dimensions allowed for discrimination between instars. Durations required after 1 January for 100% hatch of C. verbasci eggs in the Okanagan Valley of B.C. varied by 21 d from 1986 to 1988. This duration did not differ among six host apple varieties, or by tree quadrant. Live-caged females attracted males to sticky traps. In apple trees, traps hung at 4 and 5 m caught more males than did those at 1, 2 and 3 m. Catches of males in female-baited traps in the autumn were highly correlated with nymphal densities the following spring. Male bugs responded to fractionated female crushes and to Porapak Q-collected volatiles. Gas chromatography of female volatiles disclosed that butyl and hexyl butyrate were main volatile components, but were unattractive to males. A lure comprised butyrate and crotyl butyrate equalled the attractiveness of live-caged females.

The estimated lower developmental threshold for in both overwintering and nondiapausing summer eggs of C. verbasci was determined to be 10°C. A simple degree-day model was written and tested for three years and 31 orchard sites. It was more reliable than mean days since 1 January, or current agricultural extension recommendations, in determining the appropriate timing for limb-tap sampling. Female winter-form pear psylla, Psylla pyricola Föerster (Homoptera: Psyllidae), responded positively in a two-choice static air olfactometer to the odour of 'Anjou' pear buds. Both winter and summer-form male psyllids responded positively to the odour of live females and pentane-based extracts of females. Both female seasonal morphs were attractive to winter form males; females were not attracted to males.

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1. GENERAL INTRODUCTION

1.1. The Impact of Orchard Pests

Since the beginning of agriculture, man has been in direct competition with insects for both food and fiber. In North America many cultivated plants were introduced from Europe, often with accompanying pests but without the pests' natural enemies. A further complication has been the expansion of the host range of native insects to include commercial crops. In orchards this phenomenon has been documented for the apple maggot, Rhagoletis pomonella (Walsh) (Bush 1969) and the roundheaded apple tree borer, Saperda candida Faber (Davidson and Lyon 1979). Under favourable climatic conditions insect numbers have shown remarkable increases despite efforts to eradicate or suppress the numbers. In 1974 insect-caused losses to agricultural products in North America were estimated at $25 billion (U.S.) plus an additional $5 billion spent on control measures (Ross et al. 1982).

In Canada, from 1960 to 1980, pest control in apple orchards cost $22 million annually (1980 dollars), with approximately 46% accounted for by pesticides (Stemeroff and George 1983); however, in a somewhat different perspective, pesticides (including application costs) represent only an estimated 6.5% of total production costs of apples in British Columbia (B.C.) (Geldart 1986) and 12% in Nova

Scotia (Benard 1988). In the western United States orchard pest control, as a percent of fruit production costs, is reported at ca. 6% and 18% of $1320 and $1097 per ha for Washington and Oregon State, respectively (Croft and Hull 1983).

1.2. Development of Integrated Pest Management in Orchards

Because pesticide sprays represent a small portion of total costs, there is a natural tendency to apply prophylactic treatments as insurance against possible crop loss. However, mounting concerns for personal and environmental poisoning, development by pests of resistance to pesticides, and ever-increasing costs of production have led toward acceptance of integrated pest management (IPM).

> "IPM is a feedback and feedforward process based on environmental monitoring, biological monitoring, pest modelling, and a communication and delivery system." (Whalon and Croft 1984)

In the 1600's, the first permanent settlers to the Atlantic coast of North America brought fruit trees accompanied by associated arthropods. As orchards flourished and developed into commercial ventures, growers struggled to control the destructive pests. In Nova Scotia's Annapolis Valley, organized research efforts into chemical pest control began in 1918, although as early as 1907 insect outbreaks were reported (MacLellan 1985).

The initial successes of botanical insecticides (e.g. nicotines, pyrethrin and rotenone) were upstaged by first, organic insecticides (e.g., dinitro compounds), then DDT and other chlorinated hydrocarbons in the 1940's. The years following World War II saw the adoption of a proliferation of organophosphates including parathion, malathion and diazinon, and in 1947 a new class of pesticides, the carbamates. These were followed by synthetic pyrethroids and current day "fourth generation" pesticides that include insect hormone analogues, other growth regulators, and pheromones. The evolution of orchard pest management is typified by the Nova Scotia experience about which Pickett et al. (1946) write:

> 'In Nova Scotia, as elsewhere, the economical control of apple orchard insects is becoming progressively difficult. During the early part of this century, fruit of good quality was produced with 2 or 3 applications of spray applied with hand-operated pumps. Today [1946] with greatly improved equipment and spray chemicals, 6 to 10 applications are required to produce crops reasonably free of insect damage. For the most part, the species of insects now creating the major control problem were of minor importance in the earlier days.'

Clearly there was a need for long-term studies to determine the impact of pesticides on all orchard arthropods. In Nova Scotia these investigations led to the implementation of an outstanding IPM program. The IPM concept today has progressed from 'pesticide management' to include monitoring of pest populations and the use of

selected chemical, physical and biological agents as part of a systems approach to suppress pests below a predefined economic threshold.

In New York state, growers adopting IPM reduced apple orchard sprays by 30% for insecticides, 47% for miticides and 10% for fungicides, yielding an average annual saving of \$95.80 ha^{-1}. They applied 235 kg less active ingredient ha^{-1} than under their past practices, and pest damage was held to an economically acceptable level (Kovach and Tette 1987). The same study revealed that approximately 80% of the state's 1,200 apple growers used some component of IPM.

1.3. Economic Threshold and Economic Injury Level

Paramount in establishing a workable IPM approach is the concept of "economic threshold" or "action threshold" for each pest species. The economic threshold is the density at which control measures should be applied to prevent a pest population from reaching an economic injury level (Stern et al. 1959). The economic injury level is the lowest possible density that will result in economic damage (i.e., crop loss) (Hoyt and Tanigoshi 1983).

Often overlooked is the need for quantitative studies regarding the functional relationship between crop loss and pest density. A comprehensive knowledge of the key pest species and its interaction with other arthropods

(predators, prey, and competitors) in the habitat is required; also rapid assessment of pest population levels is vital in forecasting trends. This assessment depends in turn on the sampling techniques and associated methodologies involved in arthropod monitoring, often unique to each arthropod species and geographical area. For example, in assessing populations of fruit-stinging mirids, the limb-tap technique is used in Nova Scotia, Quebec, Ontario and British Columbia. However, the number of samples per ha and the economic threshold vary between apple growing regions (Whalon and Croft 1984). Similarly, a sex pheromone trap is widely used for detection and determination of damaging numbers of codling moth, yet most production areas have established their own economic thresholds based on long-term experience under local conditions (Hoyt et al. 1983).

Monitoring per se is generally of little value unless data are available on the economic threshold and injury level, because only then does monitoring lead to prediction capability. To be incorporated into an IPM system, monitoring must meet three basic requirements: 1) it must be economical, 2) it must be relatively easy to use, and 3) it should provide a reasonably precise estimate of density and/or distribution of critical stages of the target pest.

1.4 The use of Semiochemicals in Orchard IPM

An increasingly important component of orchard IPM is the role played by message-bearing chemicals, or semiochemicals, in predicting and manipulating arthropod density. During the past decade many of these products have been isolated, identified and synthesized. Yet a general lack of knowledge regarding their fundamental biological role as well as incomplete knowledge of the pheromones used by certain key pests have impeded maximizing their true potential in IPM systems.

Sex pheromones have held much promise as a component of IPM within pome fruit ecosystems. Roelofs (1981) lists 20 fruit pests for which sex pheromones are identified. Few have been developed beyond mere detection tools, although the sex pheromone of the codling moth, Cydia pomonella L., is now routinely used as a monitoring tool to provide reliable data on which pest management decisions are made (Madsen 1981).

Three general areas of application of sex pheromones hold promise in orchard pest management: 1) monitoring of pest populations, 2) mass trapping of pest species, and 3) mating disruption. For successful implementation of each, an intimate knowledge of a species' pheromone chemistry, emission rates, periodocity of emission, perception mechanisms and behavioural response is required. Attempts

to use pheromone-baited traps to predict insect density and potential economic damage exposes our meager knowledge. Although experimentation often brings forth more questions than answers, experimental science is rapidly leading to an improved knowledge of basic biology and behavioural ecology of pest insects, and concurrently to an improved chance of incorporating pheromones effectively into IPM systems.

1.5. Temperature-Based Predictive Models

In addition to direct monitoring methods that sample the pest or its damage, the predictive capability of an IPM system may rely on an indirect monitoring method such as the use of phenological predictive models (Tauber et al. 1986). For example, management of the codling moth in B.C. involves the use of pheromone trap captures to set a "biofix" that initiates a degree-day predictive model (B.C. Ministry of Agriculture and Fisheries 1989). The model is used to generate predicted moth captures which in turn are known to be correlated with the economic injury level. Thus, the model is used to determine if and when treatments will be needed in a particular orchard.

The physiological-time or degree-day approach is frequently used to forecast pest phenology although the concept was first widely used by horticulturalists in predicting crop development (Arnold 1974). For the sake of simplicity, degree-day models assume that development and

other functions are mainly temperature-dependent and linear in relationship. Prominent in temperature-based models is the need to determine the lower threshold for development. Deriving an appropriate threshold is typically accomplished through incubation of post-diapause insects at several constant temperatures under appropriate environmental conditions. Regression analysis is performed on the linear portion of development rate data to determine the threshold temperature (X-intercept). The number of degree days above the threshold temperature required for complete development can be estimated by taking the reciprocal of the slope value (Whitfield 1984).

1.6. Thesis Objectives

Research was initiated and driven by voids in current knowledge and the pest status of two sucking insect pests of pome fruits in the Okanagan Valley of B.C., the mullein bug Campylomma verbasci (Meyer) (Heteroptera: Miridae) and the pear psylla Psylla pyricola Föerster (Homoptera: Psyllidae). In order to provide continuity in research programs, pioneering investigations on Psylla pyricola were initiated. The overall objective was to develop methods of predicting pest population levels for both species so that IPM systems could be refined and improved.

Semiochemicals were investigated for both species. The mullein bug was known to use a sex pheromone (Thistlewood

1986) and the research addressed two objectives: 1) the isolation, identification and bioassay of the pure sex pheromone and 2) testing the hypothesis that sex pheromone could be used as a predictive tool in an IPM system. Little was known about semiochemicals in the pear psylla. Thus basic research was initiated to test the hypothesis that pheromone-based communication occurred in this species with the ultimate objective of eventually developing semiochemicals into predictive tools as for the mullein bug.

For the mullein bug, limb-tap sampling had been developed as an effective assessment tool for nymphal population levels in the spring (Thistlewood et al. 1989). However, the efficacy of this tool was limited by several factors including the short time between sampling of neonate nymphs and the actual occurrence of damage to newly set fruit. Therefore, an additional objective for this species was to develop an indirect predictive tool; i.e., a temperature-based phenological model that could be incorporated into a refined IPM system. In support of both semiochemical and phenological model research on the mullein bug, supplementary studies were initiated on the rearing methodology, basic biology and development, and behavioural aspects of responses to field traps.

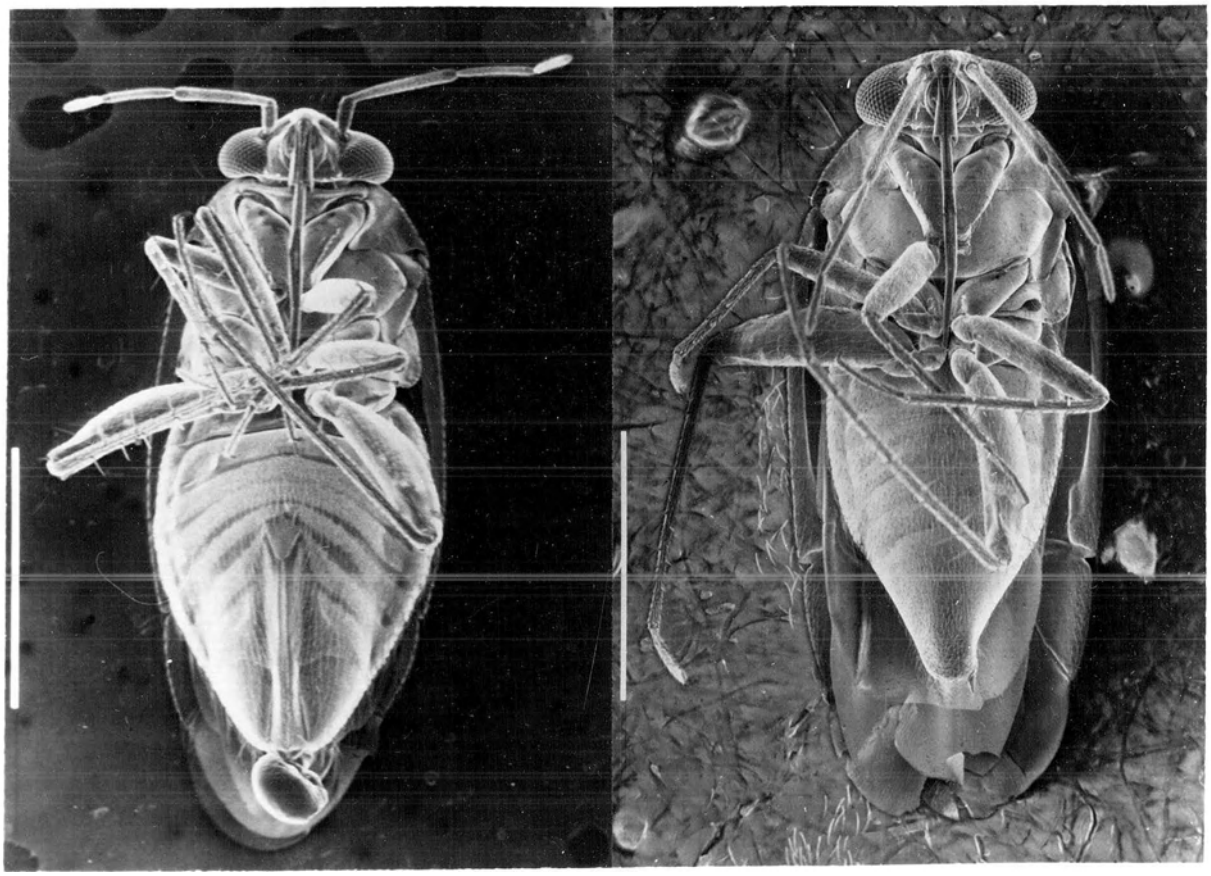
2. THE MULLEIN BUG, Campylomma verbasci

2.1. General Introduction

The mullein bug (Fig. 1) is an introduced insect that is one of over 80 mirid species in 30 genera in Canada (Kelton 1982). Knight (1941) reports C. verbasci originated in Europe and was introduced into eastern North America many years ago. In 1930 Gilliat (1935) observed this bug feeding on european red mite, Panonychus ulmi (Koch), in Nova Scotia orchards. At that time it was considered neither pest nor predator of any significance, possibly as a result of abundant prey and robust apple varieties. Erratic outbreaks of damage in the late 1930's (Pickett 1941) established its reputation as a pest on the apple varieties 'Red Delicious' and 'Northern Spy'. In later years a second fruit-stinging mirid, Atractotomus mali (Meyer) became established in Nova Scotia resulting in a two-species, "stinging bug complex" (Hardman et al. 1984, Whitman and Craig 1989). Elsewhere in Canada C. verbasci is a serious but sporadic pest, both in Ontario (Goble 1972) and B.C. (Thistlewood 1986).

Damage to sensitive apple varieties occurs when first generation nymphs puncture and feed on fruitlet juices, inducing a physiological reaction that results in corky tissue formation, dimples and pits and the downgrading of the fruit to cull status. In southwestern Quebec

Figure 1 Scanning electron micrographs of adult *C. verbasci*, ventral view: female (left) and male (right).



C. verbasci hatch after fruit set and the fruitlets may be too well developed for the nymph to damage them (Boivin and Stewart 1982a).

In the Okanagan Valley there are three or four generations of mullein bugs per year (McMullen and Jong 1970). The summer months are spent on its principal herbaceous host, common mullein, Verbascum thapsus L. After two complete generations on this plant, adults migrate to woody host plants to oviposit overwintering eggs in the bark (McMullen and Jong 1970); in agricultural areas this movement is mainly to fruit trees. Little is known of the cues and possible kairomonal stimuli involved in fall migration to orchards, although mere proximity to V. thapsus can be a factor (Thistlewood 1986).

The overwintering eggs pass through a true diapause; hatch will not occur if eggs are brought from the field prior to mid-December. With the approach of spring embryonic development accelerates. Typically, first generation egg hatch occurs during the 'bloom' through 'calyx' stages (Thistlewood 1986) of apple development. Neonate nymphs are translucent and measure ca. 0.65 x 0.25 mm (length x width). Prey are necessary for survival of early instars and within a few hours of hatch these nymphs feed on overwintering european red mite eggs (personal observation). It remains unclear what role, if any, prey

abundance has on deposition of overwintering eggs and intensity of fruitlet damage the following spring. Sanford (1964a) suggests that a correlation may exist between prey density and fruit damage caused by the apple brown bug, A. mali in Nova Scotia orchards.

Management of C. verbasci is currently based on economic thresholds or injury levels that correlate density of nymphs in the spring with subsequent fruit damage, primarily on sensitive varieties 'Red Delicious' and 'Golden Delicious' (Whalon and Croft 1984, Thistlewood et al. 1989). Sampling for mullein bug is done using a cloth-covered tapping tray onto which nymphs are jarred from the fruit tree branches (Hardman et al. 1984, Washington State University 1988, Thistlewood and McMullen 1989). Although this technique often gives reliable predictions (Thistlewood et al. 1989), the method has several serious shortcomings: 1) it is time consuming and requires many samples per ha for reliable prediction, 2) it requires that sampling be done when most eggs have hatched, yet hatch varies considerably between years, 3) there is often little time between egg hatch and the occurrence of economic damage, 4) adverse weather during the sampling period can not only disrupt hatch but also the sampling routine, 5) it is the only means of determining bug density within an orchard, so all sites must be sampled, including those which ultimately show sub-economic levels of nymphs, and 6) samples may contain nymphs

of several species that can be easily misidentified by inexperienced personnel.

Therefore, my objective was to conduct research that would lead to alternative and effective predictive systems that could replace or supplement limb tap sampling in IPM for the mullein bug.

2.2. Aspects of *C. verbasci* biology

2.2.2. Effect of Cultivars, Orchard Site and Tree Quadrant on Overwintering Egg Hatch

2.2.1.1. Introduction

Two alternate techniques to the limb-tap sampling method have been proposed: 1) collection of fruit wood samples for incubation, assessment of numbers of hatching nymphs, and prediction of bug density in the field (MacPhee 1976), 2) visual stimuli traps (Boivin et al. 1982, Thistlewood 1986). Neither method has been widely accepted for monitoring mirids and, unless further information is available, there is little hope for their eventual use as efficient, reliable tools. Moreover, there are necessary assumptions made for the limb tap sampling method that are not yet based on sound research. For example, there is no prediction tool to determine completion of hatch; orchards must be checked two or more times to be certain that sampling is truly portraying nymphal density. This extra

sampling can require considerable time under present recommendations of 50 limb taps per ha. The sequential sampling scheme developed by Thistlewood (1986) may overcome this shortcoming in part once it has been operationally tested.

The hatching dates of overwintering eggs can vary considerably from one year to the next. McMullen and Jong (1970) suggested that overwintering eggs enter a true diapause and, only after sufficient chilling followed by warm temperature, will hatch occur. On pear in the Okanagan Valley, they report that field hatch is normally complete within one week, while in Poland hatch extends over two weeks (Niemczyk 1978), commencing a few days before bloom. Jonsson (1985) reported that C. verbasci begin to hatch just prior to bloom in the variety 'Cox Pomona' in Norway.

In 1988 in addition to monitoring development on woody plants, weekly observations were made on bug abundance in common mullein to ascertain dynamics in the Okanagan Valley. Abundance and timing of a late summer generation could influence the intensity of oviposition by C. verbasci on fruit trees in the fall.

Other assumptions have not been addressed adequately; for example, is the rate of egg hatch the same regardless of apple variety? Presently, all varieties are sampled at the same time. Campylomma verbasci are present in all apple

varieties (Pickett 1938, Thistlewood 1986) and are considered to be a beneficial predator in pear (McMullen and Jong 1970). 'Red Delicious' and 'Golden Delicious' are the most sensitive to feeding injury, but occasionally economic damage results on other varieties (e.g., 'Northern Spy', 'Spartan' and 'McIntosh'). Field observations indicate that damage is not always density-related and it remains unknown what induces the nymph to attack the fruit.

In this study, detailed hatch records were taken both under laboratory and field conditions to determine if significant inter-varietal differences exist.

A second question pertains to the possible effect of tree quadrant sampled on field hatch in the spring. Solar radiation during the winter is known to be disproportionate on fruit tree wood with the southwest portion of the tree occasionally encountering structural damage from extreme temperature contrasts of day and night. Detailed field hatch records were taken in spring 1988 and tree quadrants compared to establish whether egg hatch was significantly influenced by tree quadrant.

2.2.1.2. Materials and Methods

Field development time. In the winter of 1986-1987, 12 - 15 sections of fruit wood 30 - 40 cm long were cut from all quadrants of 5 -8 'Red Delicious' apple trees in a

standard orchard block at the Agriculture Canada Research Station, Summerland, B.C. Samples were taken on 3 December 1986 and on six subsequent dates. Cuttings were incubated in an environmental cabinet under a 16:8 h L:D photoperiod (37.9 μ $Es^{-1}m^{-2}$, 3018 lux) at 22° ± 0.5°C and checked daily for neonate C. verbasci.

In the fall of 1987 a 25 x 25 m field was planted with common mullein rosettes, transplanted in a 2 x 2 m grid. These were well rooted and established by late autumn, and the following spring through fall were monitored at 7 d intervals for C. verbasci abundance. Adult bugs were counted on each of five randomly chosen plants.

Cultivars. Field hatch of C. verbasci was monitored in two orchard blocks during 1987 and 1988 at the Agriculture Canada Research Station, Summerland, B.C. Limb-tap sampling was conducted at 24 h intervals on randomly chosen limbs of known apple varieties grown in the same orchard site. Both orchards were ca. 20 years old, grown on semi-dwarf rootstock and maintained under typical horticultural management without pesticides. Block A was located on level bench land, elevation 455 m, and block B on a delta at lakeside, elevation 339 m.

Effect of Orchard Site on Overwintering Egg Hatch. In 1988, field hatch of C. verbasci overwintering eggs was monitored by the limb tap method in three geographical areas

within the B.C. interior, spanning a distance of approximately 200 km in a north-south direction. Twenty-five to 30 individual branches of 'Red Delicious' apples were tagged and limb tapped at 24 h intervals throughout the field hatch period. Daily maximum and minimum temperatures were recorded at each site using thermometers set within Stevenson screens. Mean rate of hatch was compared within orchard sites.

Influence of Tree Quadrant on Rate of Field Hatch. Prior to C. verbasci hatch in 1988, five limbs were randomly picked and tagged on each of five fruit trees in two orchards. One orchard was a mature (> 20 years old) standard rootstock planting of 'Spartan' located at Winfield, the second a 10-year-old, semi-dwarf block of 'Golden Delicious' at the Agriculture Canada Research Station, Summerland, B.C. Branches were limb-tapped at 24 h intervals throughout the hatching period, concluding when five days elapsed with no further nymphs collected. Quadrants of the trees were assigned a directional status relative to true magnetic north. Mean rates of hatch by quadrant were compared after arcsine transformation of data (Least Significance Test, SAS 1985).

2.2.1.3. Results and Discussion

Field development time. In the winter of 1986-1987, eggs sampled from the field on 3 and 15 December 1986 did

not hatch when incubated at 22°C for 40 days, while subsequent collections on and after January 11, 1987 hatched. There was a progressive reduction in days required to complete hatch as the season progressed (Fig. 2). The data suggest that embryonic development occurs during the post-diapause period. They imply that diapause had been broken between mid-December and 11 January in agreement with the observation made by McMullen and Jong (1970) that eggs enter a true diapause which in the British Columbian interior is not broken before mid-December.

The date of first hatch by C. verbasci in the Okanagan Valley differed by 21 days during 1986-1988 (Table 1). Duration of the total hatching interval ranged from 8 to 19 days. In 1988 hatch had begun 7 d prior to full bloom.

In 1988 there were two generations of C. verbasci on mullein in the Okanagan Valley of B.C. (Fig. 3). The first peak of adults by mid-June represented adults that migrated from fruit trees and other woody hosts. Numerous teneral bugs were found aggregating on elongating mullein flower stalks, even before flowers were in bloom. By late July a second generation peaked, followed by a third extended generation in late August through mid-September. Adults

Figure 2 Advancement of the pre-eclosion period in a sequence of field samples from 'Red Delicious' apple wood infested with overwintering C. verbasci eggs, Summerland, B.C., 1987. Each cumulative hatching curve identified by sampling date.

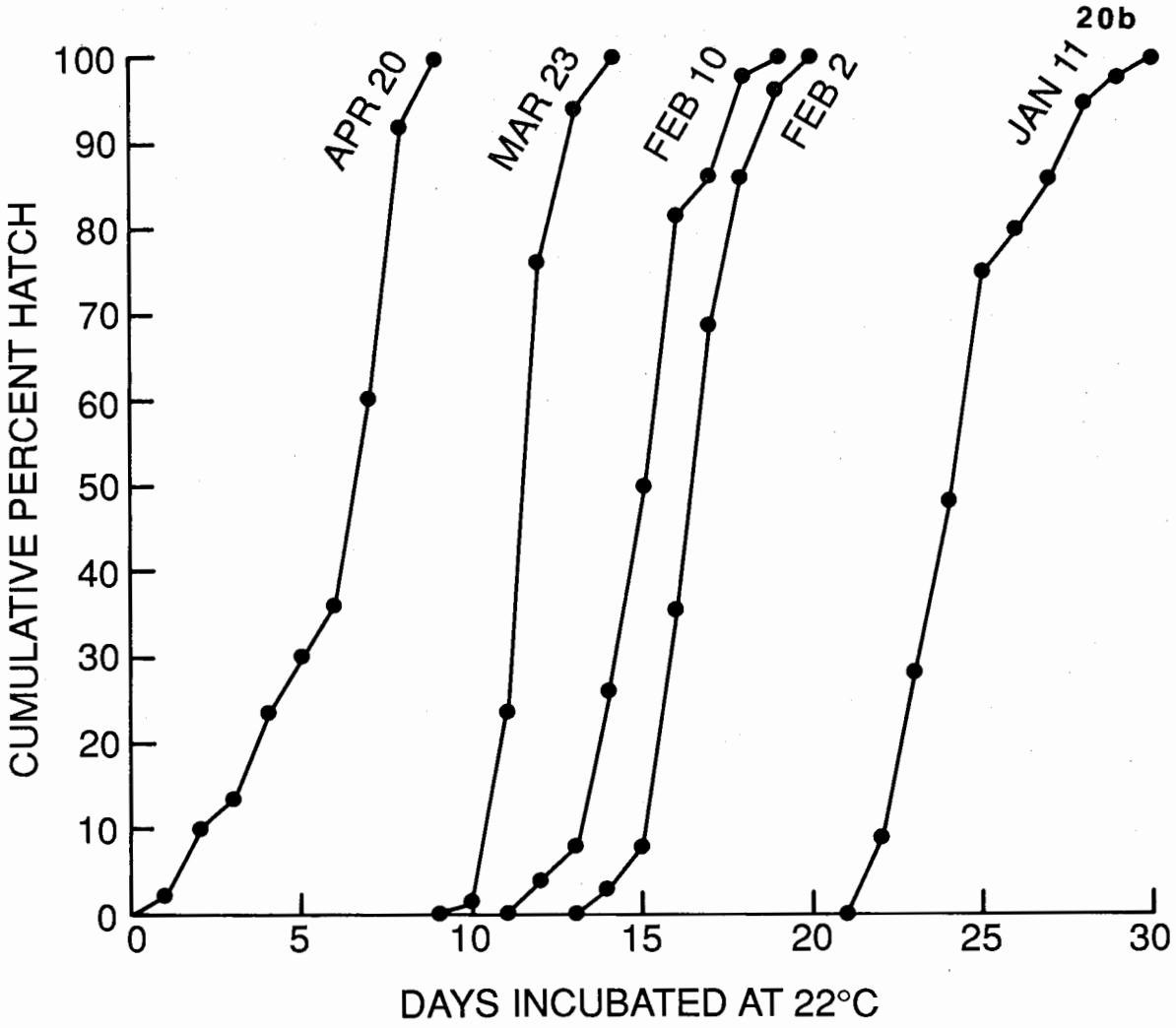
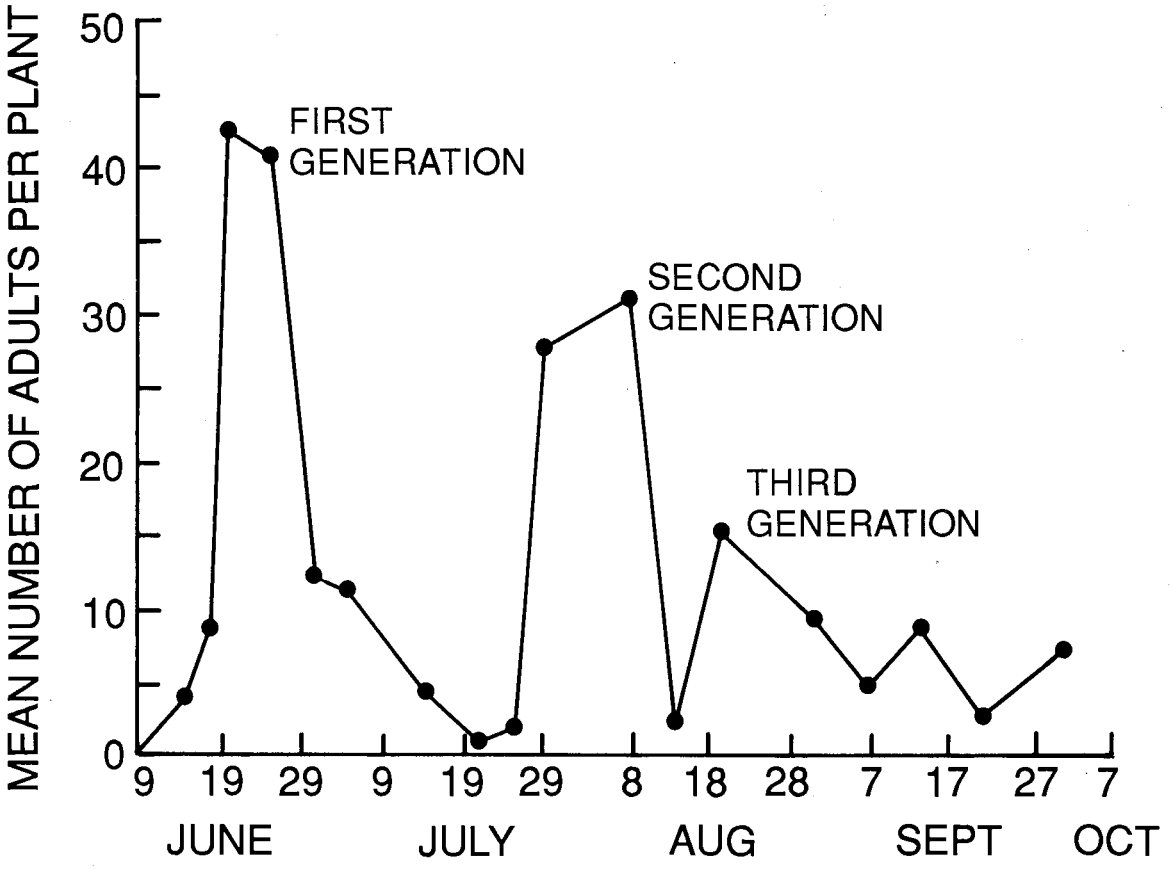

20b
CUMULATIVE PERCENT HATCH
100
90
80
70
60
50
40
30
20
10
0
APR 20
MAR 23
FEB 10
FEB 2
JAN 11
0
5
10
15
20
25
30
DAYS INCUBATED AT 22°C

Table 1 Field hatch of overwintering C. verbasci in 'Red Delicious' apples, Summerland, B.C. based on limb-tap samples taken at 24 h intervals on the same limbs (within years) and orchard site over three years.

	Date of full bloom		Days from 1 January at which hatching stage reached				
Year	Calendar date	Days from 1 January	First hatch	50% hatch	90% hatch	100% hatch	Total number of nymphs
1986	15 May	135	140	148	150	155	62
1987	30 Apr	120	126	129	132	134	154
1988	6 May	126	119	132	137	138	30

Figure 3 Abundance of adult C. verbasci on common mullein in the Okanagan Valley of B.C. showing three generations in 1988, the first having migrated from woody hosts and the next two having developed on mullein. Each data point is the mean adult population on five plants.


MEAN NUMBER OF ADULTS PER PLANT
50
40
30
20
10
0
FIRST GENERATION
SECOND GENERATION
THIRD GENERATION
9 19 29 9 19 29 8 18 28 7 17 27 7
JUNE
JULY
AUG
SEPT
OCT

from this third generation fed for a short time on mullein, then left to deposit overwintering eggs in woody hosts. Limb-taps of adjacent orchards confirmed their movement as mature, dark-colored adults to the trees; few tenerals were taken on limb-taps or in pheromone traps that were being evaluated in orchard lands. Madsen and Proctor (1982) report at least three generations of mullein bug in the Okanagan Valley; adults migrated to woody hosts by mid-September. It is the females of this migrating generation that oviposit overwintering eggs in the fruit wood; subsequent hatch of these eggs the next spring yields nymphs that can inflict economic injury to sensitive apple varieties.

Sampling the orchard blocks during the autumn flight period may yield density data that would correlate with nymphal numbers the upcoming spring. If this were proven, then prediction could be made several months prior to the actual period when damage occurs. The limb-tap technique is not particularly suited to sampling adult bugs (Thistlewood 1986) and the rapid flight of the jarred insects could result in underestimated numbers. The known existence of a sex pheromone for C. verbasci (Thistlewood et. al 1989) may allow pheromone-based monitoring of this insect.

Cultivars. Overwintering eggs of C. verbasci hatched sooner from 'Anjou pear' than 'McIntosh' in 1987, and

'Golden Delicious' in 1988. (Table 2). Mean developmental times for both orchard sites differed by less than 3 d between years; within years there was no difference among mean hatch values from different apple varieties. Frequency distributions of field hatch showed a general unimodal trend over the four varieties (Fig. 4).

These data indicate that the limb-tap sampling method should be an equally suitable monitoring tool, regardless of apple variety sampled. The sampling period in pear may allow some fruit damage to occur before economic injury is predicted, but pear has a higher tolerance to bug feeding and, in B.C., little damage is encountered if limb-tap counts are less than 15 nymphs per tray (B.C. Min. of Agric. and Fish. 1989).

Effect of orchard site on overwintering egg hatch. Osoyoos in the southern end of the Okanagan Valley in B.C. showed advanced hatching of overwintering C. verbasci eggs compared to the Summerland and Winfield areas (Table 3). Egg hatch was complete in Osoyoos before 50% hatch occurred in the Summerland or Winfield areas. Fruit tree advancement followed a similar trend (personal observations) with 'full bloom' of 'Red Delicious' first noted on days 110, 122, and 129 respectively, for Osoyoos, Summerland and Winfield.

Table 2 Ranked days from 1 January in 1987 and 1988 for 100% field hatch of overwintering C. verbasci eggs from five fruit varieties in two orchard sites, Agriculture Canada Research Station, Summerland, B.C.

Sample Site	Year	Variety	No. nymphs in sample	Days from 1 January Mean	95% C.I.
Block A elev. 455 m	1987	Anjou pear	183	127.7	127.3-128.1
		Spartan	342	127.8	127.4-128.2
		McIntosh	441	128.7	128.5-128.9
	1988	Anjou pear	59	128.8	127.1-130.5
		McIntosh	85	130.2	129.1-131.3
		Spartan	64	130.2	128.8-131.6
		Red Delicious	57	130.5	128.8-132.2
		Golden Delicious	142	131.9	131.1-132.7
Block B elev. 339 m	1987	Newtown	52	132.1	131.5-132.6
		Spartan	66	132.3	131.4-132.9
		Red Delicious	97	132.6	132.2-133.0
		McIntosh	105	132.8	132.3-133.3
	1988	McIntosh	24	129.6	128.0-132.2
		Spartan	29	130.2	127.9-132.5
		Red Rome	36	130.6	128.8-131.4
		Red Delicious	44	131.6	130.0-133.2
		Newtown	38	131.7	129.8-133.6

Figure 4 Frequency distribution for field hatch of overwintering C. verbasci eggs in four apple varieties in one orchard site, spring 1987, Summerland, B.C.

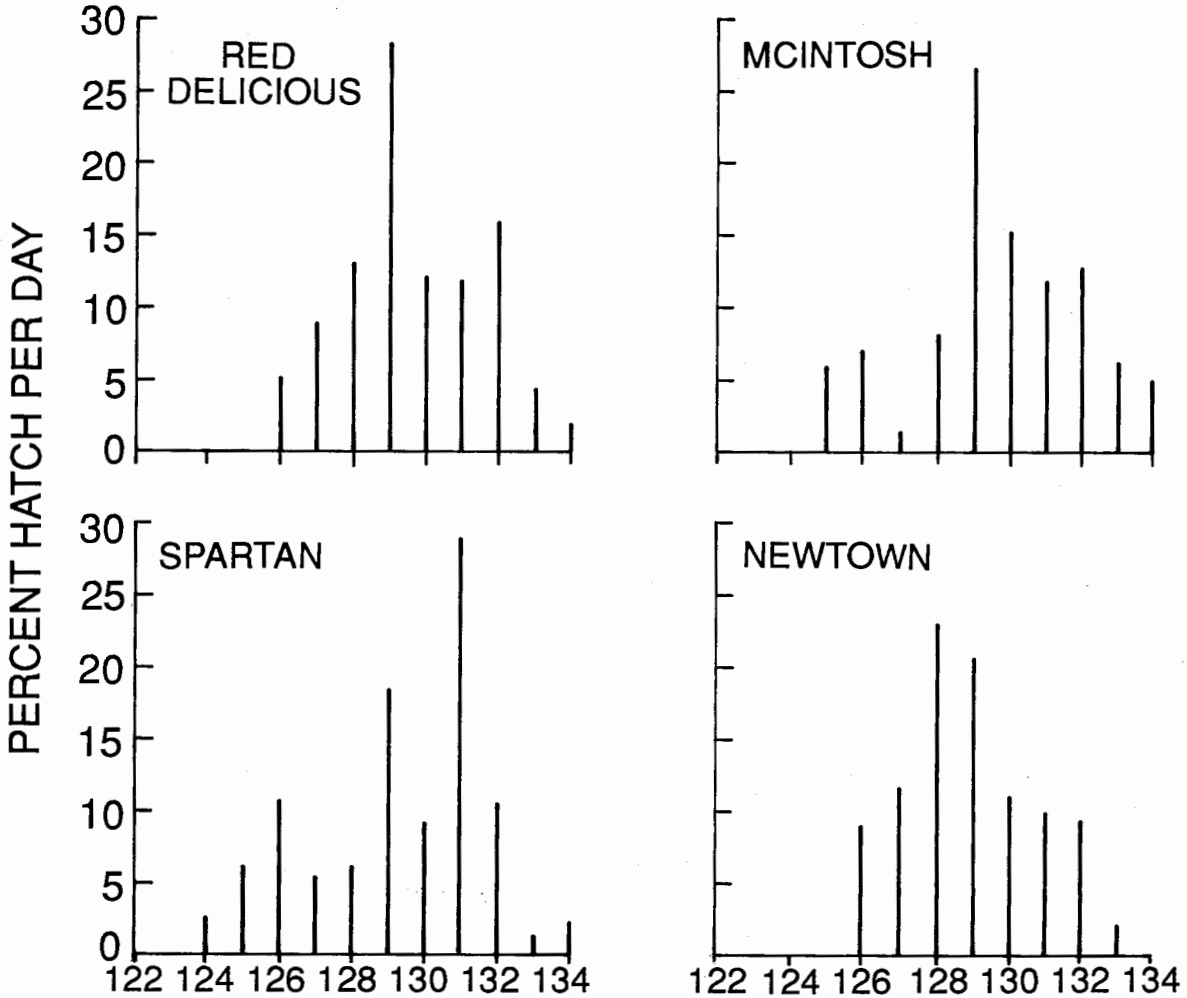

RED DELICIOUS
MCINTOSH
SPARTAN
NEWTOWN
PERCENT HATCH PER DAY
0
5
10
15
20
25
30
122 124 126 128 130 132 134
DAYS FROM 1 JANUARY, 1987

Table 3 Observed field hatch of C. verbasci overwintering eggs in three geographical areas of the B.C. interior, spring 1988. Limb-tap sampling was conducted at 24 h intervals on 'Red Delicious' apple limbs in commercial orchards.

Orchard location south to north	No. of orchards	Days ($\bar{x}$ ± S.E.) from 1 January at which hatching stage reached			
		First hatch	50% hatch	90% hatch	100% hatch
Osoyoos	4	111.0 ± 0.4a	119.5 ± 0.3a	123.8 ± 0.3a	125.0 ± 0.0a
Summerland Res. Stn.	4	119.8 ± 1.4b	130.4 ± 0.4b	136.8 ± 0.7b	140.4 ± 0.2bcd
Summerland Entomology	8	121.4 ± 1.2b	131.0 ± 0.5b	137.1 ± 0.6b	139.1 ± 0.4bc
Winfield	3	126.3 ± 0.9b	132.7 ± 0.9b	138.0 ± 0.0b	142.0 ± 1.0d

Means within a column sharing a common letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison, SAS Institute 1985.

This trend is generally consistent each year and parallels heat unit accumulation within the three areas (unpublished data).

For purposes of monitoring and control practices, pest management would be better served by considering the Osoyoos area as a separate and discrete zone. A systems approach to IPM could easily include adjustment factors to incorporate the effect of geographical area on insect phenology. A current attempt to compensate for this discrepancy is the recommendation for 3, 5 and 10 d post-bloom sampling intervals for limb-tap monitoring of C. verbasci.

Influence of tree quadrant on rate of field hatch. It has been assumed, but not proven, that tree quadrant does not influence rate of egg hatch. My data (Table 4) suggest that this assumption is correct. Tree quadrant had no influence on mean field hatching date for overwintering eggs of C. verbasci on either 'Spartan' or 'Golden Delicious' apples. The limb-tap method presently used to determine bug density within orchards used a randomly selected sample of 50 limbs (B.C. Min. Agric. and Fish. 1989). My results indicate that this procedure is acceptable and that cardinal direction need not be taken into account.

Table 4 Dates of mean field hatch for overwintering *C. verbasci* eggs in two Okanagan apple orchards in relation to cardinal direction, spring 1988.

Variety and Location	Quadrant	No. nymphs in sample	Days from 1 January ($\bar{x}$ ± S.E.)*
Spartan, Winfield	East	151	133.1 ± 0.39
	North	149	133.0 ± 0.40
	South	97	132.5 ± 0.48
	West	116	132.7 ± 0.44
Golden Delicious, Summerland	East	95	133.6 ± 0.49
	North	80	133.7 ± 0.52
	South	115	133.7 ± 0.44
	West	149	133.7 ± 0.38

*Conversion to reciprocal of days from 1 January made to achieve normal distribution prior to statistical analysis. No significant difference between mean hatching dates, $P > 0.05$, Least Significant Difference test (SAS Institute 1985).

2.2.2. Establishment of a Laboratory Colony

2.2.2.1. Introduction

McMullen and Jong (1970) raised C. verbasci on pear at 21° ± 0.8°C and found that development from egg to adult took 23.3 ± 0.6 days. The duration of the five nymphal stadia was 4.9, 3.4, 3.5, 5.3 and 6.1 days, respectively. These data vary somewhat with those presented by Niemczyk (1978) in Poland, where, under controlled conditions and a temperature of 25°C, durations were 1.2, 3.1, 3.5, 2.5 and 5.5 days. Part of the variation in the latter data may be attributed to a small sample size (n = 7). Jonsson (1985) compared C. verbasci development with apple phenology but did not discuss how instars were sorted in field samples.

My objective was to establish a cycling, vigorous colony of C. verbasci under controlled environmental conditions generating sufficient numbers of bugs to supply ongoing experiments, to document development and longevity of subsamples from this population, and to compare variables with natural populations.

2.2.2.2. Materials and Methods

Campylomma verbasci was maintained on eggplant cv 'Black Beauty' infested with twospotted spider mite (TSSM), Tetranychus urticae Koch, and grown under a 16:8 h L:D photoperiod at 25° ± 2°C. To minimize inbreeding, a new

colony was established each year for 1987 and 1988 using neonates taken from fruit wood. Campylomma verbasci was reared on eggplant because common mullein is difficult to maintain under laboratory conditions.

An overabundance of prey, T. urticae, was maintained to minimize the possibility of starvation or cannibalism. McMullen and Jong (1970) and Niemczyk (1978) reported that both first and second instars die without prey, as do nymphs of Deraeocoris signatus (Distant.) raised on cotton (Chinajariyawong and Harris 1987).

To reveal the impact of temperature on hatch rate, mature C. verbasci were gathered from the established colony and confined to eggplant seedlings infested with T. urticae. Multiple pairs were allowed to feed and oviposit on the eggplants held for 24 h at 22° ± 1°C, then all adults were dislodged and the plants incubated at one of the following temperatures: 20°, 22°, 25° and 27° (± 0.5°C). Neonates were counted and removed daily.

2.2.2.3. Results and Discussion

Colony establishment. From January through September, in both 1987 and 1988 the laboratory colony of C. verbasci was successfully maintained on eggplant. Exact counts were not routinely taken to monitor population dynamics, but sufficient numbers were produced to supply frequent

experiments with neonates and teneral bugs. An occasional over abundance of T. urticae caused premature leaf-drop and care was exercised to retrieve nymphs which often gathered in the fallen, withered eggplant leaves.

Tenerals were frequently found in groups of 3 - 7 bugs (mixed sexes) on terminal shoots and in flower blossoms. Mating pairs were never observed, yet it was not uncommon to find 12 or more neonates on a lateral leaf, indicating that unobserved matings did occur.

When disturbed, nymphs ran to a lower leaf surface; adults also would hide, often in the axis of a leaf stem. Only as a last resort would the adults take flight to avoid capture; generally they flew in a spiraling upward direction toward any bright light source. In the presence of dense aggregations of T. urticae eggs, both nymphs and adults were found feeding together. Cannibalism was not observed, but dead bugs of all instars were found, suggesting that host plant and/or prey were not supplying completely adequate nutrients. No measure of age class-based mortality was taken.

Hatch rate. Duration of egg hatch ranged from 7.2 ± 0.1 d at 27°C to 13.0 ± 0.2 d at 20°C (Table 5). This result compares with 5.9 ± 0.3 (30°C) to 12.3 ± 0.7 (20°C) (mean ± S.D.) for Lygus hesperus Knight reared at constant temperatures on green beans (Champlain and Butler 1966). In

Table 5 Duration of summer egg hatch for C. verbasci ovipositing on eggplant at 25°C and incubated at one of four constant temperatures.

Temperature (°C)	Number of nymphs	Days for 100% Hatch ($\bar{x}$ ± S.E.)*
20	95	13.0 ± 0.2a
22	119	10.1 ± 0.1b
25	145	8.2 ± 0.1c
27	138	7.2 ± 0.1d

*Means sharing a common letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison, General Linear Model (SAS Institute 1985).

Champlain and Butler's (1966) study, no differences in hatch duration occurred when eggs were reared at constant or fluctuating temperatures.

Cumulative percent hatch (Fig. 5) became progressively faster in response to increased temperature. The frequency distributions of hatching were unimodal and approximated normal distributions (Fig. 6). First hatch occurred at day 9, 7, 6, and 5 for eggs held at 20°, 22°, 25° and 27°C, respectively.

Campylomma verbasci dynamics on herbaceous plants has important implications. The summer generations of C. verbasci determine the abundance of bugs that eventually migrate to fruit trees for deposition of overwintering eggs. These are the source of nymphs that inflict economic injury to sensitive fruit varieties the following spring.

The development of a standardized rearing method makes possible the study of population dynamics and phenology; this may lead to new possibilities for manipulating populations and subsequently reducing damage to agricultural crops.

Artificial diets for mirids have met with limited success; early reports of success with Lygus disponsi (Hori 1972) and L. lineolaris (Vanderzant 1967) may have been the result of nymphal cannibalism enhancing survival through the

Figure 5 Cumulative percent hatch at 16:8 h L:D and four constant temperatures (± 0.5°C) of summer generation eggs from a laboratory colony of C. verbasci raised on eggplant infested with T. urticae. Each curve identified by rearing temperature.

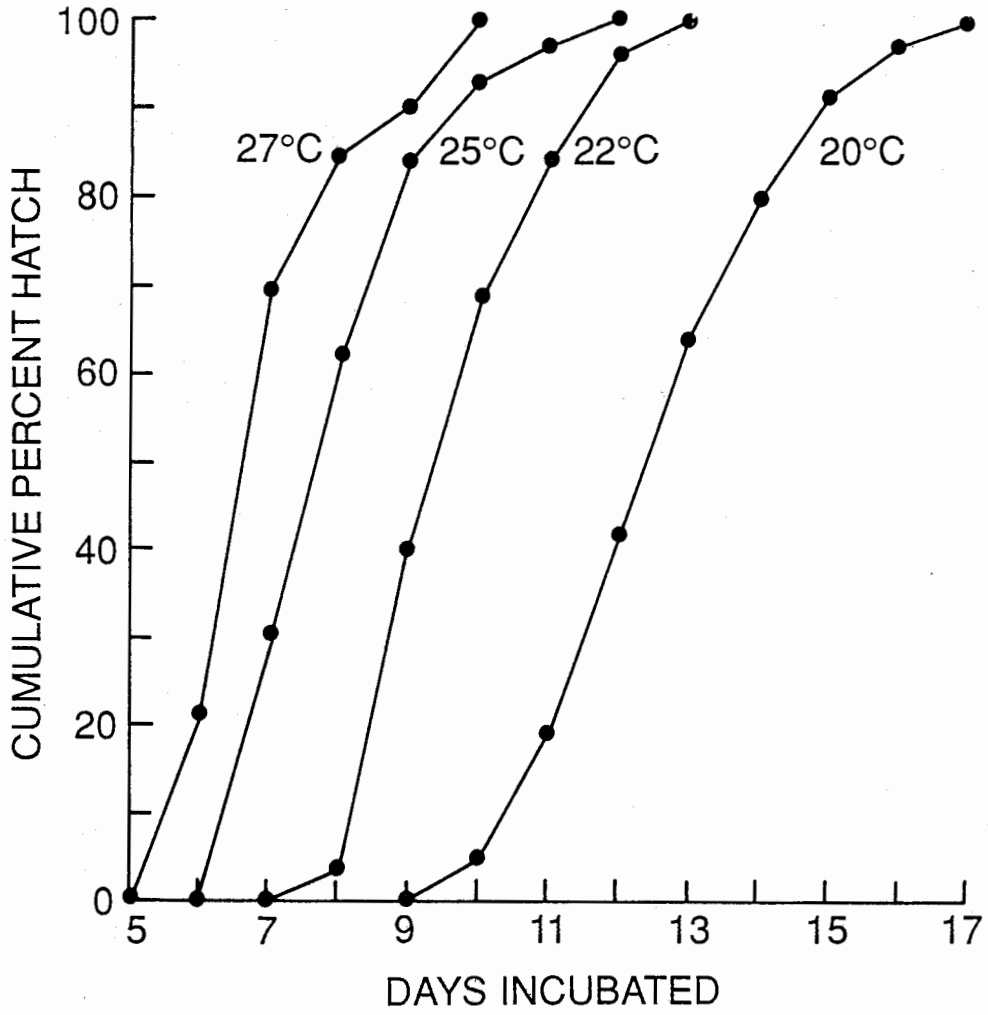
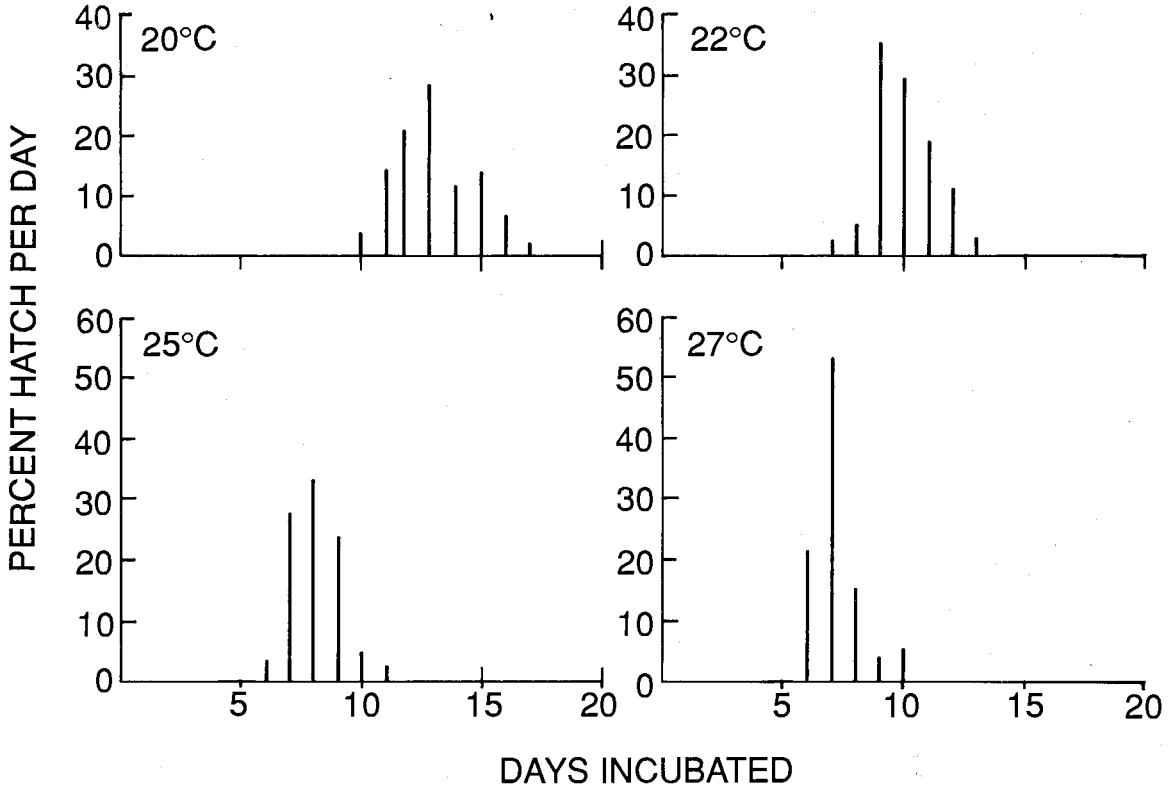

100
80
60
40
20
0
CUMULATIVE PERCENT HATCH
27°C
25°C
22°C
20°C
5
7
9
11
13
15
17
DAYS INCUBATED

Figure 6 Frequency distribution for hatching of C. verbasci eggs at four constant temperatures following oviposition on eggplant.


20°C
22°C
25°C
27°C
PERCENT HATCH PER DAY
DAYS INCUBATED
0
10
20
30
40
50
60
5
10
15
20

first few instars. However, Debolt (1982) reared over 13 generations of L. hesperus on a synthetic diet; fecundity and longevity equalled or exceeded that on a standard bean and prey diet.

This research indicates that C. verbasci can be reared successfully on alternate herbaceous plants; however, further refinement and definition of nutritional needs are required if the method is to achieve acceptance as an aid in the study of this mirid's biology under controlled environmental conditions.

2.2.3. Discrimination Between Nymphal Instars by Size

2.2.3.1. Introduction

Leonard (1915) separated the nymphal instars of C. verbasci by size, but did not report sample size nor degree of variance for his data. Similarly, Collyer (1953) suggested that gross body measurements could aid in separating nymphal instars, but gave only sample size (n = 12) and no variance for the mean values reported. She also included antennal segment length as a further guide in mirid identification (Collyer 1952, 1954).

To date, there are no life tables for C. verbasci, in part because studies on population dynamics require a means of separating nymphal instars. My objective was to discern

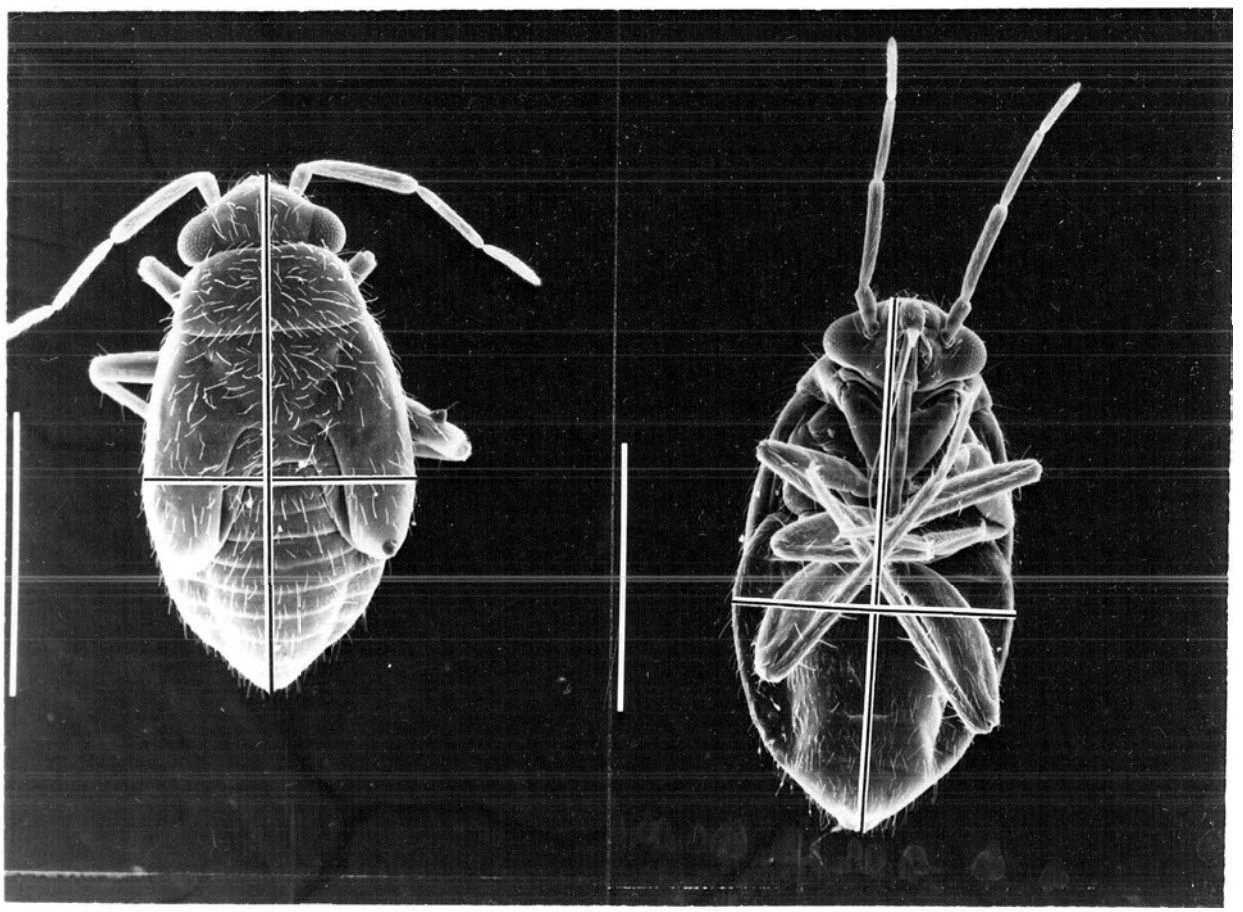
whether simple external body measurements can be used to distinguish between the five nymphal instars of C. verbasci.

2.2.3.2. Materials and Methods

Campylomma verbasci nymphs ≤ 24 h old were collected from a laboratory colony on eggplant and transferred to a single eggplant leaf with an abundance of twospotted spider mites. The leaf was then placed on a moist filter paper disc, ca. 9.0 cm in diameter in a plastic petri dish. Ventilation was supplied through a 5.0 cm diameter screen-covered hole in the lid. Prior to initial release and at the time of successive molts, each nymph was lightly dusted with a few particles of Day-glo fluorescent pigment. Petri dishes were held at 25° ± 0.5°C under ≤ 60% R.H. and a 16:8 h L:D photoperiod. Fresh prey and leaves were supplied at 48 h intervals. Every 24 h, each nymph was immobilized with CO_2, and measured under a dissecting microscope using a micrometer graduated in 0.1 mm units. Body length was taken from the rostrum trunk to the distal portion of abdomen, and body width across the widest point of the abdomen (Fig. 7).

Means values were subjected to ANOVA and statistical analysis using the Least Significant Difference Test (SAS 1985). Measurements were evaluated for possible correlation with instar, using the Pearson Correlation coefficient (SAS Institute 1985).

Figure 7 Scanning electron micrographs of C. verbasci fifth nymphal instar showing axes for dimensional measurements, ventral view (left), dorsal view (right). Bar beside insect represents 1 mm.



2.2.3.3 Results and Discussion

There was no apparent adverse effect caused by the fluorescent pigments on nymph longevity and their use allowed speed plus accuracy in determining when individual bugs had molted. A necessary assumption of this experimentation was that development and survival approximated that of a wild population.

There were significant differences between each instar in both body length and width (Table 6). There were highly significant correlations between increases in body dimension and instar ($r = 0.956$ and 0.936, $p < .0001$ for body length and width, respectively). Both parameters were normally distributed in each instar (Fig. 8). The results indicate that either length or width give a measure for sorting field populations into nymphal instars. In Nova Scotia where A. mali is the dominant fruit-stinging mirid, Sanford (1964a) reports that head capsule width provides a reliable means separating nymphal instars. Because of the small size of these insects, whole body measurements would be a more confident means of discriminating between instars.

In spite of overlap in measurements between instars (Fig. 8), the confidence intervals for the measurements of each instar (Table 6) indicated that there is a good chance of separating insects in any two subsequent instars, particularly when both length and width are measured.

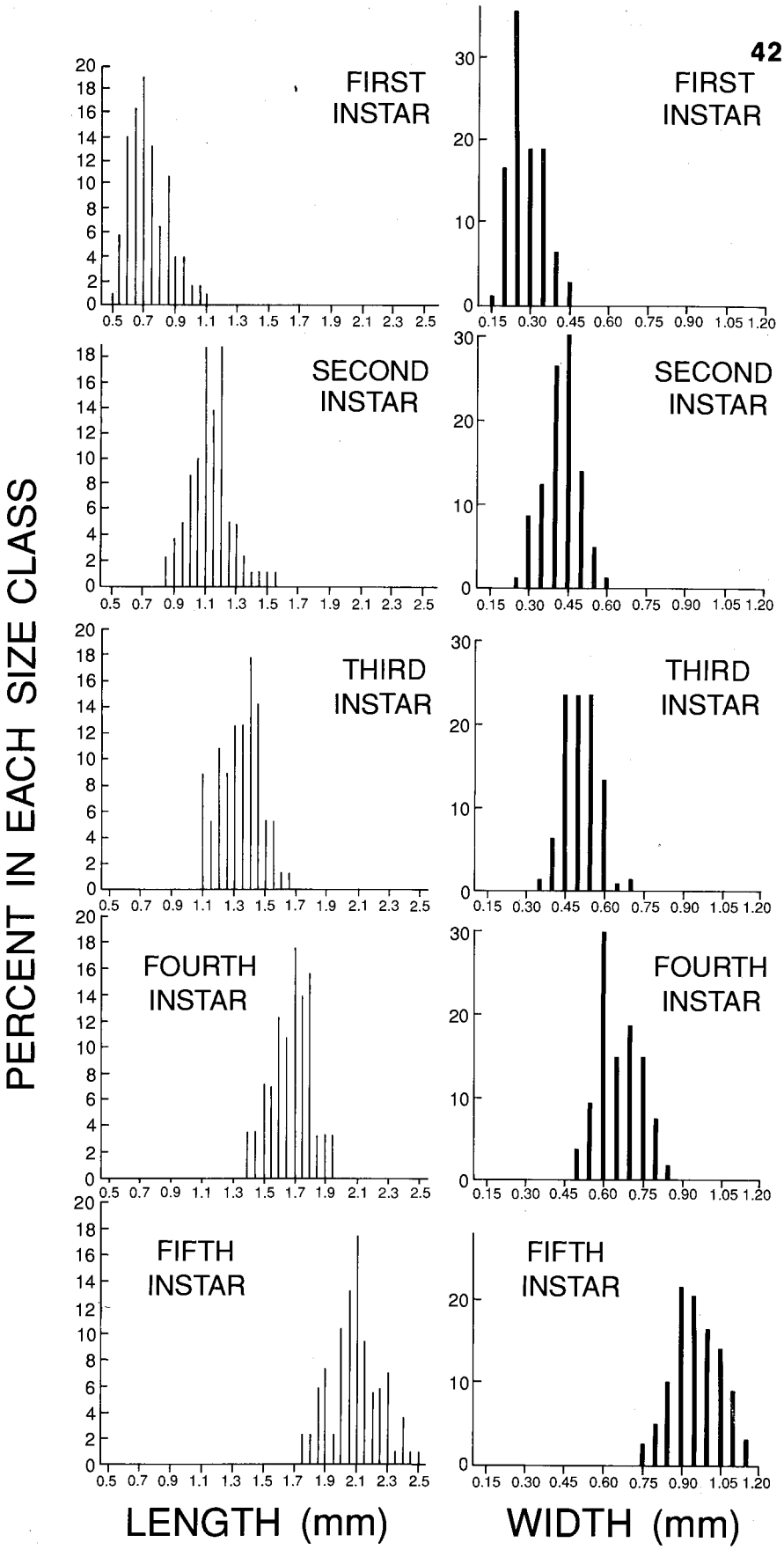
Table 6 Body size measurements (Fig. 7) of C. verbasci nymphs from a laboratory colony on eggplant.

Instar	Sample Size	Dimensions (mm) ($\bar{x}$ ± S.E.)[a] Width	Length
First	121	0.28 ± .01a (0.26 - 0.30)[b]	0.74 ± .01a (0.72 - 0.76)[b]
Second	79	0.42 ± .01b (0.40 - 0.44)	1.12 ± .02b (1.08 - 1.16)
Third	60	0.52 ± .01c (0.50 - 0.54)	1.33 ± .02c (1.28 - 1.37)
Fourth	58	0.66 ± .01d (0.64 - 0.66)	1.69 ± .02d (1.65 - 1.73)
Fifth	82	0.91 ± .01e (0.89 - 0.93)	2.11 ± .02e (2.07 - 2.15)

[a]Means within a column followed by different letters are significantly different, $P < 0.05$, Least Significant Difference Test, SAS Institute 1985.

[b]95% Confidence intervals α (2).

Figure 8 Frequency distributions of numbers of C. verbasci according to length (left) and width (right) for five nymphal instars raised on eggplant. Sample sizes for instars 1-5 are 121, 79, 60, 58 and 82 nymphs, respectively.


PERCENT IN EACH SIZE CLASS
FIRST INSTAR
FIRST INSTAR
SECOND INSTAR
SECOND INSTAR
THIRD INSTAR
THIRD INSTAR
FOURTH INSTAR
FOURTH INSTAR
FIFTH INSTAR
FIFTH INSTAR
LENGTH (mm)
WIDTH (mm)

2.2.4. Longevity and Fecundity

2.2.4.1. Introduction

Little is known of C. verbasci fertility and fecundity owing in part to the difficulty until now of rearing this species in the laboratory. McMullen and Jong (1970b) raised only one female from the egg until oviposition occurred (14 d after the final molt); this female deposited 39 eggs in 3 d and contained developing eggs at the time of her death. When mullein bugs were held on apple twigs and fed eggs of the angoumois grain moth, Sitotroga cerealella (Oliver), females first contained eggs in the ovaries when 6 d old, but eight male-female pairs averaged only ten oviposited eggs each, and dead females contained up to 22 eggs in the ovaries (Niemczyk 1978).

It is very difficult to determine the fecundity of mirid species that oviposit in woody hosts. Collyer (1955), Leonard (1915) and Sanford (1964b) describe oviposition sites of several mirids including C. verbasci. The eggs (less than 1 mm long) are thrust into corky tissue, e.g. lenticels, with only the operculum visible externally. Further confounding detection is the cryptic colouration and slightly depressed egg cap, blending uniformly with debris and weathered bark. In my research, the most practical approach to monitoring fecundity in woody plants may be to count hatched nymphs and to disregard egg mortality.

Other mirids, particularly Lygus spp. utilize only herbaceous plants as oviposition sites. Cave and Gutierrez (1983) using a developmental threshold of 11.9°C, determined a preoviposition period of 136 ± 27.0 degree-days (D.D.) for L. hesperus on cotton, with a longevity of 385 ± 90.0 D.D. and total fecundity averaging 49.7 ± 28.5.

There is meager information regarding C. verbasci dynamics on V. thapsus, yet phenology on its herbaceous host ultimately influences the number of bugs available to infest orchards in the autumn. This, in turn, determines nymph density and subsequent fruit damage the following spring. Temperature-based models have been suggested as a means of tracking mirid seasonal development (Gutierrez et al. 1977) assuming sufficient biological data are available. To support such eventual models as well as studies on population dynamics, my objective was to determine the potential longevity and capacity for C. verbasci to express its full oviposition potential.

2.2.4.2. Materials and Methods

Adult C. verbasci were collected from a stock colony established on eggplant. Only teneral bugs showing a light green colouration were used; preliminary observations (n = 16) indicated that females and males with this colouration were ≤ 5.6 ± 0.3 d and ≤ 4.7 ± 0.3 d old, respectively.

Individual females were confined with two males on potted eggplant seedlings, previously infested with T. urticae, beneath a clear plastic drinking cup. New host plants were given at 48 h intervals and additional males supplied as needed to maintain a female to male ratio of 1:2 until the female died. This procedure was repeated over each female's life span. Plants were labelled and incubated at 25° ± 1°C under a 16:8 h L:D photoperiod. Eggplants were searched daily for neonate nymphs and records kept for fecundity and oviposition frequency of each female.

Teneral mullein bugs were also collected from V. thapsus and confined to eggplant under identical conditions as above. This was undertaken to compare longevity and fecundity of wild bugs with those from the colony raised on eggplant.

The caged insects were held in a controlled environment chamber under a 16:8 h L:D photoperiod at 50% R.H. and 25° ± 0.5°C. Light from fluorescent bulbs measured within the cabinet with a LI-COR Integrating Quantum/Radiometer/ Photometer averaged 37.9 μ E s^{-1} m^{-2} (3018 lux). Infested eggplants were incubated as above and counts of nymphs were taken at 24 h intervals.

2.2.4.3. Results and Discussion

Over 1,200 nymphs were collected from eggplant on which female C. verbasci were held. Colony-raised and wild females lived on average 17.4 ± 0.8 d (n = 36) and 15.2 ± 1.2 d (n = 22), respectively. The shorter life span of wild females may suggest a behavioural resistance to accepting eggplant as a herbaceous host.

Ovipositing females from the eggplant colony produced 6.7 ± 0.6 nymphs per 48 h (range 0 - 36). Fecundity peaked at 13 percent total progeny on day 8 and declined steadily beyond day 16 (Fig. 9). Fifty percent of the nymphs were from eggs laid in the first 12 days of oviposition (Fig. 9). Over the females' life spans, those from the eggplant colony averaged 38.6 ± 8.3 (range 2 - 184) nymphs compared to 15.5 ± 11.6 (range 2 - 124) from wild females; one wild female produced 124 of the total 155 nymphs.

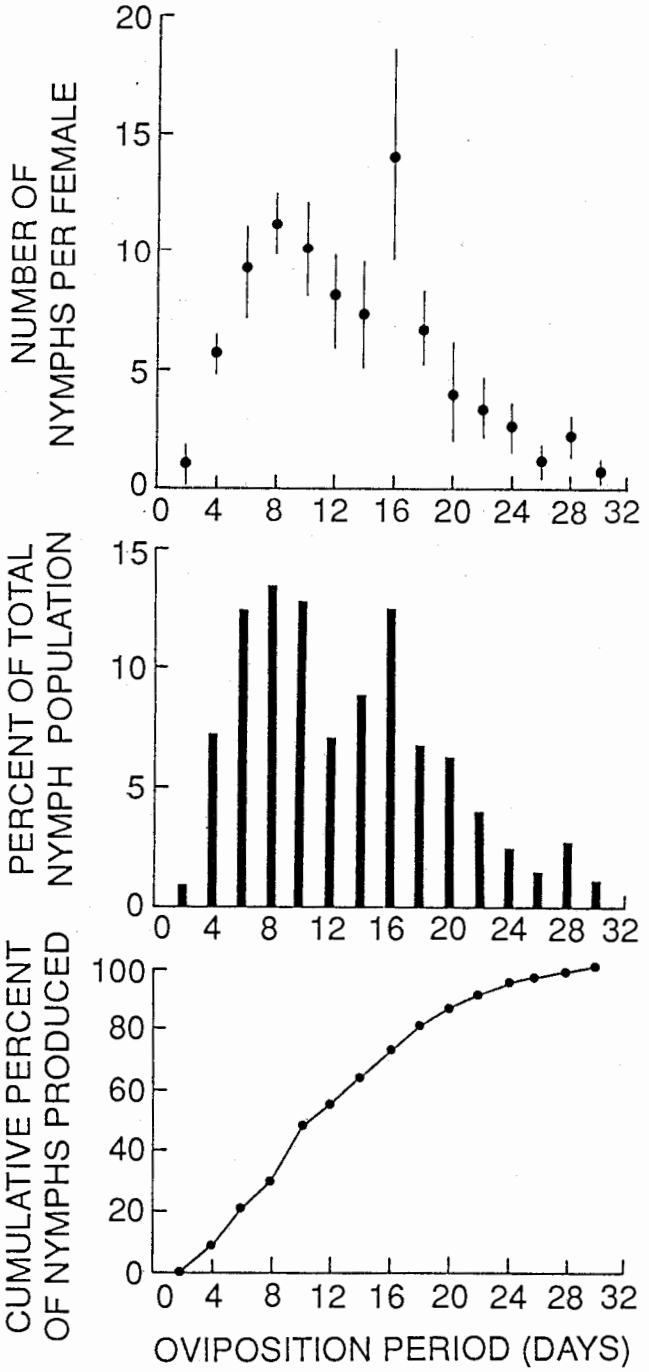
Glen (1973) reports that oviposition in the field by the black-kneed capsid, Blepharidopterus angulatus (Fall.), extends over five weeks with ca. 1.2 eggs deposited per day and 44 ± 2.5 (x ± S.E.) (n =10) for the entire life span.

2.3. Chemical Ecology of C. verbasci

2.3.1. Introduction

It has been shown by Thistlewood et al. (1989b) that potential exists for pheromone-based monitoring of

Figure 9 Mean numbers of nymphs produced (top), mean percent of nymphal population (middle), and mean cumulative percent of nymphs produced (bottom) per female C. verbasci reared and held on eggplant at 25° ± 0.5°C. Lines through data points in top subgraph represent ± 1 S.E.


NUMBER OF NYMPHS PER FEMALE
20
15
10
5
0
0 4 8 12 16 20 24 28 32
PERCENT OF TOTAL NYMPH POPULATION
15
10
5
0
0 4 8 12 16 20 24 28 32
CUMULATIVE PERCENT OF NYMPHS PRODUCED
100
80
60
40
20
0
0 4 8 12 16 20 24 28 32
OVIPOSITION PERIOD (DAYS)

C. verbasci. Such a program would be species-specific, and would give advanced warning of possible damage. It would impart considerable benefit, given the sporadic nature of C. verbasci outbreaks and the inability thus far to predict their occurrence. However, several major obstacles must be overcome before pheromones are incorporated into an IPM approach. These include:

1. correlation of trap captures with economic injury levels, establishment of a data base demonstrating a consistent predictive ability, and establishment of an economic threshold for trap captures;

2. identification of key pheromone components sufficient to produce a synthetic a sex lure that is competitive with female bugs.

3. establishment of standardized trapping materials and methodologies, including selection of a controlled release device and emission rate of pheromones, optimum trap type, and appropriate height and placement of baited traps.

2.3.2. **Design and Placement of Pheromone-Baited Traps**

2.3.2.1. Introduction

Trap design and placement within a crop canopy can have a significant effect on the capture rate of target species.

Morrill (1988) outlined for noctuid moths several criteria necessary if a trapping program is to supply consistent, reliable results. These criteria also apply to the fauna of pome fruits. A trap must withstand adverse weather and protect catches from destruction. If an adhesive is used, saturation of a trap with specimens needs to be anticipated, and deployment of traps within the monitoring site must give reliable results.

Riedl et al. (1979) demonstrated that both trap height and placement in the tree canopy had a dramatic effect on captures of the codling moth, Cydia pomonella (L). Similarly, Ahmad (1987) captured almond moths, Cadra cautella (Walker), with greatest success when traps were at heights of 3-6 m.

There are no published reports of the influence of pheromone trap height on mirid bug captures. Thistlewood et al. (1989b), in demonstrating the presence of a sex pheromone in C. verbasci, used 2 L ice-cream cartons baited with live females hung 1 - 1.5 m high in a mullein field or within the canopy of apple trees.

Boivin and Stewart (1984) using a visual stimulus trap concluded that most C. verbasci captures in a Quebec apple orchard were between 2.0 and 3.5 m. McPherson et al. (1983) presented seasonal flight patterns of 79 mirid species in a North Carolina black walnut plantation. Captures using a

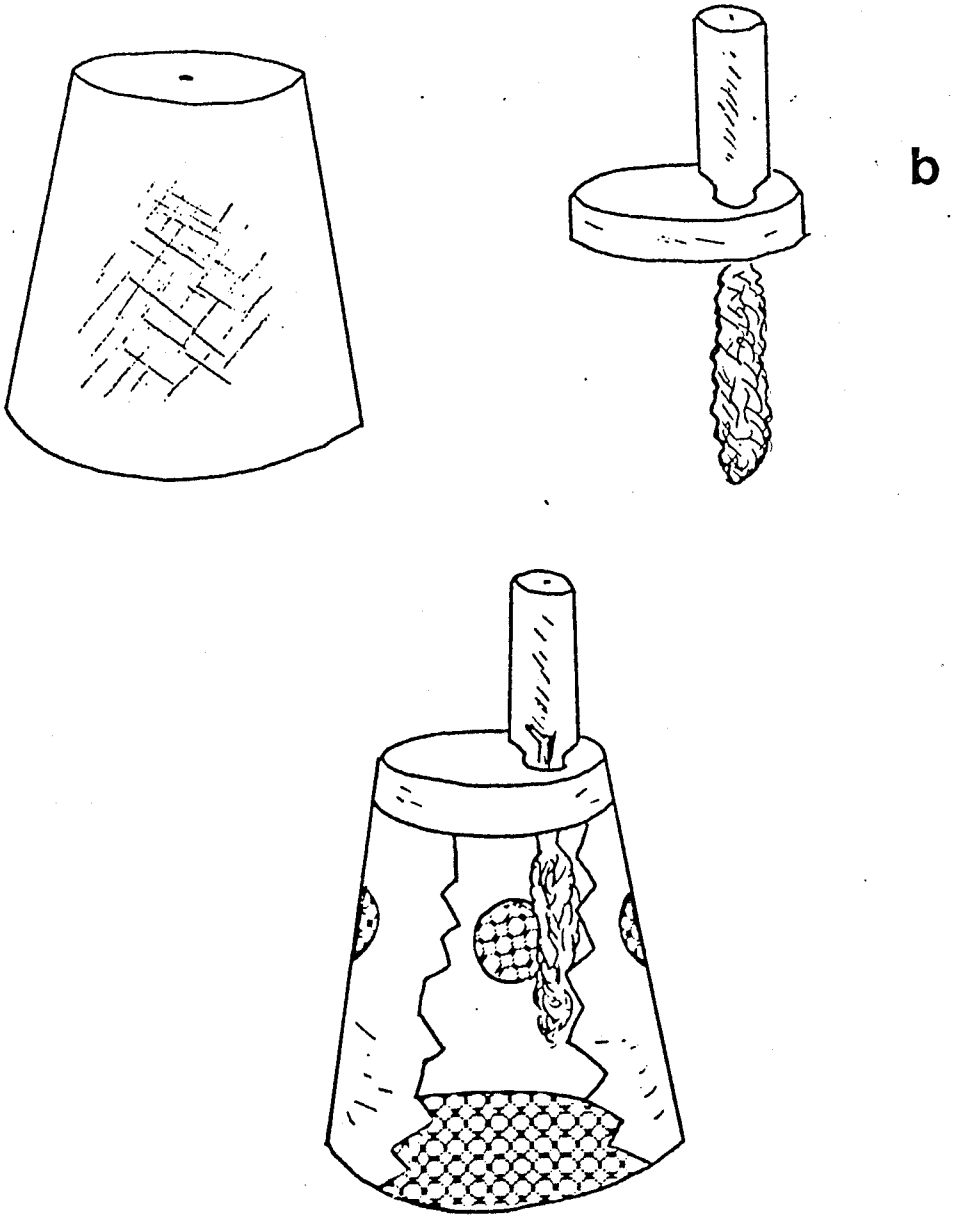
'window trap' were recorded at 1 m intervals to a height of 7 m; four of the five principal mirid species were taken primarily at heights less than 4 m and only one favoured elevations greater than 4 m. Sixty percent of Lygus lineolaris were taken at 1-2 m and only 3% at 7 m. Lygus hesperus in proximity to a safflower field in the San Joaquin Valley of California were trapped mainly at heights ≤ 4 m using a non-attractive sticky trap (Mueller and Stern 1973).

My objectives were: 1) to select an effective trap type, and 2) to determine the most practical height for monitoring C. verbasci.

2.3.2.2. Materials and Methods

Three types of traps were evaluated: a 'Delta triangular form', a 'Wing trap', (both manufactured by Albany International Inc.[1]) and a 2 L ice-cream carton (18.5 x 13 cm O.D.) (Thistlewood 1986). Female C. verbasci were collected from common mullein and confined on a small piece of flower stalk in a plastic cage, 10 females per cage (Fig. 10). The caged females were suspended from the inside top of each trap type. Control traps were baited with a caged mullein flower stalk or left unbaited.

Figure 10 Cage used to confine C. verbasci females in pheromone traps: a) unmodified plastic cup, 5.5 x 6.5 cm, b) petri dish insert with mullein flower stalk inserted in water vial, c) cut away view of assembled cage showing 5 mm diam. vents and bottom covered with mesh screening.


a
b
c

Treatments (traps) were replicated five times in a completely randomized block design and tested from 27 June to 4 July 1987 in a mature pear orchard (variety 'Bartlett') at the Agriculture Canada Research Station, Summerland, B.C. Within each replicate traps were spaced 4.0 m apart and hung 1.5 m high and 0.5 m within the tree canopy; replicates were 5.0 m apart. Every 48 h, captures were recorded and the traps rerandomized within each replicate.

Two L ice-cream carton traps were used to test the effect of height on capture of male C. verbasci responding to sex pheromone from live females caged as above. Traps were placed at heights of 1, 2, 3, 4 and 5 m in a 3-replicate, completely randomized design in a standard orchard block of 'Red Delicious'. The data were transformed to $\sqrt{(n + 0.5)}$ prior to ANOVA and Tukey's pairwise comparison of the mean total captures.

2.3.2.3. Results and Discussion

Trap type. All three types of traps baited with live C. verbasci females caught more males than did unbaited traps and those baited with mullein only (Table 7), corroborating the results of Thistlewood et al. (1989b) that female C. verbasci produce a sex pheromone. Female-baited Delta traps caught fewer males than either the 2 L ice-cream carton or the Wing trap. Possibly the folded flaps on the Delta trap may have disrupted the pheromone plume or acted

Table 7 Captures of male C. verbasci in three types of traps within an orchard. Each treatment was replicated five times.

Lure	Trap type	No. males caught ($\bar{x}$ ± S.E.)*
10 females on mullein	2 L ice-cream carton	22.8 ± 2.6a
	Wing	21.0 ± 2.5a
	Delta	11.2 ± 1.9b
Mullein only	2 L ice-cream carton	0.2 ± 0.1c
	Wing	0.4 ± 0.3c
	Delta	0.0 ± 0.0c
Blank	2 L ice-cream carton	0.0 ± 0.0c
	Wing	0.0 ± 0.0c
	Delta	0.0 ± 0.0c

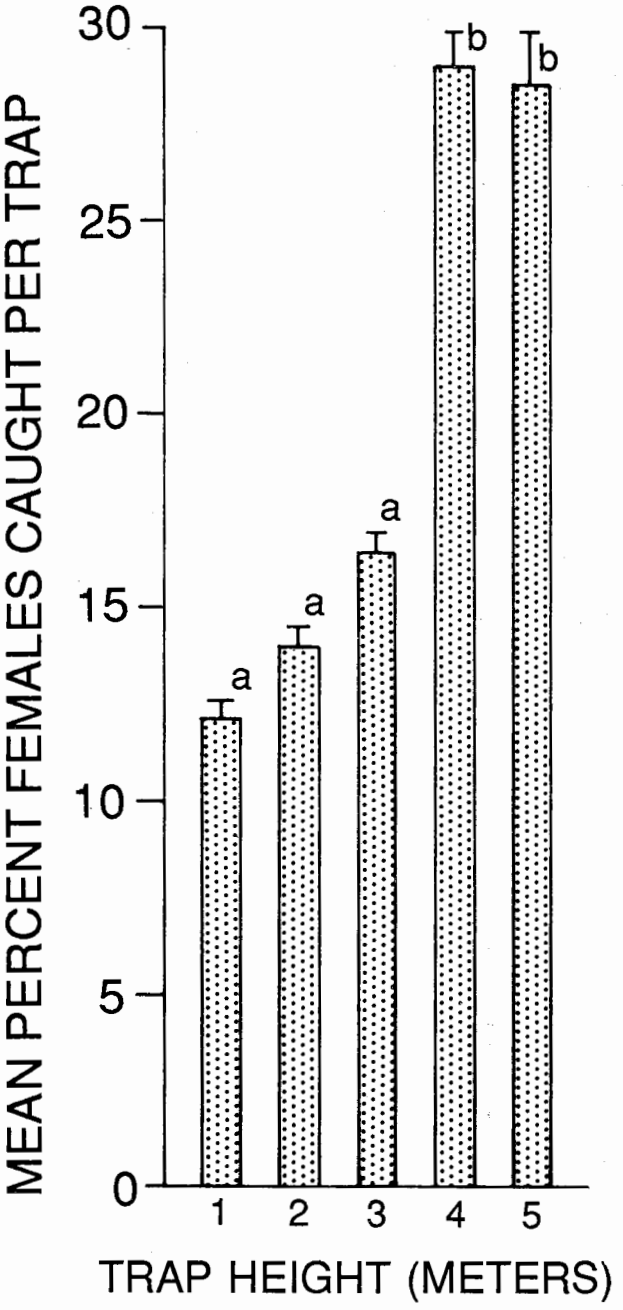
*Means followed by the same letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison, SAS Institute 1985.

as a barrier to approaching males. Because the 2 L ice-cream carton with its wide mouth opening was easiest to maintain, this trap was chosen for use in subsequent research.

Trap height. Traps set 4 and 5 m high within the apple orchard caught the largest numbers of male C. verbasci, while the traps at the lower 3 heights did not differ in catches (Fig. 11). The catches at 5 m, which were above the canopy suggest a trend of high flight into the orchard; a similar flight pattern was demonstrated by Boivin et al. (1982) using visual stimuli traps. It is not known how far the males moved in response to the chemical stimuli.

It would be impractical to use pheromone-baited traps for population monitoring if they were set at heights of 4 or 5 m. Maximum captures are not necessary so long as numbers at the other elevations are consistent. Therefore, in further experiments to elucidate pheromone identity, or to test female-baited traps as a monitoring tool,traps were placed with confidence at 1.5 - 2.0 m within the tree canopy.

Figure 11 Mean proportions (with S.E.) of 163 male *C. verbasci* taken in female-baited 2 L ice-cream carton traps at five heights in an Okanagan Valley apple orchard, September 1988. Bars topped by the same letter are not significantly different, Least Significant Difference test, $P < 0.05$, SAS Institute 1985.


MEAN PERCENT FEMALES CAUGHT PER TRAP
30
25
20
15
10
5
0
a
a
a
b
b
1
2
3
4
5
TRAP HEIGHT (METERS)

2.3.3. Relationship Between Catches of C. verbasci in Traps Baited with Females in the Fall and Density of Nymphs in the Spring

2.3.3.1. Introduction

Current management of C. verbasci is based on economic thresholds that correlate spring nymphal density with subsequent fruit damage, primarily to the apple varieties 'Red Delicious' and 'Golden Delicious', although other varieties can be injured (Madsen et al. 1975, B.C. Ministry of Agriculture and Fisheries 1988, Thistlewood 1989).

Sampling for C. verbasci is done using a 40 x 40 cm tapping tray; nymphs are jarred from the branch by several sharp blows with a stick (Hardman et al. 1984, Washington State University 1988). Although it generally leads to effective predictions (Thistlewood and McMullen 1989), the method is deficient in several ways. It is time-consuming and requires many limb tap samples per ha for reliable prediction. There is often little time between egg hatch and the moment at which injury to the fruit occurs. Adverse weather during the sampling period can prolong both egg hatch and/or the sampling routine. The limb-tap method assumes that the majority of overwintering eggs have hatched, while maximal hatching varies considerably from year to year (Thistlewood 1986). Finally, although only a few orchards in any given year may sustain damage, it is necessary to sample all orchards intensively because there

is no means of predicting beforehand which ones are most likely to harbour populations above the economic threshold.

Pheromones have been used to monitor such orchard pests as the codling moth, C. pomonella L., the peach twig borer, Anarsia lineatella Zeller, and the peachtree borer, Synanthedon exitiosa (Say). Thistlewood et al. (1989a) have shown that female mullein bugs emit a sex pheromone that attracts males to female-baited traps in a manner similar to that found in the other mirids: Lygus lineolaris (P. de Beauvois) (Scales 1968), Lygocoris communis (Knight) (Boivin and Stewart 1982b), Distantiella theobroma (Dist.) (King 1973) and Helopeltis clavifer (Walker) (Smith 1977, Staddon 1986). The exact identity of the pheromone for this species, or any mirid, has yet to be determined (Aldrich 1988).

Our objective was to test the hypothesis that the catch of C. verbasci males in the autumn in response to female sex-produced pheromone could be used as a predictor of nymphal density in apple orchards in the following spring, at the time that injury to fruitlets occurs. If this hypothesis were to be upheld, we judged that the results might lead to an effective method of determining in the fall which orchards would require intensive limb-tap sampling the following spring.

2.3.3.2. Materials and Methods

Females obtained from common mullein, V. thapsus (L.), were used as a pheromone source, five being confined in a 140 mL plastic cup in which three 5 mm diam. holes were cut. Both the cup mouth and the holes were covered with fine mesh screening. A small portion of a flower stalk of mullein was inserted through the cup top and held in a 3 dram vial of water (Fig. 10). Females maintained on mullein remain attractive for ca. 7–10 d (Thistlewood 1986).

The cage containing the females was pinned inside the top of a horizontal 2 L ice-cream carton trap (18.5 x 13 cm O.D.) lined with a cardboard insert covered with Stiky Stuff[2]. Two or three traps were deployed per orchard in the Okanagan Valley of B.C. Twenty-one such traps were in operation from 6–11 September in seven orchards, and 27 were in operation from 12 September to 13 October in 10 orchards. Traps were hung 1.5 m above ground level, ca. 0.5 m inside the tree canopy. They were at least 8 m apart; none was placed in a border row. At least once a week from 11, September to 13 October, males were removed from the traps and all 5 females were replaced.

Five limbs on each trap-placement tree and one limb on each of four adjacent trees were tagged with plastic survey tape in the fall of 1987. The nymphal population of each tagged branch was sampled in the spring by tapping at 48 h

intervals beginning at 'king bloom' and continuing until the mullein bug hatch was complete in each orchard. Simple linear regression (SAS Institute 1985) was performed between the mean nymphal density per limb (spring 1988) and the mean male bugs caught per trap day (fall 1987) for each of five trapping intervals and for the entire period from 12 September to 13 October when 27 traps were in operation.

2.3.3.3. Results and Discussion

The captures of male C. verbasci in the fall varied greatly (Table 8) suggesting the traps were sensitive to different population levels. Movement of bugs to the orchards had begun prior to trap placement (Table 8) resulting in high numbers caught from the beginning of the experiment. Captures remained high in the first week of October, but by 13 October, they dropped to very low levels.

Densities of nymphs per limb in the spring were also variable (Table 9). Mean numbers of nymphs per limb did not differ significantly ($P > 0.05$) between trap and adjacent trees (Tukey's HSD Test, using a general linear model, SAS Institute 1985).

There was a highly significant positive relationship between numbers of male C. verbasci trapped during most trap count intervals in the fall and density of nymphs in the spring in the trap trees (Fig. 12). A similar but slightly

Table 8 C. verbasci capture rates in the fall and nymphal densities in spring, in ten Okanagan Valley orchards. All means based on 27 replicates. Trap interval 6 September to 13 October 1987.

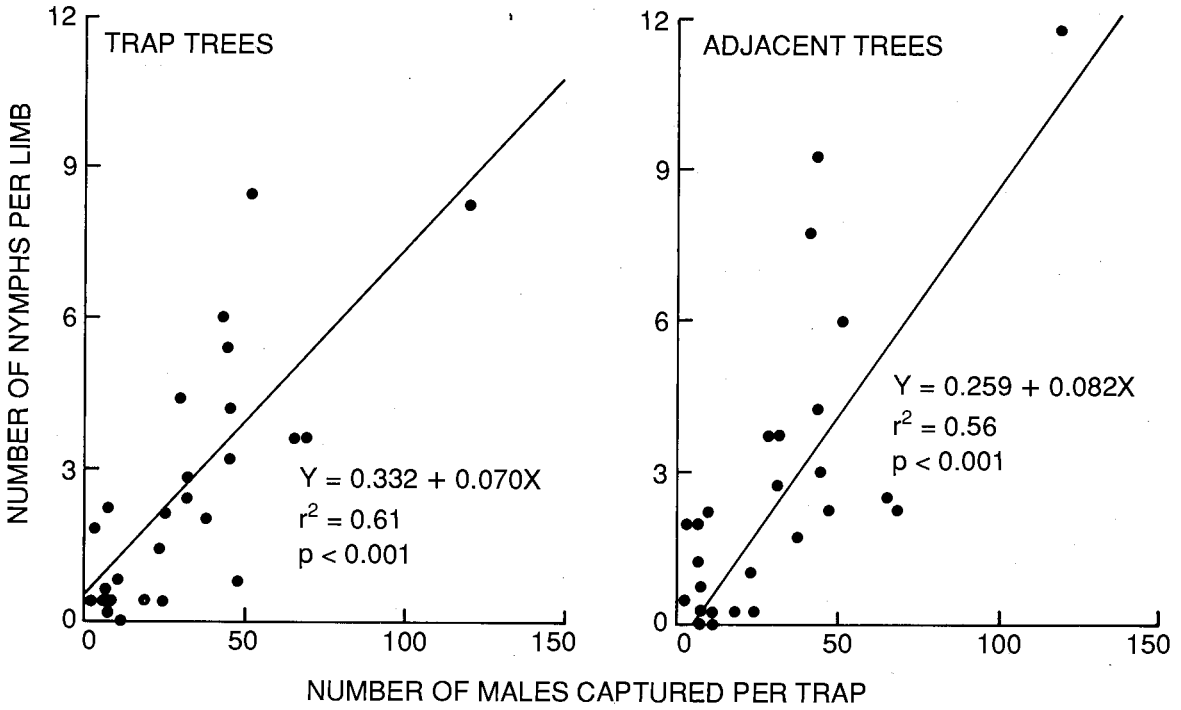
Season	Criterion Assessed	Range	Mean ± S.E.
Fall	Total males trapped per tree	3-120	35.9 ± 5.8
	Males per trap per day	0.1-4.1	1.1 ± 0.2
Spring	Nymphs per trap tree limb	0-11	2.4 ± 0.5
	Nymphs per adjacent tree limb	0-9	2.7 ± 0.6

Table 9 Relationship between C. verbasci captures by trapping interval in the fall 1987 and nymphal densities in the spring 1988 in ten Okanagan Valley orchards.

Trapping Interval	No. traps in operation	No. adults captured	Trap trees r^2	Trap trees p	Adjacent trees r^2	Adjacent trees p
6-11 Sept.	21	153	0.55	0.0001	0.50	0.0003
12-15 Sept.	27	82	0.01	0.55	0.06	0.24
16-22 Sept.	27	185	0.31	0.003	0.38	0.0006
23 Sept.- 2 Oct.	27	360	0.41	0.0003	0.45	0.0001
3-13 Oct.	27	33	0.06	0.23	0.03	0.43

P values based on regression analysis, General Linear Model, SAS Institute 1985.

Figure 12 Relationship between catches of male C. verbasci in female-baited traps from 14 September to 13 October in 1987 and numbers of nymphs per limb the following spring.


TRAP TREES
Y = 0.332 + 0.070X
r2 = 0.61
p < 0.001
ADJACENT TREES
Y = 0.259 + 0.082X
r2 = 0.56
p < 0.001
NUMBER OF NYMPHS PER LIMB
NUMBER OF MALES CAPTURED PER TRAP
0
3
6
9
12
0
50
100
150

weaker relationship occurred for the trees adjacent to the ones in which the traps were placed. The relationships were also significant for the individual trapping intervals with the exception of the final interval in October when the flight of adults had declined to a very low level (Table 9).

The development of a pheromone-based, predictive monitoring system for C. verbasci would be a positive achievement for integrated pest management. While significant relationships between fall and spring populations occurred for several sampling intervals (Table 9), additional research would be required to determine precisely such factors as the entire duration of the fall flight and the optimal time window for sampling in the fall. In the spring research would be needed to determine the effective distance from pheromone-baited traps for accurate prediction of population density.

The B.C. Ministry of Agriculture and Fisheries (1989) recommends treatment against C. verbasci during the "calyx stage" when the economic threshold is reached. In some cases prophylactic sprays are applied. A pheromone-based monitoring system should find immediate use as an early warning system for high nymphal populations that can be further quantified by limb-tap sampling and suppressed if necessary. Ultimately it may prove to be reliable enough that populations exceeding the economic threshold could be

predicted on the basis of pheromone traps alone. It should also be effective in identifying "safe" orchards in which no further sampling would be necessary, allowing limb-tap sampling to be concentrated where most needed in the limited time available in the spring.

There is scant knowledge of overwintering mortality in C. verbasci eggs, but Thistlewood (1986) detected no egg parasites while conducting extensive orchard samplings. Normal winter temperatures are unlikely to kill mullein bug eggs because their mean freezing point is ca. -30°C (MacPhee 1964). We postulate that there would be minimal egg mortality between fall oviposition and spring hatch and thus such mortality should not confound a pheromone-based predictive system in the fall. However, other factors, e.g., proximity to V. thapsus and predation acting at or just after the time of oviposition may initiate variation in numbers of overwintering eggs from year to year. Such yearly fluctuations should be anticipated, but should not negate the potential of pheromone-based monitoring.

Once a synthetic pheromone has been developed, the apple industry should benefit considerably from the implementation of a pheromone-based monitoring system that gives advanced warning of economic injury.

2.3.4. Isolation, Identification and Bioassay of the Sex Pheromone for C. verbasci.

2.3.4.1. Introduction

To date, determination of the identity of any mirid sex pheromone has been an elusive goal, although suspect components in several species have been identified (Aldrich 1988). Thistlewood et al. (1989b) demonstrated the presence of a sex pheromone in C. verbasci. Butyl butyrate, hexyl butyrate and hexyl acetate were significant components of female-produced volatiles. Male bugs responded to traps baited with either live females, their extracts or extracts of their captured volatiles. I have shown that, using live females as a pheromone source, fall populations can be correlated with subsequent densities of nymphs in the following spring (Chapter 2.3.3). However, a monitoring program cannot rely on such a variable and uncertain stimulus as live females. Therefore, my objectives were: 1) to isolate, identify and synthesize the sex pheromone for C. verbasci, and 2) to determine the bioactivity of synthetic pheromone in the field. Dr. H.D. Pierce Jr., Dept. of Chemistry, Simon Fraser University conducted all extractions, fractionations, spectrometric analyses and synthesis.

2.3.4.2. Materials and Methods

2.3.4.2.1. Chemical and Instrumental Methodology

Butyl butyrate (1-butyl butanoate), hexyl butyrate (1-hexyl butanoate), butyryl chloride (butanoyl chloride), 2 (E)-crotonaldehyde (2 (E)-buten-1-al), and 1-hexanol were purchased from commercial sources. Hexyl acetate (1-hexyl acetate) was prepared by reaction of 1-hexanol with acetic anhydride in pyridine in the usual way. Reduction of 2 (E)-crotonaldehyde with sodium borohydride in 50% aqueous ethanol gave a 2 (E)-crotyl alcohol containing 4.3% 1-butanol and 1.7% Z isomer. 2 (E)-crotyl butyrate (2(E)-butenyl butanoate) was prepared by reaction of 2 (E)-crotyl alcohol with butyryl chloride in ether in the presence of triethylamine. After work-up and distillation at reduced pressure the ester was 90.6% pure and contained 4.5% butyl butyrate.

Hewlett-Packard 5830, 5880 and 5890 gas chromatographs equipped with capillary inlet systems and flame-ionization detectors were employed for analyses by gas-liquid partition chromatography (GC). Glass columns (30-40 m x 0.5 mm ID) coated with SP1000[3] and fused silica column (15 m x 0.25 mm ID) coated with DB-1[4] were used. The injection port and detector temperatures were 260° and 270°C, respectively.

A Hewlett-Packard 5895B GC/MS/DS was employed for coupled gas chromatography-mass spectroscopy (GC-MS). Fused silica columns (0.32 mm ID) coated with DB-1 (30 or 60 m) or DB-WAX (60 m)[4] were coupled directly into the ion source. The injection port, transfer line and ion source temperatures were 260°, 250° and 200°C, respectively. Helium was the carrier gas for GC and GC-MS.

2.3.4.2.2 Test of Known Female-Produced Volatiles

Reagent grade n-butyl butyrate and n-hexyl butyrate were tested alone and in a 2:1 ratio using four replicates in a completely randomized block design of 2 L ice-cream carton traps set in September, 1986, in a semi-dwarf orchard of 'Red Delicious', Agriculture Canada Research Station, Summerland, B.C.

The traps were separated within replicates by 5 m and between replicates by 10 m; limb-tap samples at the time of the experiment averaged 0.5 C. verbasci per tray with a sex ratio of 1:2 (male:female). Treatments evaluated were:

1. n-butyl butyrate, 0.2, 0.02, 0.002, or 0.0002 mL in 5 mL of paraffin oil;
2. n-hexyl butyrate, 0.1, 0.01, 0.001, or 0.0001 mL in 5 mL of paraffin oil;
3. a 2:1 (vol:vol) mixture of n-butyl butyrate + n-hexyl butyrate, 0.3, 0.03, 0.003, or 0.0003 mL in 5 mL of paraffin oil; and
4. 5 mL of lightweight paraffin oil (control).

The paraffin oil solutions were placed in 10 mL vials suspended from the center of 2 L ice-cream carton traps hung 1.5 m high just inside the apple tree canopy.

In a second experiment, the (2:1) combination of n-butyl butyrate and n-hexyl butyrate was tested alone or in combination with a 1% solution of hexyl acetate. The test site was an established second-year planting of V. thapsus grown in a 2 x 2 m grid. Traps were hung 1.5 m high on posts in a completely randomized design; treatments were spaced 5 m apart with 6 m between each of 3 replicates.

If appropriate, mean capture rates were subjected to statistical analysis and separation of the means by Tukey's Pairwise Comparison (SAS Institute 1985).

2.3.4.2.3. **Isolation and Identification of the Pheromone**

Isolation and identification of the sex pheromone of C. verbasci followed the protocol outlined in Fig. 13 Mullein bugs were mass collected from natural stands of V. thapsus and sorted by sex.

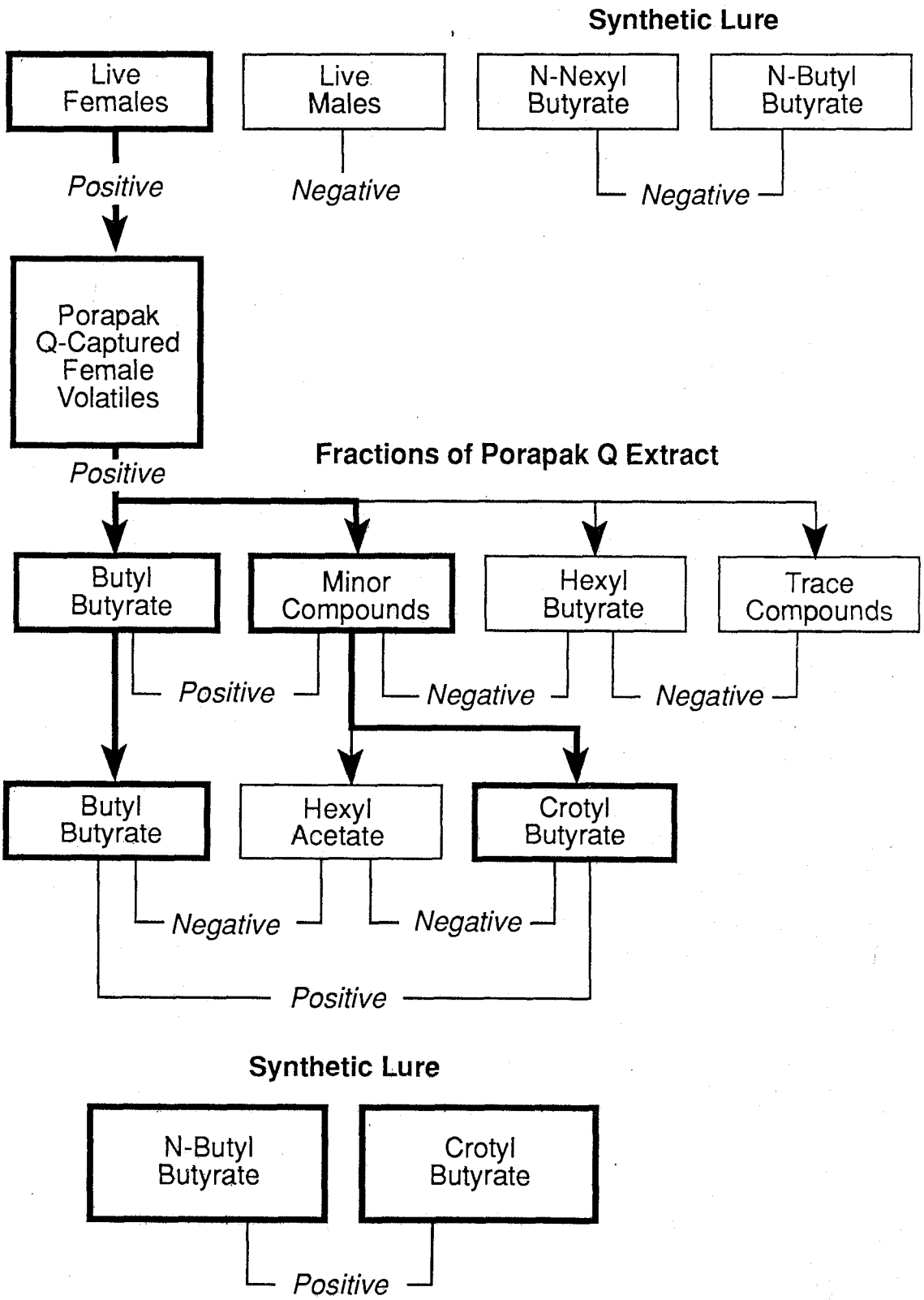
Some females were crushed in double distilled pentane at -40°C, and the extracts were stored at -20°C in screwcap vials with Teflon-lined lids. The strength of extracts was expressed as bug equivalents (b.eq.); i.e., one crushed female bug or any undiluted fraction thereof = 1 b.eq.

Volatiles from live C. verbasci females were also collected in Porapak Q (ethylvinyl benzene-divinyl benzene copolymer, 50-80 mesh, Applied Science Laboratories Inc.) using methods similar to those employed in capturing the pheromones of stored grain insects (Pierce et al. 1984). Air was drawn at a rate of ca. 4 L per min through a glass aeration chamber (30 cm O.D. by 50 cm) containing females on mullein stalks. The air passed through a humidifier and an air scrubber (2.4 cm O.D., by 12 cm) filled with 50-80 mesh activated coconut charcoal™. The apparatus was maintained under constant fluorescent light and an ambient temperature of ca 22°C. Under these conditions, females survived 7-10 days. The aeration chamber was cleaned and fresh plant material and female bugs added at approximately 48 h intervals. Captured volatiles were expressed as bug-hours (b.h.) (i.e., one b.h. = volatiles produced by 1 female for 1 h).

Porapak Q trapped volatiles. Volatiles from feeding female bugs or mullein were recovered by overnight extraction of the Porapak Q in a Soxhlet extractor with pentane. The solution was then concentrated to approximately 10 mL by distilling off the pentane through a 30 cm Dufton column.

Isolation of Volatiles by Steam Distillation. A micro steam distillation-continuous extraction apparatus

Figure 13 Flow chart depicting sequence of experiments culminating in the identification of the sex pheromone for C. verbasci.


Synthetic Lure
Live Females
Live Males
N-Nexyl Butyrate
N-Butyl Butyrate
Positive
Negative
Negative
Porapak Q-Captured Female Volatiles
Positive
Fractions of Porapak Q Extract
Butyl Butyrate
Minor Compounds
Hexyl Butyrate
Trace Compounds
Positive
Negative
Negative
Butyl Butyrate
Hexyl Acetate
Crotyl Butyrate
Negative
Negative
Positive
Synthetic Lure
N-Butyl Butyrate
Crotyl Butyrate
Positive

(Godefroot et al. 1985) was employed for the isolation of volatiles from the pentane extracts of crushed bugs.

Fractionation of Volatiles by Gas Chromatography and Preparation of Samples for Field Bioassays. The micropreparative gas chromatograph has been described elsewhere (Pierce et al. 1985). A stainless steel column (3.05 m x 3.18 mm OD) packed with 10% SP1000 on Supelcoport (100/120) was used for fractionation of steam-distilled or Porapak Q-trapped female volatiles. A portion of the solution containing total volatiles was set aside for field tests; the remainder of the sample was separated and concentrated under a stream of nitrogen at -10 to 0°C to approximately 30 µL before injection into the chromatograph. Fractions were rinsed from the collection tubes into 1 mL volumetric tubes containing ca. 200 µL of hexane or pentane which were transferred up to volume with hexane. Aliquots from these were transferred to screw cap vials for later release in field traps.

2.3.4.2.4. Bioassay of Extracts, Fractions and Candidate Pheromones

Because C. verbasci is difficult to work with in the laboratory, five bioassay experiments were done in the field at the Agriculture Canada Research Station, Summerland, B.C. Unless stated otherwise, all treatments were replicated four times in a completely randomized design. The 2 L ice-cream

carton trap with a sticky liner insert was used in all experiments, and set at a height of 1.5 m in both orchard and mullein field test sites. Those in an orchard were placed 0.5 m from the outer canopy edge. All bait receptacles were suspended inside the centre of the trap. Detailed experimental data are given in Table 11. Data were transformed to $\sqrt{(n + 0.5)}$ prior to statistical analysis to meet the assumptions for analysis of variance prior to Tukey's pairwise comparison of the means (SAS Institute 1985).

Crushed C. verbasci fractionates. In Exp. 1, fractionates of crushed bug extracts or unfractionated extracts were dissolved in 2 mL of pentane and held in a 5 mL glass vial. The screw cap for each vial was drilled to give a 2 mm vent. Traps were deployed in a mixed planting of 'Red Delicious' and 'Golden Delicious' for four days commencing 29 August 1986. Treatments were separated by at least 6 m, and replicates by 8 m. Migration to woody hosts had begun; limb-taps at this time averaged 1.25 bugs per tray in a ratio of 3.2 female per male. The unfractionated extract represented 100 b.eq.

Concentration response. Sensitivity of male C. verbasci to Porapak Q-collected pheromone or fractions thereof was field-tested in the above orchard site. Concentrated extract in a diethyl ether/pentane solvent was

transferred by syringe into a 2 mL centrifuge tube and the cap sealed. Treatments were extracts at 29,400, 9,800, and 2,900 b.h., solvent control (ether/pentane), and a caged-female control (five per trap). The caged female treatment was replicated three times; all other treatments had four replicates. This experiment was conducted over a 6 d period commencing 6 September 1987.

Porapak Q-Collected Fractions. Porapak Q extract fractions were syringed in Exp.3 into a 2 mL centrifuge tube through a 2 mm diam. hole in the cap. Fractions were tested at a strength of 8,000 b.h. Control stimuli were five caged females and solvent. The tests ran for 11 days commencing 21 September 1987, when third generation bugs were numerous in the orchards. The objective was to verify the activity zone, initially defined by the fractionates from the crude insect crushes. In particular, since the Porapak Q method was now the sole means of lure collection, confirmation of previous results served to double check this procedure's accuracy. This experiment was set in an apple orchard; live-caged females had three replicates, all others had four. A fourth experiment using 10,000 b.h. was undertaken in the same orchard to resolve whether butyl butyrate alone had any attractiveness.

The fifth and final experiment involving 7,000 b.h. was conducted to determine the identity of the minor component

that interacts in combination with butyl butyrate. It was set up in a mullein field setting in a 2 x 2 m grid in August 1988. There were 4 m between treatments and 8 m between replicates; the mullein field was heavily populated with teneral, third-generation C. verbasci.

Concentration response to synthetic sex lure. Synthetic n-butyl butyrate and crotyl butyrate were field tested (16:1 w/w) in a 3-replicate concentration response experiment conducted in September 1988 in a 'Bartlett' pear orchard. This orchard block had a history of abundant C. verbasci populations and at the time of the experiment, third generation adults were depositing overwintering eggs. Persistence of the lure was enhanced by mixing the butyrates with lightweight paraffin oil. Treatments were 4 mL oil in a 6 mL glass vial containing butyl/crotyl butyrate (16:1) at 2%, 1%, 0.1% and 0.01%, paraffin oil controls and caged-female controls. Numbers of males captured were transformed to $\sqrt{(n + 1)}$ prior to statistical analysis and pairwise comparison of the means using Least Significant Difference t test (SAS Institute 1985).

Comparison of synthetic lure release devices. Butyl butyrate and crotyl butyrate (16:1, w/w) were field tested as candidate pheromones in three release devices and compared to five live-caged females for attraction of males. Dispensers were: 1) coagulation tubes 0.98 ± .03 mm I.D.

x 40 mm, 2) capillary tubes 1.21 ± .03 mm I.D. x 40 mm, and 3) 5.3 dram glass vials. Four μL of the butyrate mixture was transferred by syringe into the tubes, while the lure for the 5.3 gram vial was mixed in 4 mL lightweight paraffin oil. All dispensers were suspended from the center of a 2 L carton trap, hung at 1.5 m in an orchard block of 'Red Delicious', September, 1988. Traps were set in a completely randomized design with each treatment having three replicates. Data were transformed to $\sqrt{(n + .5)}$ prior to ANOVA and Least Significant Difference test, $P < 0.05$, SAS Institute 1985.

Release rate for both coagulation and capillary tubes was determined in the laboratory (25° ± 1°C) by measurement of daily evaporation rate. Depletion of 5 μL synthetic lure was monitored in seven tubes for each device type and regression of the miniscus incorporated into the following equation to estimate release rate per day:

$$\frac{\pi \cdot r^2 \cdot l \cdot d}{t}$$

where r = radius of tube (cm)

l = length of miniscus regression (cm)

d = density of lure (0.856 g/mL)

t = observation time (days)

2.3.4.3. Results and Discussion

2.3.4.3.1. Inactivity of Known Volatiles

Gas chromatograms of volatiles from female and male C. verbasci are shown in Fig. 14. Although butyl and hexyl butyrate are dominant compounds in the volatiles from females, neither butyrate alone, or in combination, lured mullein bugs of either sex to traps in the apple orchard setting (Table 10). Moreover, hexyl acetate also had no attractive effect.

In the female volatiles, there were several minor and trace components (Fig. 14). Since butyl butyrate is female specific, I hypothesized that it and at least one of the minor components acted synergistically. To identify this compound, the female volatiles were fractionated and the field bioassay was used to guide and monitor the progress of its isolation.

2.3.4.3.2. Activity of Extracts, Fractions and Candidate Pheromones

Crushed C. verbasci fractionates. The progression of experiments leading to isolation and identification of the mullein bug sex pheromone is given in Fig. 13. Pheromone activity was centered in fraction #2 of the bug distillate extract (Fig. 14a) including butyl butyrate and minor

Figure 14 Gas chromatograms of C. verbasci volatiles. A) volatiles from steam distillate of females; B) Porapak Q-trapped volatiles from females feeding on mullein; and C) volatiles from steam distillate of males. BB = butyl butyrate, HA = hexyl acetate, CB = 2 (E) -crotyl butyrate, H = 1 -hexanol, HB = hexyl butyrate, and O = 1-octen-3 ol (from mold growing on mullein).

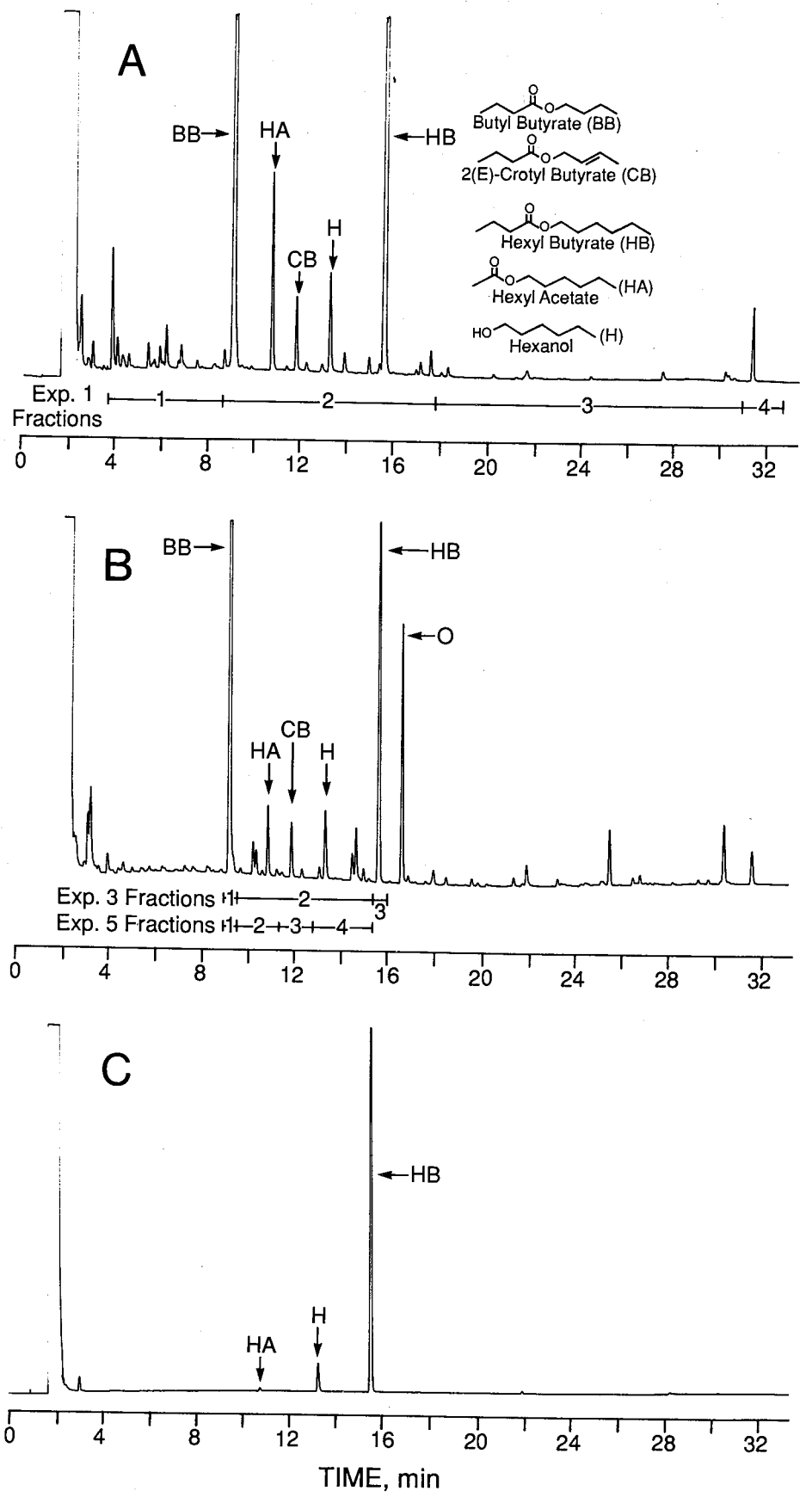

A
BB
HA
CB
H
HB
Butyl Butyrate (BB)
2(E)-Crotyl Butyrate (CB)
Hexyl Butyrate (HB)
Hexyl Acetate (HA)
HO
Hexanol (H)
Exp. 1 Fractions
1
2
3
4
0
4
8
12
16
20
24
28
32
B
BB
HB
O
CB
HA
H
Exp. 3 Fractions
Exp. 5 Fractions
1
2
3
4
C
HB
HA
H
TIME, min

Table 10 Response of C. verbasci to synthetic lure components tested in an apple orchard (Experiment #1, four replicates) and in a field of mullein (Experiment #2, three replicates).

Exp. No.	Lure	Vol. mL of test materials in 5 mL paraffin oil	No. bugs trapped (± S.E.)* Males	Females
1	n - butyl butyrate	0.2	.25	--
		0.02	0	--
		0.002	0	--
		0.0002	0	--
	n - hexyl butyrate	0.1	0	--
		0.01	0	--
		0.001	0	--
		0.0001	0	--
	n - butyl butyrate + n - hexyl butyrate (2:1) (v:v)	0.3	.25	--
		0.03	.25	--
		0.003	.25	--
		0.0003	.50	--
	mineral oil	--	0	--
2	n - butyl butyrate + n - hexyl butyrate + hexyl acetate (1%) (2:1)	0.3	4.0 ± 0.6	5.7 ± 2.0
		0.03	5.0 ± 1.7	2.7 ± 1.6
		0.003	2.3 ± 0.9	3.7 ± 1.2
		0.0003	3.7 ± 0.7	7.0 ± 1.0
	hexyl acetate	0.003	6.7 ± 1.9	6.7 ± 0.9
	mineral oil	5.0	6.7 ± 1.2	4.0 ± 1.2

*In neither experiment was there a significant difference between the means, Tukey's Pairwise Comparison test, $P > 0.05$ (SAS Institute 1985).

compounds eluting after it and before hexyl butyrate (Table 11, Exp. 1). The total extract, despite being 1.5 times less concentrated, trapped numbers of males. Because the bug crush technique rapidly depleted the limited supply of available C. verbasci, further efforts were concentrated on Porapak Q-collected volatiles.

Concentration response. Porapak Q-captured female volatiles were as active at 29,400 b.h. as five females (Table 12, Exp. 2). Attraction was less at 9,800 or 2,900 b.h., but still higher than the solvent control at the latter concentration. The capture rates in comparison to that of live females may be misleading because the longevity of the extracts was < 4 days and attraction must have declined rapidly once they were placed in the traps.

Porapak Q-collected fractions. The Porapak Q extract and a combination of fractions #1 and #2 (Fig. 14b) achieved captures approaching those of caged females (Table 11, Exp. 3, 4), verifying the response to fraction #2 of the female extract (Table 11, Exp. 1). Hexyl butyrate (fraction #3) did not influence male captures either alone (Table 10) or in combination with other fractions (Table 11, Exp. 1,3). Therefore, hexyl butyrate was eliminated as a candidate semiochemical. Butyl butyrate alone was inactive (Tables 10, 11) yet attraction was achieved when it was combined with the minor compounds in fraction #2, which in turn were

Table 11 Captures of male C. verbasci in traps baited with fractions of crushed female extract or the extract of Porapak Q-captured female volatiles, 1986-1988.

Exp. no. and description	Treatment*	Stimulus strength	No. of replicates	Mean no. males captured ± S.E.b
1 Crushed bug fractions	Female extract	100 b.eq.	3	17.3 ± 1.8b
	Fraction #1	250 b.eq.	4	0.3 ± 0.3d
	Fraction #2	250 b.eq.	4	35.8 ± 5.4a
	Fraction #3	250 b.eq.	4	0.5 ± 0.3cd
	Fraction #4	250 b.eq.	3	2.0 ± 0.6c
	Pentane	5 mL	4	0.0 ± 0.0d
2 Concent. response Porapak Q collected volatiles	5 live females		3	8.3a
	Captured volatiles	29,000 b.h.	4	5.8ab
	Captured volatiles	9,800 b.h.	4	3.3bc
	Captured volatiles	2,900 b.h.	4	2.0c
	Pentane	5 mL	4	0.0d
3 Porapak Q extract fractions	5 live-caged females		4	17.0 ± 3.8a
	Porapak Q extract	8,000 b.h.	4	8.3 ± 0.6b
	Fractions #'s 1 and 2	8,000 b.h.	4	11.5 ± 3.6ab
	Fraction #2	8,000 b.h.	4	0.5 ± 0.5c
	Fraction #'s 2 and 3	8,000 b.h.	4	0.0c

Table 11 (continued)

Exp. no. and description	Treatment[a]	Stimulus strength	No. of replicates	Mean no. males captured ± S.E.[b]
4 Porapak Q extract, test of Fraction 1 (butyl butyrate) alone	5 live-caged females		3	7.7 ± 1.2a
	Porapak Q extract	10,000 b.h.	4	12.1 ± 1.1a
	Fraction #'s 1 and 2 from from Exp. 3	10,000 b.h.	4	9.8 ± 2.9a
	Fraction #1 from Exp. 3	10,000 b.h.	4	0.0b
5 Porapak Q extract, identity of minor component	5 live-caged females		4	5.0 ± 0.6a
	Porapak Q extract	7,000 b.h.	4	4.0 ± 0.4ab
	Fraction #1 + crotyl butyrate		4	3.3 ± 0.6b
	Fraction #1 + hexyl acetate		4	1.0 ± 0.5c
	Hexane	5 mL	4	1.1 ± 0.5c

[a]Fraction numbers correspond to those on GLC traces of female extracts or extracts of Porapak Q-captured female volatiles (Fig. 14).

[b]Means followed by a common letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison test, SAS Institute 1985.

Table 12 Mean number of male C. verbasci captured in concentration response experiment with butyl and crotyl butyrate (16:1) in 4 mL paraffin oil. Each treatment was replicated three times in a completely randomized design in an apple orchard, September 1988.

Synthetic lure concentration	No. of males caught ($\bar{x}$ ± S.E.)*
2.0%	11.3 ± 2.3a
1.0%	8.7 ± 1.3a
0.1%	4.3 ± 1.8b
0.01%	2.0 ± 0.6bc
5 live females	1.0 ± 0.6c
Blank only	0.0 ± 0.0c

*Means followed by a common letter are not significantly different, $P < 0.05$, Least Significant Difference test, SAS Institute 1985.

inert when tested alone (Table 11, Exp. 3). Further research then focused on these minor compounds.

Structure of peak CB. The mass spectrum of peak CB exhibited a base peak at m/z 89 ($C_4 H_9 O_2^+$), the base peak in the spectrum of butyl butyrate (MW = 144). Since females of several Lygus spp. contain and emit hexyl and 2 (E) -hexenyl butyrate (Aldrich et al. 1988), peak CB was hypothesized to be an unsaturated companion to butyl butyrate, i.e., 2 (E)-crotyl butyrate. Comparison of the mass spectrum and retention time of the unknown to those of the synthetic sample confirmed this hypothesis.

Present in both male and female volatiles were hexyl acetate and 1-hexanol. These compounds were identified by GC-MS and search of reference spectra. The assignments were confirmed by comparison of their mass spectra and retention times to authentic samples.

GC-MS revealed crotyl butyrate and hexyl acetate as two of the trace chemicals in fraction 2. Recombining crotyl butyrate, but not hexyl acetate, with butyl butyrate gave capture rates equalling those of the complete extract and approaching that of the five live-caged females (Table 11, Exp. 5).

Concentration response to synthetic lure. More male C. verbasci were trapped using synthetic lure at 1.0% and 2.0% concentration than at lower concentrations (Table 12). A concentration as low as 0.1% induced a significant response even under field conditions using a crude pheromone dispenser. Possibly an improved release device would enhance and prolong lure persistence.

Comparison of synthetic lure release devices. Attraction of the lure in three release devices equalled that of live females (Table 13). Therefore, I conclude that there is a 2-component pheromone in C. verbasci comprised of butyl butyrate and crotyl butyrate and that these occur naturally in a ratio of 16:1 (Fig. 14). This is the first successful identification of a sex pheromone in the family Miridae.

2.4. Temperature-Based Prediction Models to Forecast C. verbasci Egg Hatch and Field Development.

2.4.1. General Introduction

For all temperature-based prediction models, basic assumptions must be made and certain biological parameters determined. In these models rate of development by insects is predominantly governed by temperature. Enzyme-catalyzed reactions within the organism are assumed to be limited by temperature and the insect is perceived as incapable of regulating its own body temperature. The models assume that

Table 13 Mean number of male C. verbasci captured in traps using three lure release devices containing 4 μL of synthetic lure. Each treatment was replicated three times in a completely randomized design in an apple orchard, September 1988.

Release device	Release rate[b]	No. of males caught (± S.E.)[a]
Coagulation tube	1.63 ± .076	11.7 ± 1.5a
Capillary tube	0.34 ± .013	7.7 ± 1.9ab
5.3 gram vial	0.25	5.7 ± 1.8b
Unbaited control	--	0.0c
5 live-caged females	--	11.0 ± 2.9ab

[a]Means followed by a common letter are not significantly different, $P < 0.05$, Least Significant Difference test, SAS Institute 1985.

[b]Release rate g/day ($\times 10^{-4}$) determined at 25° ± 1°C in the laboratory.

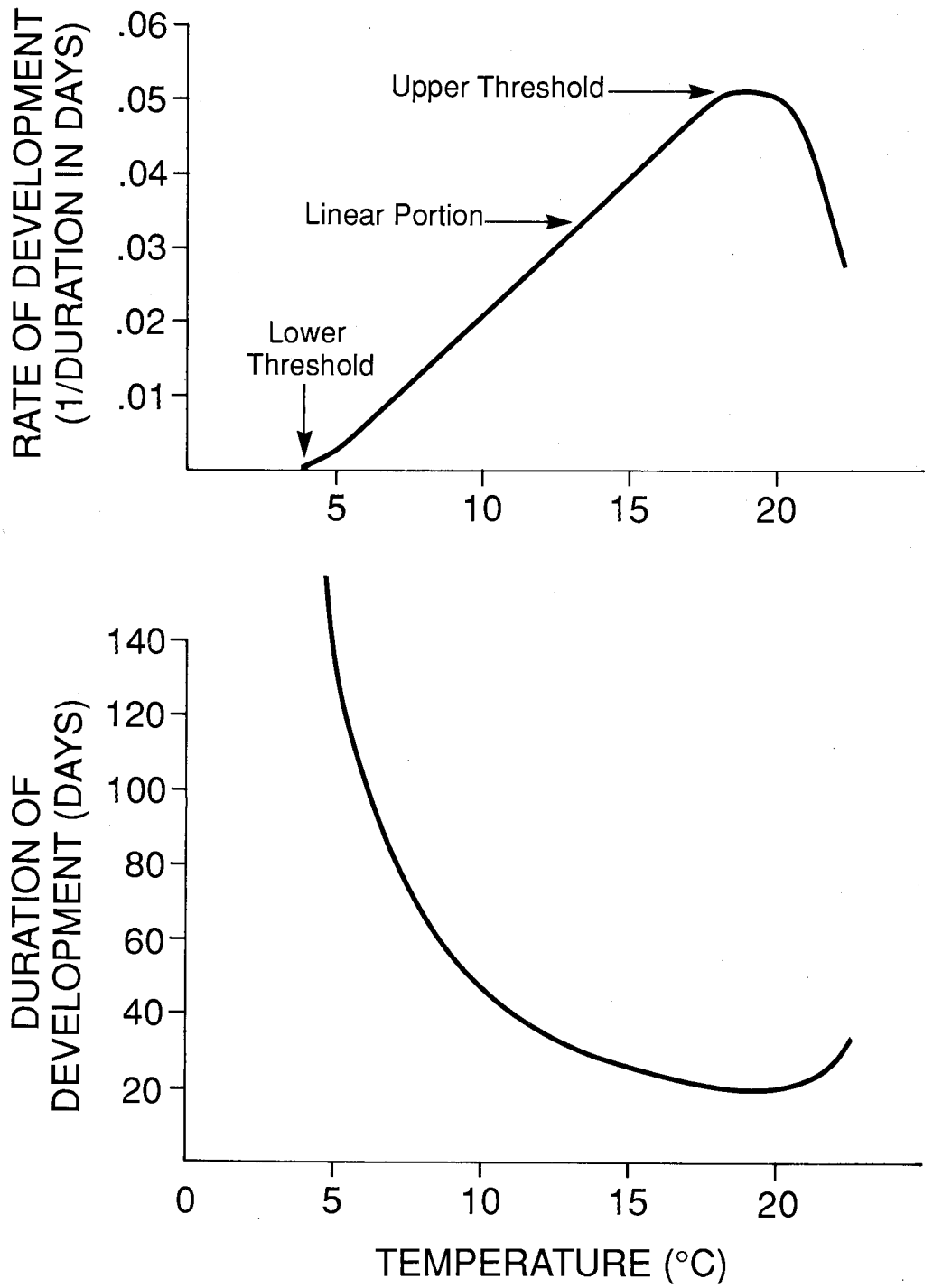
air temperatures as recorded at a meteorological station represent conditions experienced by the insect in its microhabitat. A fundamental difficulty is to know when to begin the collection of temperature data. This decision is particularly troublesome when dealing with overwintering life stages for which little is known about diapause termination (e.g., C. verbasci overwintering eggs).

Once diapause ceases to inhibit development, temperatures above the species' developmental threshold permit growth to occur (Fig. 15 top). In a narrow perspective, lower threshold has been defined as a temperature below which no detectable development occurs (Campbell et al. 1974). The determination of this estimated value is an essential component of any predictive model.

There is an upper threshold, above which growth proceeds at a suboptimal rate (Fig. 15 bottom). In a temperate climate post-diapause development in the spring seldom involves prolonged exposure to these upper temperatures and incorporation of this parameter into temperature-based model may be considered optional (Higley et al. 1986). Physiological time can be gauged in degree-days; 1 degree-day unit equals 1° above lower threshold over 24 h (Zalom et al. 1983).

Degree-day models are but one temperature-based predictive tool proposed in pest management; their use in a

Figure 15 Development time (top) and development rate (bottom) for hypothetical organism in relation to temperature.


RATE OF DEVELOPMENT (1/DURATION IN DAYS)
.06
.05
.04
.03
.02
.01
Upper Threshold
Linear Portion
Lower Threshold
5
10
15
20
DURATION OF DEVELOPMENT (DAYS)
140
120
100
80
60
40
20
0
5
10
15
20
TEMPERATURE (°C)

pest management system depends on several factors including ease of implementation, costs incurred, and a basic assumption that the degree-day approach yields a net gain in accuracy compared with presently used methods.

Complicating the wide-spread validation and use of degree-day models is the common occurrence of geographically-based biotypes that differ in their responses to temperature (Campbell et al. 1974, Tauber and Tauber 1976). Most temperature-based models deal with a single insect species, e.g., those for the western cherry fruit fly, Rhagoletis indifferens Curran (Van Kirk and Aliniazee 1981), and the bagworm, Thyridopteryx ephemeraeformis (Haworth) (Neal et al. 1987). However, Pruess (1983) urges merging of multiple species' components into one model that would also incorporate degree-day development of the agricultural crop. This approach might enhance acceptance and utility of the model with necessary adjustments made as needed for adoption into other locations.

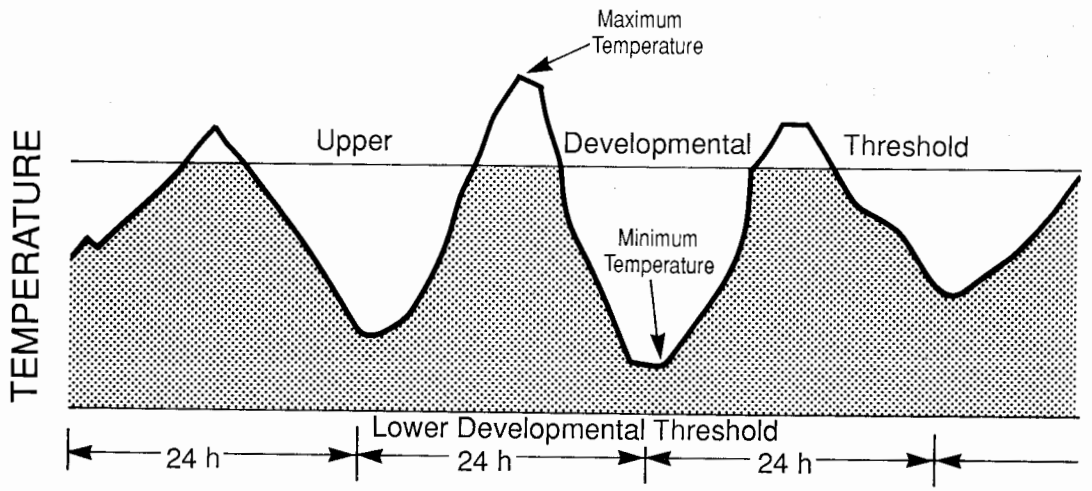
Several techniques can be used to derive accumulated degree-day units for a particular 24 h interval; each involves assumptions concerning the area (shading, Fig. 16) between the developmental threshold and temperature curve. 'Simple averaging' (Funderburk et al. 1984), 'sine wave' (Allen 1976), 'triangle method' (Stark and Aliniazee 1982), and the 'rectangular approach' (Arnold 1959) are examples of

the calculation methods available. All are considered linear models because rate of development is presumed to be a straight line directly related to temperature as in the linear portion of the hypothetical curve (Fig. 16). Pruess (1983) reviews assumptions and virtues of each and suggests that the 'sine wave' most closely approximates temperature accumulation for springtime in temperate regions.

Presently in B.C., 3, 5 and 10 days post-bloom are suggested as times for sampling the nymphal population of C. verbasci eggs (B.C. Min. Agric. and Fish. 1989). The assumption is made that at least one of the three intervals will encompass the majority of egg hatch. However, this method has not been rigorously tested. The standard limb-tap technique used to monitor nymphal density would be inaccurate if sampling were conducted before 50% hatch occurred.

My objectives were: to estimate durations of embryonic development at different controlled temperatures; to use these data to derive a lower developmental threshold for C. verbasci which would then be incorporated into a degree-day model to describe mullein bug development; and finally, to compare the model's performance in B.C. orchards with simple three year mean Julian day predictors and the recommended 3, 5 and 10 d post-bloom samples (B.C. Min. of Agr. & Fish. 1989).

Figure 16 Hypothetical three day interval depicting developmental thresholds and degree-day accumulation (shaded area).


Maximum
Temperature
Upper
Developmental
Threshold
TEMPERATURE
Minimum
Temperature
Lower Developmental Threshold
24 h
24 h
24 h

2.4.2. Determination of lower hatch threshold for *C. verbasci* eggs

2.4.2.1. Introduction

The small size and cryptic nature of overwintering *C. verbasci* eggs within the fruit wood (Sanford 1964b) preclude counts of their abundance or mortality. The effect of fluctuating temperature and other environmental factors on mirid embryonic development and hatch are unknown. Presumably gas and moisture exchanges occur between eggs and their microhabitat. Temperature is assumed to play a prominent role in embryonic development driving enzyme-mediated reactions that are linear within a yet undetermined range of temperatures. Even if the relationship is not linear, it may be possible to use linear models through choice of "effective" rather than "actual" developmental thresholds; the results may yield a practical predictor (Pruess 1986).

The first objective was to test the null hypothesis that no relationship existed between temperature and time to hatch. A second objective of this study was to document developmental time under controlled environmental conditions and, by using rate of development (the reciprocal of duration), derive an estimated lower threshold.

Note that by taking the reciprocal of duration, rate of development is expressed as the proportion of total

developmental time taken per day. These data could then be incorporated into an appropriate temperature-based predictive model to improve timing of the limb-tap sampling of orchard blocks for the evaluation of C. verbasci nymphal density. Currently, there is a potential sampling error because there is no means of predicting what percent of overwintering eggs have hatched.

Summer populations of C. verbasci ultimately produce a fall generation which oviposits overwintering eggs; these yield nymphs that inflict damage on sensitive varieties of apples. Tracking this mirid's summer development with a temperature-based model may aid in a pheromone-based trapping protocol for telling when peak numbers will begin migration to orchards. Therefore, estimations of developmental time and, ultimately, hatch threshold were sought. This was accomplished through controlled temperature incubations of C. verbasci eggs from the laboratory colony reared on eggplant.

2.4.2.2. Materials and Methods

Overwintering eggs. During the winter of 1987-1988, fruit wood containing post-diapause overwintering eggs of C. verbasci was collected from several orchard sites at Summerland, B.C. Thirty to 40 cm sections of wood were incubated at constant temperatures ranging from 10° to 30°C (± 0.5°C) in controlled environment cabinets set for a

16:8 h L:D photoperiod and 60% R.H. In addition to the constant 10°C temperature, one cabinet was set to cycle between 8° and 12°C in 0.5°C hourly increments to give a 24 h mean of 10° ± 0.5°C; all other conditions were identical to those in other cabinets. Wood was checked daily for neonates, misted with distilled water to deter desiccation and returned immediately to its incubation temperature.

As previously indicated, the reciprocal of mean days for hatch (1/days) is an expression of developmental rate. By plotting the rates derived from constant temperature experiments versus incubation temperature, the range of temperatures within which rate of development responds linearly to temperature could be determined. At least three temperature regimes were used to estimate developmental threshold in each experiment. Apple varieties were evaluated separately in 14 runs; three each on 'Spartan', 'McIntosh' and 'Golden Delicious' and five on 'Red Delicious'. Each experiment used 10 - 15 branches of fruit wood at each temperature.

Because field hatch of C. verbasci eggs was not influenced by host apple variety (see Section 2.2.2), developmental thresholds were pooled. A general lower threshold temperature for development was then calculated as the mean of the 14 estimated values derived from regressing

developmental rate (within the linear region) against temperature.

Nondiapausing summer eggs. Teneral C. verbasci were collected from a colony established on eggplant and multiple pairs were confined for 24 h at 22°C on individual eggplant seedlings infested with T. urticae. The seedlings were then incubated at 20°, 22°, 25° or 27° (± 0.5°C). Plants were checked daily; neonates were counted and removed. In a similar manner to that used for overwintering eggs, regression analysis was performed on rate of development against temperature to derive an approximate lower threshold temperature for development.

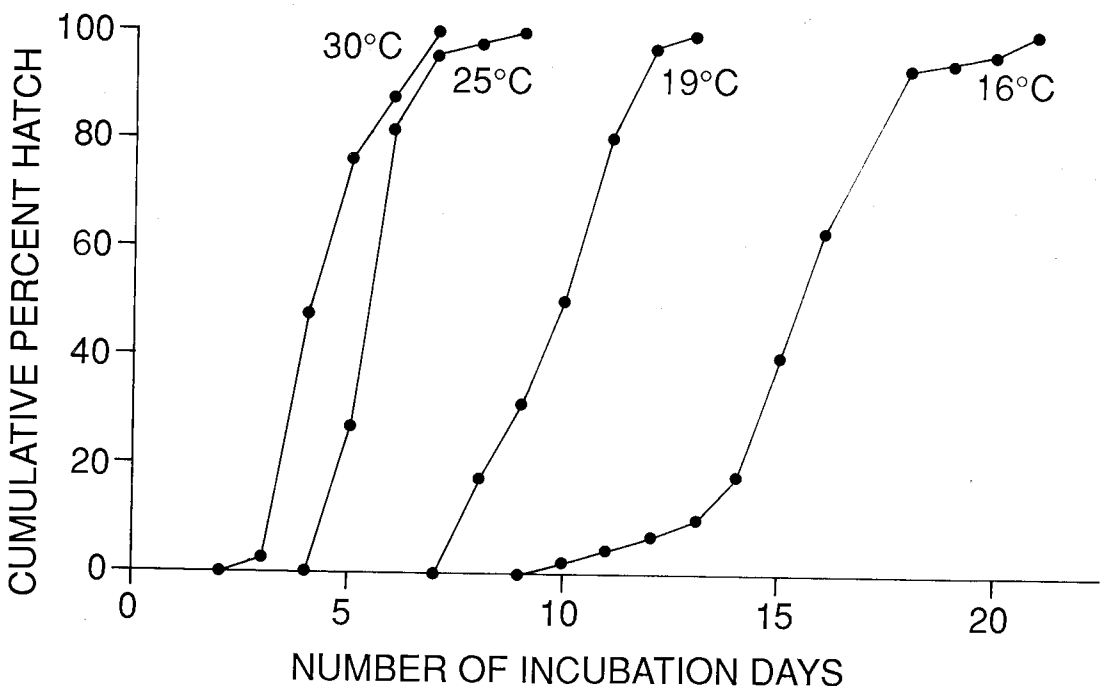
2.4.2.3. Results and Discussion

Overwintering eggs. Hatch proceeded most rapidly at the highest constant temperature as exemplified by samples shown in Fig. 17. First hatch occurred on days 3, 5, 8 and 10, respectively at 30°, 25°, 19° and 16°C.

No hatch occurred at a constant 10°C, or at fluctuating temperatures having a mean of 10°C during the 120 d observation period. Similarly, Champlain and Butler (1966) reported that non-diapausing eggs of Lygus hesperus Knight did not hatch at a constant 10°C.

Regression of developmental rate with temperature gave a reasonable fit with r^2 values ranging from 0.71 to 0.96

Figure 17 Cumulative percent hatch of C. verbasci overwintering eggs from 'Red Delicious' apple taken from the field 6 April 1987 (Julian day 096), Summerland, B.C. and incubated at one of four constant temperatures.


CUMULATIVE PERCENT HATCH
100
80
60
40
20
0
30°C
25°C
19°C
16°C
0
5
10
15
20
NUMBER OF INCUBATION DAYS

(Table 14). The 14 samples in Table 14 gave a mean estimated lower developmental threshold of 9.9° ± 0.2°C (range 9.2° to 10.7°C). A typical data set for 'Red Delicious', sample day 096, (Fig. 18 left) yielded the equation:

Rate of development = - 0.12323 + 0.011747 Temperature.

Data sets were too few for statistical comparison of thresholds from different apple varieties on any one sample date. For the same sample day (Julian day 096) 'Spartan' and 'Golden Delicious' gave slightly lower estimated thresholds, 8.9° ± 0.5°C and 9.6° ± 0.1°C respectively, while 'McIntosh' (10.4° ± 0.2°C) was close to the predicted value given by 'Red Delicious' (10.3° ± 0.4°C). For further modelling the pooled value was rounded to the nearest integer and treated as an estimate of 10°C.

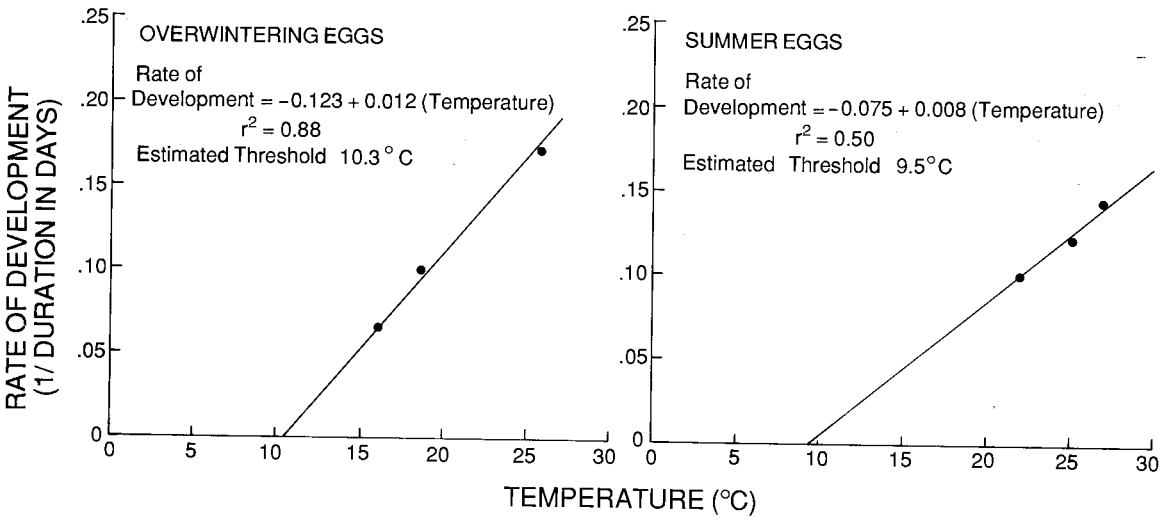
Nondiapausing summer eggs. Rate of development for summer eggs was nearly linear in relation to temperature within the range tested (Fig. 18 right), and regression analysis estimated 9.5°C as the lower threshold. This is similar to Champlain and Butler's (1966) 10°C estimate for hatch threshold for Lygus hesperus eggs.

Incubation temperatures were generally within the range encountered in the field by C. verbasci on herbaceous plants

Table 14 Estimated lower threshold for hatch of overwintering C. verbasci eggs incubated at constant temperatures. Date represents days from 1 January 1987. Only developmental rates within the linear portion of the development curve (Fig. 18) were used in the regressions of developmental rate against temperature.

Sample Date	Variety	Temperature (°C)	Estimated Threshold	r^2
082	Spartan	16,22,25	9.4	0.87
090	Spartan	16,19,22,25	10.6	0.90
096	Spartan	16,19,25,30	8.9	0.89
079	Golden Delicious	16,19,22,25	9.6	0.84
090	Golden Delicious	16,19,22,25	9.9	0.85
096	Golden Delicious	16,19,25,30	9.6	0.77
082	McIntosh	16,19,22	9.8	0.89
096	McIntosh	16,19,25,30	10.4	0.84
110	McIntosh	16,19,25,30	9.9	0.71
082	Red Delicious	16,19,25	9.2	0.96
082	Red Delicious	16,22,25	10.7	0.95
082	Red Delicious	16,19,22,25	10.7	0.86
091	Red Delicious	16,19,22,25	9.9	0.86
096	Red Delicious	16,19,25,30	10.5	0.87

Figure 18 Relationship between hatch rate and incubation temperature for C. verbasci overwintering eggs in 'Red Delicious' sampled day 096 (left) and summer eggs in eggplant (right). Line represents regression equations derived from calculations. Rate of development for winter eggs at 30°C was 0.215; summer eggs at 20°C was 0.075; both values were slightly off the linear portion of development and therefore not included in formulation of the regression equations.


OVERWINTERING EGGS
Rate of
Development = −0.123 + 0.012 (Temperature)
r² = 0.88
Estimated Threshold 10.3 °C
SUMMER EGGS
Rate of
Development = −0.075 + 0.008 (Temperature)
r² = 0.50
Estimated Threshold 9.5°C
RATE OF DEVELOPMENT
(1/ DURATION IN DAYS)
.25
.20
.15
.10
.05
0
0
5
10
15
20
25
30
TEMPERATURE (°C)

with the possible exception of 20°C. It is acknowledged that host plant (e.g., eggplant) may have an impact on embryonic development and subsequent rate of hatch. A comparison of developmental rates between populations raised on eggplant and common mullein, V. thapsus, would provide useful data.

2.4.3. Embryonic development below the estimated hatch threshold.

2.4.3.1. Introduction

Embryonic development is a complex process possibly having many temperature thresholds (Howe 1967). Threshold temperatures below which hatch will not occur may be independent of the threshold temperature for embryonic development. Chapman (1982) suggests that three thresholds could be present for any species, one at which 'some' development takes place, another for 'full embryonic development' and a third for 'eclosion'.

From section 2.4.2.1, I have established 10°C as an approximate lower threshold for hatching. It remains to be determined whether embryonic development proceeds below this temperature. If this were verified, the prediction of field hatch may be complicated and more than one threshold might need to be incorporated into a temperature-based model.

It is unknown at what stage of development C. verbasci enter diapause; post-diapause overwintering eggs incubated at constant temperatures show a unimodal frequency distribution of hatching about the mean duration of development with an occasional skewed tail towards 100% hatch (Fig. 4). This pattern suggests that embryonic development is synchronized early in the post-diapause period.

My objective was to determine if embryonic development was occurring at or below 10°C. in the overwintering eggs.

2.4.3.2. Materials and Methods

Thirty to 40 cm sections of fruit wood were cut from 'Spartan' apple trees at Winfield, B.C. on 13 February 1988. Weekly samples indicated that diapause in C. verbasci eggs had terminated by this date. Samples were stored with cut ends set in jars of water, placed in a controlled environment cabinet at 10° ± 0.5°C with a 16:8 h L:D photoperiod (commencing 06:00 h, 37.9 μ E s^{-1} m^{-2}, 3018 lux) and 60% R.H.

To deter desiccation, branches were misted daily with distilled water. Prior experiments indicated that hatch would not occur at 10°C when branches were incubated for > 120 days. A subsample taken from the collection was set directly in a growth cabinet with similar light and humidity

but held at 22° ± 0.5°C. At 10 d intervals, six consecutive subsamples were taken from the 10°C cabinet. These were incubated at 22°C and examined daily for neonate nymphs by tapping individual branches with several sharp blows over a white enamel tray (60 x 30 cm). Examination of each subsample was continued until five days elapsed with no further egg hatch noted. A final portion of infested wood was held at 10°C for a total of 90 days and checked daily for neonates.

In a similar manner, branches taken from the same orchard were held at 1° ± 0.5°C. Subsamples were removed and incubated at 22°C after 16, 27, 37, 54 and 87 d.

2.4.3.3. Results and Discussion

There was no accurate means of determining egg mortality or abundance prior to hatch and early attempts to assess these factors proved unreliable (unpublished data). No C. verbasci eggs hatched from wood held at 10°C for 90 days.

Although overwintering eggs did not hatch at 10°C, embryonic development was in progress as suggested by the reduced time for hatch when subsamples were subsequently incubated at 22°C (Table 15). Mean days for complete hatch declined from an initial 17.9, to 4.6 d after only 60 d held at 10°C.

A similar trend occurred for C. verbasci eggs held at 1°C and incubated at 22°C (Table 15). The duration required for 100% hatch showed a significant decline after only 16 d at 1°C. Prolonged exposure to this temperature may have adversely affected developing embryos and was reflected in the increased duration of development for those hatching after 87 d at 1°C.

It remains unknown at what point embryonic development is initiated in C. verbasci overwintering eggs. Possibly development may begin shortly after oviposition in late fall. An unseasonally warm autumn might advance eggs to a stage at which post-diapause growth above the 10°C "hatching threshold" would cause serious inaccuracies in a degree-day model's predictive ability.

Conversely, further research may yield information that would allow incorporation of pre-diapause growth into a model. Attempts to use degree days (base 10°C) from fall through to field hatch in a predictive capacity proved very inaccurate (unpublished data) suggesting that there was a nonlinear relationship for embryonic development prior to diapause termination.

Table 15 Mean number of days for 100% hatch of C. verbasci overwintering eggs laid in fruit wood of the variety 'Spartan' held at 10°C or 1°C and subsequently incubated at 22°C.

Holding temperature	Days held	Number of days ($\bar{x}$ ± S.E.) for hatch	Number of nymphs
10°± 0.5°C	0	17.9 ± 0.25a	115
	10	12.1 ± 0.19b	157
	20	10.8 ± 0.09c	210
	30	8.5 ± 0.12d	131
	40	7.5 ± 0.09e	114
	50	5.8 ± 0.17f	62
	60	4.6 ± 0.13g	78
1°± 0.5°C	0	17.9 ± 0.25a	115
	16	12.3 ± 0.07bc	260
	27	12.2 ± 0.12bc	119
	37	11.5 ± 0.08d	127
	54	11.3 ± 0.24cd	26
	87	12.6 ± 0.23b	51

* Means sharing a common letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison, General Linear Model (SAS Institute 1985).

2.4.4. Test of Temperature-based models in the prediction of C. verbasci egg hatch.

2.4.4.1. Introduction

Presently, pest managers must use limb-tap monitoring at 3, 5 and 10 d after bloom (B.C. Min. Agric. and Fish. 1989) because it is unknown when C. verbasci egg hatch has finished. If a more precise predictor than this time interval can be found, considerable savings would be realized. In my three field seasons of observations, spring hatch and full bloom varied considerably from year to year (Table 1), yet it is unknown if hatch and bloom are strongly correlated. A temperature-based predictive model may prove useful in optimizing the timing of limb-tap sampling for C. verbasci in the spring.

Prediction of 1st and 50% hatch may have merit in the timing of control measures, especially if a pheromone-based monitoring system in the autumn could forecast potential economic injury by the subsequent spring generation. More important is the estimation of 90% and 100% hatch in conjunction with the limb-tap sampling method. An accurate prediction of these proportions hatched should enable one-step sampling with reasonable assurance that the limb-tap technique is portraying true nymphal density. Thus, a single sample could replace the currently recommended three

repeated samples, and at the same time yield more reliable data.

2.4.4.2. Materials and Methods

Degree-day model. A computer program was written to calculate accumulated degree days using maximum and minimum daily temperatures (Appendix A). This was similar to a program for the personal computer written by Higley et al. 1986, but my version had the speed and storage capacity associated with a mainframe VAX computer. An average data set containing 365 days' temperature records took less than 5 sec. to calculate degree-days determined by the sine, rectangular and triangular methods. The program generates a report file which can be printed at the researcher's convenience.

My first objective was to determine if degree-days would accurately describe C. verbasci egg hatch and secondly, to resolve which method (among the degree-day estimates) gave the best prediction. Lower and upper hatching thresholds of 10°C and 30°C were used for these evaluations.

Overwintering egg hatch. In each of four areas weather stations in close proximity to orchard study sites were carefully chosen to represent the most appropriate temperature records. Maximum and minimum daily temperatures

were recorded at each geographically distinct orchard site; most temperature records were taken within 0.5 km of the orchards.

Although the exact date for diapause termination is unknown, it has been demonstrated typically to end during mid- to late-December (McMullen and Jong 1970b), (Section 2.0); therefore, commencing 1 January, mean numbers of degree-days during 1986-1988 were calculated and cumulative totals established for observations of first, 50%, 90% and 100% field hatch of overwintering eggs. Actual days for each year and location correspond to accumulated degree-days taken from the report file generated by the computer model. Absolute differences between actual and projected percent hatches were compared for the 1986-1988 study period.

Nondiapausing eggs. Eggplant infested with twospotted spider mite served as an oviposition site for C. verbasci raised in a laboratory colony (Section 2.2.3). Following a 24 h oviposition period, plants were incubated at constant temperatures of 20°, 22°, 25°, or 27°C under a 16:8 h L:D photoperiod in a controlled environment chamber. Plants were examined daily for neonates; first, 50%, 90% and 100% hatch of the population from each eggplant were calculated. Corresponding degree-days above 10°C were tabulated and mean values were established for percent hatch and compared

statistically using Tukey's Pairwise Comparison, General Linear Model (SAS Institute 1985).

Post-bloom sampling interval. The B.C. Ministry of Agriculture and Fisheries (1989) recommend sampling for C. verbasci nymphs at 3, 5 and 10 d intervals post-bloom. In this study 'full bloom' is defined as the date on which a limb-tap causes the majority of flower petals to drop. Repeated observations over the bloom period defined this stage for each orchard site. Mean values were compared statistically and graphically with other predictors of hatch.

Comparison of predictors for egg hatch. Both degree-day and post-bloom intervals were compared with mean Julian days (from January 1st) using a 3-year average for observed percentages of field hatch, and these data were based on results from 31 orchard sites (1986-1988). Absolute days' deviations from observed 1st, 50%, 90% and 100% field hatch were subjected to pairwise comparison of the means using Waller/Duncan K-ratio T-test (General Linear Model, SAS Institute 1985).

Validation of the degree-day technique as a predictive model. Previous sections have demonstrated the descriptive utility of a temperature-based model in tracking hatch of C. verbasci eggs. The 'sine wave' method, which proved to be equal to or better than the other degree-day methods,

was used in subsequent tests for validation of the degree-day approach in predicting egg hatch.

The 1987 data from seven orchard sites in Summerland, B.C. were tested as a predictor of field hatch for the years 1982, 1986 and 1988. Degree-day units for 1987 were calculated from daily minimum and maximum temperature records and mean values corresponding to observed first, 50%, 90% and 100% hatch of C. verbasci overwintering eggs. Estimates of hatching dates were compared with mean Julian days required for first, 50%, 90% and 100% hatch (1987) and the currently recommended 3, 5, and 10 d post-bloom sampling interval for accuracy in forecasting hatch (1982, 1986, and 1988). The method having the smallest deviation from observed field values was taken to be the most suitable approach. Data were analyzed and comparisons of mean deviations (days) conducted using the Waller/Duncan K-ratio T-test (SAS Institute 1985).

2.4.4.3. Results and Discussion

General description of field hatch. During 1982-1983 and 1986-1988, actual days for hatch (first to 100%) of overwintering eggs averaged 14.3 ± 0.8 days (range 5 - 25 days); average degree-days per day in this time interval was 6.5 ± 0.8 (range 4.0 - 11.4) (Table 16). Because each actual day is represented by relatively few degree-days, errors in calculation have a more serious consequence than

would computations for summer generations when each actual day was represented by nearly a tenfold increase in accumulated degree-days. By permission, the 1982-1983 data of Dr. H.M.A. Thistlewood are included for comparison and generally fall within the range of values collected in my study.

Degree-Day Model. Overwintering egg hatch. During three years and based on 31 orchard sites, the degree-day model proved to be a more accurate predictor of overwintering egg hatch than did mean Julian days (Fig. 19). There was no significant difference among means for sine wave, rectangle and triangle calculations of degree days. Estimation of 90% and 100% spring hatch are the more useful proportions that could be utilized by the limb-tap technique. Absolute predictions from actual observed hatch by degree days were < 4 d for 50% through 100% hatch. These predictors should give ample warning for orchard blocks to be sampled before economic injury would occur.

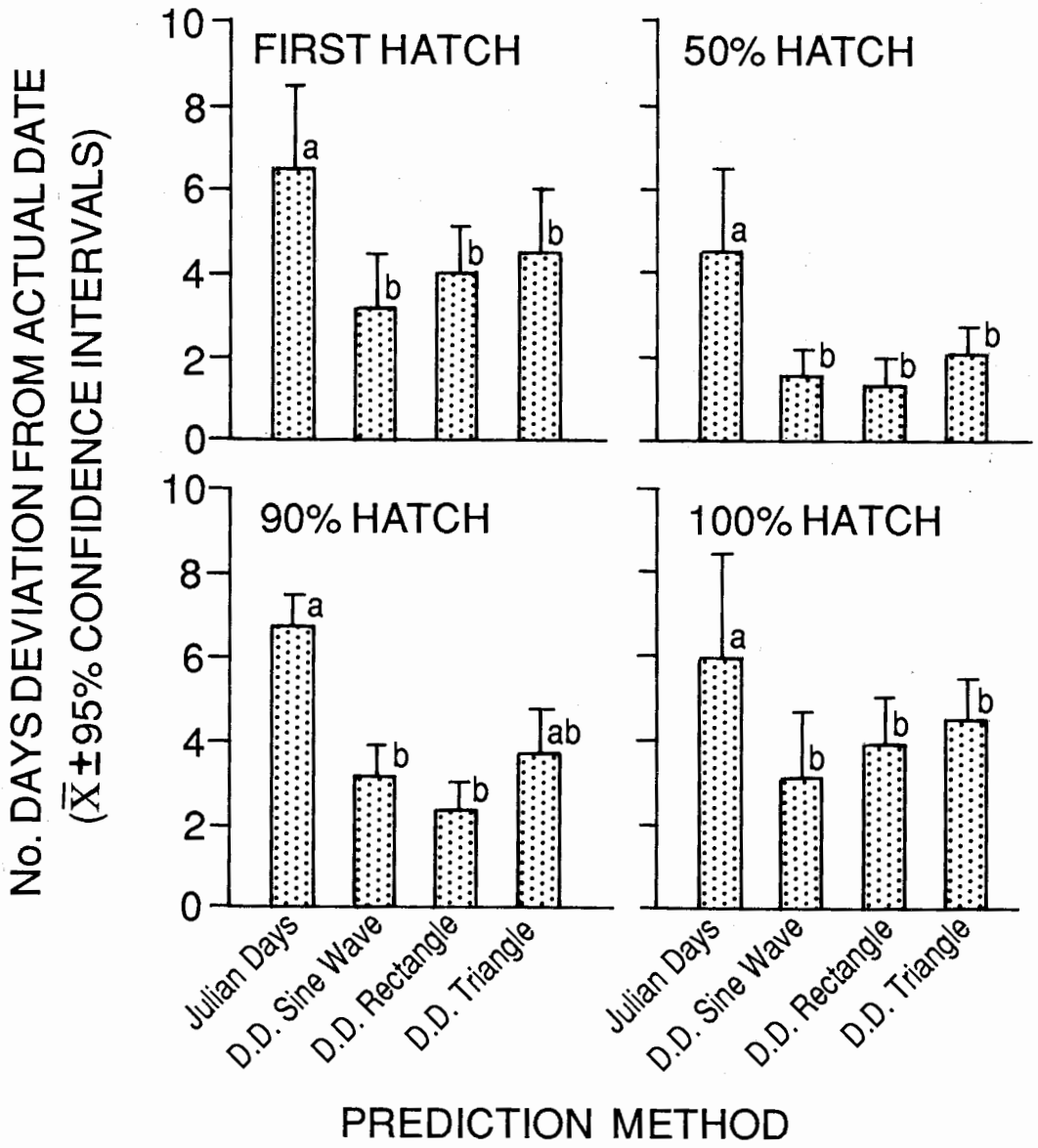
Nondiapausing egg hatch. First hatch occurred on eggplant at 111.1 ± 2.28 degree-days following a 24 h oviposition period at 22°C. Over the four temperatures of incubation, values ranged from 108.2 (22°C) to 113.0 (25°C) degree-days. Fifty percent hatch required an additional 16 degree-days (mean 127.1) while 90% and 100% accumulative

Table 16 Duration C. verbasci field hatch of overwintering eggs and degree-day (D.D.) (base 10°C) accumulations during hatch.

Year	Location	No. of sites	Julian day for Red Delicious full bloom	Observed hatching period			
				Range (days)	Mean days (± S.E.)	Total D.D calculated	D.D. per day
*1982	Summerland	4	138	10 - 17	12.0 ± 1.7	92.3	7.7
*1983	Summerland	6	125	5 - 10	7.2 ± 0.8	28.9	4.0
1986	Summerland Res. Station	1	134	--	16.0 ± 0.0	145.0	9.1
	Summerland Entomology	3	134	9 - 15	12.3 ± 1.8	140.0	11.4
1987	Summerland Res. Station	3	122	13 - 18	17.0 ± 1.0	111.2	6.5
	Summerland Entomology	4	122	8 - 13	9.0 ± 0.7	76.0	8.4
1988	Summerland Res. Station	5	122	18 - 23	20.6 ± 1.2	92.4	4.5
	Summerland Entomology	8	125	14 - 25	17.8 ± 1.4	84.4	4.7
	Winfield	3	129	12 - 23	18.0 ± 3.2	86.9	4.7
	Osoyoos	4	111	13 - 15	14.3 ± 0.4	51.0	3.6
	Average, all locations	41	126.2	5 - 25	14.3 ± 0.8	90.0	6.5

*data supplied by Dr. H.M.A. Thistlewood, Agriculture Canada, Vineland, Ontario.

Figure 19 Comparison of mean Julian day and degree-days (base 10°C) as predictors of C. verbasci overwintering egg hatch, 1986-1988, in B.C. interior valleys. Degree-days and Julian days are measured from 1 January. Lines on bars represent 95% confidence intervals; those bars sharing a common letter are not significantly different, $P < 0.05$, Tukey's Pairwise Comparison, SAS Institute 1985.


No. DAYS DEVIATION FROM ACTUAL DATE
($\bar{X}$ ± 95% CONFIDENCE INTERVALS)
FIRST HATCH
50% HATCH
90% HATCH
100% HATCH
10
8
6
4
2
0
a
b
b
b
a
b
b
b
a
b
b
ab
a
b
b
b
Julian Days
D.D. Sine Wave
D.D. Rectangle
D.D. Triangle
PREDICTION METHOD

hatch utilized 148.5 and 159.6 degree-days, respectively (Table 17). Required degree-day accumulation for each percent hatch did not differ among the four constant temperatures (Table 17). It may be worthy of research to track field development of C. verbasci on its herbaceous host, Verbascum thapsus using a degree day model. Abundance and development on herbaceous plants influence the numbers of bugs migrating to orchards for the deposition of overwintering eggs. Occasional injury is caused by C. verbasci when they aggregate on horticultural crops and orchard nursery stock during the summer months (personal observation). A predictive model for the summer generations may have utility in managing these populations.

Post-bloom sampling interval. Preliminary data from my 1986-1988 research indicated that 3, 5, and even 10 d post-bloom samples as recommended by B.C. Min. of Agric. and Fish. (1989) underestimated the date of complete hatch in some years (Table 1). First hatch on 'Red Delicious' had occurred in eight of nine occasions by the 3 d post-bloom period (Table 18). Because limb-tap counts are assumed to represent true nymphal density, sampling at 90% to 100% hatch would give less chance of error; i.e., low counts interpreted as sub-economic injury levels when, in fact, a sufficient proportion of eggs had not yet hatched. Even use of the maximum 10 d time interval would have suggested that sampling was complete on four occasions when hatch was < 90%

Table 17 Mean degree-day (base temperature 10°C) requirement for hatching of C. verbasci nondiapausing eggs in eggplant incubated at constant temperatures.

	Mean degree-days (± S.E.) required[a]			
Temperature	1st	50%	90%	100%
20°C	114.2±3.8	129.0±2.5	146.0±2.5	158.0±3.7
22°C	108.2±5.2	121.0±3.9	144.0±6.9	157.3±7.1
25°C	113.0±4.2	125.0±5.0	150.0±4.0	160.0±12.3
27°C	110.5±4.6	136.0±4.0	154.8±1.8	161.5±5.8
Overall means	111.1±2.3	127.1±2.1	148.5±2.1	159.6±2.5

[a]No significant difference between means in each column, P > 0.05, Tukey's Pairwise Comparison, General Linear Model, SAS Institute 1985.

Table 18 Observed field hatch of C. verbasci overwintering eggs, Okanagan Valley, in relation to limb-tap sampling interval as recommended by the B.C. Ministry of Agriculture and Fisheries, 1989.

Year	Location	N[a]	Mean no. of days after 1 January (S.E.) 1st	50%	90%	100%	Days post 'full bloom' 'Red Delicious' 3	5	10
1982	Summerland	4	136.8 (1.90)	--	147.3 (0.48)	148.8 (0.48)	141	143	148
1983	Summerland	6	127.7 (1.04)	--	132.2 (0.72)	135.5 (0.43)	128	130	135
1986	Summerland	4	139.8 (0.85)	144.5 (1.44)	149.0 (1.10)	155.0 (0.40)	137	139	144
1987	Summerland Res. Stn.	3	114.0 (1.00)	126.0 (0.00)	128.3 (0.33)	131.0 (0.00)	125	127	132
	Entomology	4	125.3 (0.48)	128.8 (0.25)	131.5 (0.23)	133.8 (0.48)	125	127	132
1988	Summerland Res. Stn.	5	119.8 (1.38)	130.4 (0.41)	136.8 (0.67)	140.4 (0.24)	125	127	132
	Entomology	8	121.3 (1.19)	131.0 (0.46)	137.0 (0.62)	139.1 (0.35)	128	130	135
	Winfield	3	126.3 (0.89)	132.6 (0.90)	138.0 (0.00)	142.0 (1.00)	132	134	139
	Osoyoos	4	111.0 (0.40)	119.5 (0.29)	123.8 (0.25)	125.0 (0.00)	114	116	121

[a]Number of orchard sites included in description.

complete and five occasions when 100% hatch was not reached. In these instances, even three sampling intervals totaling 150 limb taps per ha, may not have detected impending economic injury.

Based on these data, sampling at 3 and 5 d post-bloom should be seriously challenged; it is also questionable if the 10 d interval merits continued use, particularly if degree-day models prove to be more accurate predictors of hatch.

Comparison of predictors of egg hatch. The ability to predict field hatch correctly varied considerably among methods, both within and between categories of hatch (Table 19). First hatch was difficult to forecast regardless of the method considered; however, the degree-day estimates showed the least deviation (3.3 - 4.6 d) from observed values (Fig. 20). The low level of accuracy for early hatch may be due in part to field error of the limb-tap technique in detecting the first few neonates within the orchard.

Correct prediction of 50% hatch was accomplished in approximately 60% of 31 sites (Table 19, Fig. 20) and within 1.5 - 2.1 d of observed values by all three degree-day estimators. This performance was better than Julian days and days post-bloom predictors. Sampling at ten days post-bloom did correctly predict populations on ca. 50% of the

study sites, but overestimated date of hatch in the remaining orchards.

Post-bloom and Julian day estimates of both 90% and 100% overwintering egg hatch were consistently too early (Fig. 20), while 50% - 60% of all three degree-day estimates were typically too late. Ninety to 100% hatching categories are crucial to the timing of limb-tap sampling; efficiency and increased utility would be accomplished if only one set of limb-taps (50 per ha) were known to represent the majority of hatched eggs. The consistent earliness of the 10 d post-bloom recommendation is then a more serious error than the 3 or 4 d overestimation (or lateness) as projected by the degree-days predictors.

A closer "best fit" value could be sought through trial and error until overestimations are significantly reduced with an equal increase in correct predictiveness. Nevertheless, based on these limited data sets, the degree-day approach is a positive and significant improvement over current methods in forecasting hatching of overwintering C. verbasci eggs.

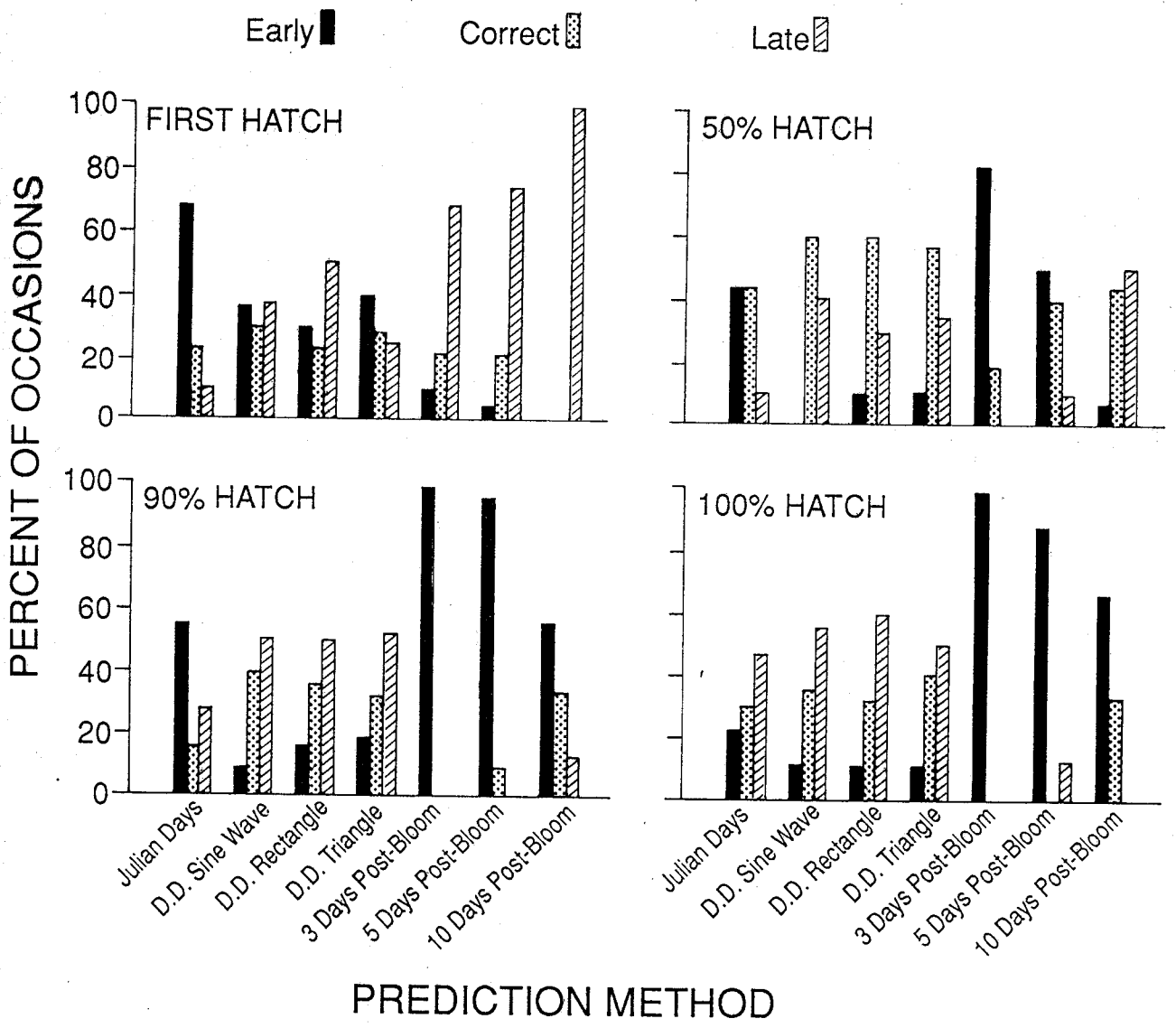
Validation of the degree-day technique as a predictive model. Testing of this degree-day model will require detailed field records for both temperature and field hatch.

Table 19 Comparison of predictors of C. verbasci overwintering egg hatch expressed as deviations in absolute days from observed field hatch, 1986-1988, Okanagan Valley, B.C., n = 31 orchard sites.

	Mean no. days deviation (± S.E.)				95% confidence intervals of deviation			
Predictor	First hatch	50% hatch	90% hatch	100% hatch	First hatch	50% hatch	90% hatch	100% hatch
Julian days from 1 Jan.	6.6±1.0b	4.5±0.9a	5.7±0.8c	6.0±1.1c	4.5-8.6	2.7-6.4	4.0-7.4	3.9-8.2
Degree-days, Sine wave	3.3±0.6d	1.5±0.2c	2.9±0.4de	3.2±0.5e	2.1-4.5	1.1-2.0	2.0-3.7	2.1-4.3
Degree-days, Rectangle	4.0±0.6d	1.5±0.3c	2.3±0.4e	3.7±0.6e	2.8-5.3	0.9-2.1	1.6-3.0	2.6-4.8
Degree-days, Triangle	4.7±0.6cd	2.1±0.2c	3.6±0.5d	4.1±0.5de	3.4-5.9	1.6-2.6	2.7-4.6	3.2-5.1
3 days post-bloom	4.9±0.6bc	4.0±0.4a	8.8±0.6a	11.7±0.7a	3.7-6.3	3.2-4.9	7.7-9.9	10.3-12.9
5 days post-bloom	6.3±0.8bc	2.5±0.4bc	6.8±0.6b	9.8±0.7b	4.7-7.8	1.8-3.2	5.7-7.9	8.5-11.1
10 days post-bloom	10.1±0.8a	3.5±0.4ab	3.0±0.3de	4.9±0.6cd	8.5-11.6	2.8-4.2	2.3-3.7	3.8-6.2

Means within a column sharing a common letter are not significantly different, $P < 0.05$, Waller/Duncan K-ratio T test, SAS Institute 1985.

Figure 20 Proportion accuracy for predictors of C. verbasci egg hatch in the Okanagan Valley, B.C. Estimated means are based on 31 year/orchard sites (1986-1988) and categorized as early, correct or late in relation to observed field hatch. Julian days and degree-day accumulations (base temperature 10°C) commence on 1 January of each year.


Early
Correct
Late
FIRST HATCH
50% HATCH
90% HATCH
100% HATCH
PERCENT OF OCCASIONS
100
80
60
40
20
0
Julian Days
D.D. Sine Wave
D.D. Rectangle
D.D. Triangle
3 Days Post-Bloom
5 Days Post-Bloom
10 Days Post-Bloom
PREDICTION METHOD

Should a pheromone-based monitoring tool replace the limb-tap method in determining the presence of a population above the economic threshold, then the degree-day predictive model could forecast spring hatch and allow better timing of the application of control measures.

Using the degree-day sine wave model generated with 1987 data to predict hatch in 1982, 1986 and 1989, actual days deviation (estimated minus observed) proved to be more accurate than with any other predictor (Table 20). The 'sine wave' tended to overestimate (predict too late) time for hatch, but this inaccuracy ranged from only 1.25 to 3.18 d, depending on percent hatch estimated.

Predictors of 90% and 100% hatch are of paramount importance; but these percents were consistently underestimated (too early a prediction) by both Julian day and post-bloom intervals. Julian days projected 90% and 100% hatch ca. 8 d too soon, while the post-bloom estimates ranged from 2 to 12 d too early.

The slight overestimation (too late a prediction) given by the degree-day method is of some concern; possibly some fruit may be damaged before the sampling could determine bug density. This may be an unavoidable trade-off between sampling too soon and a realistic sensitivity of the model to predict the desired proportion of hatch.

Table 20 Predictive ability of 1987 mean Julian days and sine wave derived degree-days (base 10°C) as an estimator of C. verbasci overwintering egg hatch. Values are compared with each year/site deviation of post-bloom estimation of hatch.

	Days difference (mean (SE)) from observed for 1982, 1986 and 1988				
			Days post-bloom		
Percent hatch[a]	Julian	Sine	three	five	ten
First	-3.50d[b] (1.54)	1.25c (0.82)	4.04b (0.76)	5.82b (0.81)	9.82a (0.68)
50%	-3.42b (1.00)	2.54a (0.45)	-4.38c (0.52)	-2.38b (0.52)	1.94a (0.70)
90%	-8.43cd (1.51)	2.29a (0.67)	-9.39d (0.49)	-7.32c (0.52)	-2.39b (0.49)
100%	-8.39c (1.69)	3.18a (0.91)	-12.11d (0.66)	-5.68b (1.76)	-5.25b (0.64)

[a]n=28 orchards for 1st, 90% and 100%, n=24 for 50% hatch.

[b]Means within a line sharing a common letter are not significantly different ($p < 0.05$, Waller/Duncan K-ratio T-test, SAS Institute 1985)

3. SEMIOCHEMICAL-BASED COMMUNICATION IN THE PEAR PSYLLA, Psylla pyricola FÖERSTER

3.1. Introduction

Psylla pyricola Föerster (Homoptera: Psyllidae) is a widely-occurring, host-specific pest of pears Pyrus spp. (Burts 1988). A major problem in management of the psylla is wide spread resistance to pesticides, a consequence of heavy dependence by commercial growers on insecticides to suppress populations. Area-wide resistance to pyrethroids is well documented (Burts et al. 1989), yet IPM has been difficult to implement. Three of the 20 - 25 species of pear are cultivated for agricultural purposes (Westigard et al. 1970), and most varieties are hosts for P. pyricola.

This psyllid was probably unintentionally introduced to North America from Europe. It was first reported in Connecticut ca. 1882 and subsequently in Massachusetts (Petit and Hutson 1931), the Pacific northwest in the 1930's (Riedl et al. 1981) and in British Columbia by the 1940's (Wilde and Watson 1963).

In 1987 commercial pear production in Canada was estimated at 27,995 metric tonnes of which 12,565 tonnes originated in British Columbia; the crops were valued at ca. $10.0 million (Canada) and $4.0 million (British Columbia), (Statistics Canada 1987). Production in the United States is concentrated primarily in Washington, Oregon and

California which account for 90% of that nation's production (Larsen 1982).

Psyllids cause economic losses by three types of feeding injury (Burts 1970):

1. downgrading of quality by russetting fruit skin from sooty mold that flourishes on honeydew excretions,
2. debilitation of the host caused by mass feeding on leaf fluids, which decreases productivity and inhibits fruit bud formation, and
3. transmission of diseases by vectoring fire blight and pear decline.

In British Columbia, there are four summer generations and one overwintering generation (Wilde and Watson 1963). Adults overwinter in a reproductive diapause which is broken by a photophase >13.5 h. A small portion of the winter form adults stay in the pear orchard; most seek shelter in woody plants, often several km from the nearest pear orchard. It is unknown what percent of the winter form population is mated, but in Nova Scotia Rasmy and MacPhee (1970) reported few females had mated prior to their return to pear. Because pear is the sole reproductive host plant, it is imperative that these adults find pear trees again in the spring. Coinciding with the swelling of the pear buds, winter form psyllids migrate back to pear and may mate even when ambient air temperature is slightly above 0°C. Eggs are deposited on rough bark near bud scales, and on the developing green bark tissue as the season advances.

Winter form pear psylla are darker and slightly larger than their summer form counterparts. Fecundity of the winter and summer form females averages 486 eggs at 15.6°C (McMullen and Jong 1977) and 664 at 24°C (Burts and Fisher 1967), respectively. There are five nymphal instars.

Crucial to any plan for management of pear psylla is the need for a practical, reliable monitoring system. Monitoring of winter form psylla using a limb-tap method has been suggested for early spring (Washington State University 1988). Burts (1988) sets a tentative economic peak density of 0.3 summer form nymphs per leaf. Applying chemical controls when populations reach this level would avoid economic damage from russetting of fruit. Frequent sampling within an orchard is feasible, but labour intensive.

There is little published literature pertaining to pear psylla chemoreception. P. pyricola distinguish among species of pear, possibly by kairomonal perception, and accept only some as a reproductive host (Chang and Philogene 1978). Ullman and McLean (1988) report that winter form pear psylla perceive plant stimuli before probing and determine host suitability by yet undefined chemosensors. This insect's ability to find pear trees implies that medium to long-range kairomonal responses may be involved.

Male P. pyricola have a precopulatory maturation period of approximately five days. Females can mate within a few

hours of the final molt, but require repeated matings to sustain their fecundity (Burts and Fisher 1967). Cook (1963) described the mating of a single pair of pear psyllids but did not suggest that semiochemicals were involved. R.D. McMullen[4] observed that males in the proximity of, but not in contact with, females apparently became sexually excited, showing antennal vibration and rapid movement, suggesting that they were responding to an excitatory sex pheromone. I hypothesize that if a long-range kairomonal attraction were involved in host selection, a short-range pheromonal communication would be a logical reproductive strategy since both sexes would be present, often at very high densities, on the host. If semiochemicals for pear psylla were known, they might find ready application in new monitoring techniques that could replace or supplement limb-tap sampling, or for short range excitants, as bioirritants to be used to improve the efficacy of chemical or microbial insecticides.

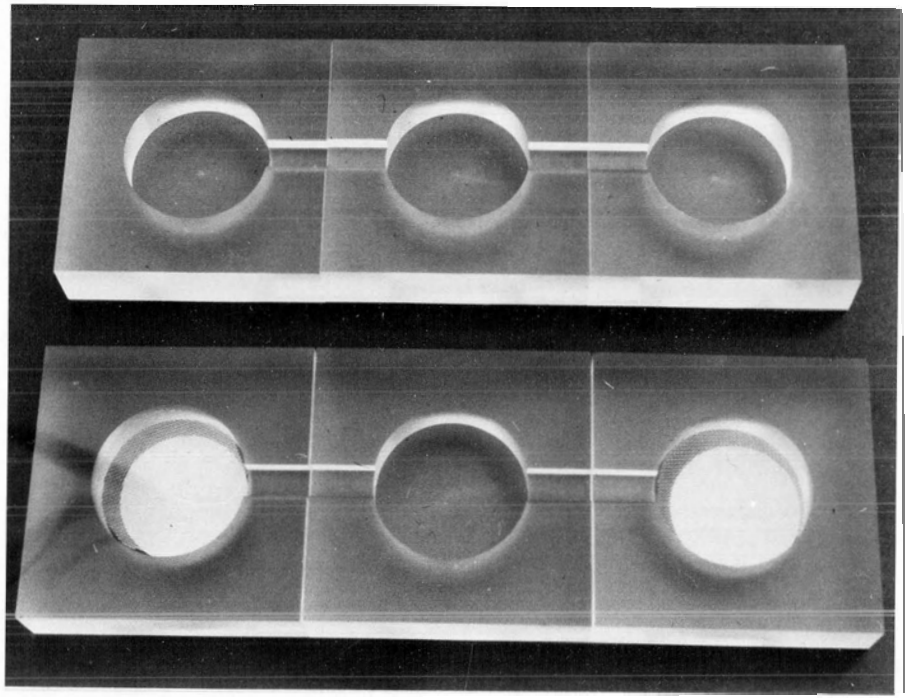
My first objective was to determine if a laboratory bioassay could be established to test the sensitivity of pear psylla to semiochemicals. My second and major objective was to investigate the hypothesis that chemical communication is involved in host selection and mate-finding by the pear psylla.

3.2. Materials and Methods

Bioassay Apparatus. A miniature version of a two-choice static air olfactometer (Vet 1983) was selected to test responsiveness of pear psylla to chemical stimuli. A single unit (Fig. 21) consists of three 50 x 50 x 15 mm plexiglass blocks hollowed out so that when placed together there are three interconnected chambers with a removable transparent glass roof. Individual chambers are 13 mm deep and the channel is 5 mm deep, 10 mm wide and 22 mm long.

Response of Winter Form Pear Psylla to Host Odour. Single fruit buds in the 'swollen bud' stage (Chapman and Catlin 1976) were dissected from 'Anjou' pear and compared with a control stimulus of water-moistened filter paper. Each end chamber of the olfactometer held a control or experimental stimulus. A cupped disk of fine mesh screening in the end chambers was used to separate the psyllids from the stimulus below them. Winter form psylla were gathered from apple trees near an orchard containing varieties 'Bartlett' and 'Anjou' pears at the Agriculture Canada Research Station, Summerland, B.C. Collections were conducted in mid-January using a 40 x 40 cm tapping tray. Psylla were immobilized with CO_2, sorted by sex, and females held on moist filter paper in petri dishes under a 16:8 h L:D photoperiod at 20° ± 1°C for 24 h. Females were segregated singly into gelatin capsules, visually inspected,

Figure 21 Perspective view of static air olfactometer composed of three plexiglass units, each 50 x 50 x 15 mm, with a clear glass cover. Individual chambers are 13 mm deep, and the channel is 5 mm deep, 10 mm wide and 22 mm long.



and, if apparently vigorous and healthy, they were gently released, one per olfactometer into the center chamber. A glass plate was placed over the apparatus to retain the insects inside.

To avoid any directional bias to photic stimuli, the olfactometers were set inside a 20 x 20 cm box with a 75 watt Grow Lux incandescent light centered over them at a height of 30 cm. Photosynthetically-active radiation was measured by a LI-COR meter (Model LI 188B integrated quantum/radiometer/photosensor) at 504.4 lux (10.3 μ E $s^{-1}m^{-2}$).

Each test lasted 1 h, during which the numbers of visits to and durations in each stimulus chamber were recorded. Between replicates the units were washed in 95% ethanol, then hot water, and air-dried.

Percent of response time in either chamber was derived from total time spent in each chamber divided by the combined sum of all time the insect spent in both stimulus chambers times 100. This latter measure tended to decrease the disparity between very active and more tranquilly responding psyllids.

Prior to comparison of paired means by t-tests (SAS Institute 1985), data were transformed as follows. Numbers of visits were subjected to $\sqrt{}$ (visits + 1), duration was

converted to log10 (duration + 1), and proportions of response to arcsine (√ (proportion)).

Chemically-mediated Communication Between the Sexes. Psyllids were collected from the same orchard as above in late January, sorted by sex, and held on Bartlett pear seedlings under a 16:8 h L:D photoperiod. Extracts were made of some psyllids immediately after sorting by sex; they were dropped into -40°C pentane and quickly fragmented with a blunt, metal probe. Extract concentrations were expressed as psyllid equivalents (p.eq.) (an extract containing an amount of material equivalent to that in 1 psyllid = 1 p.eq.).

Summer form psylla were collected from the above orchard and a colony was established on potted Bartlett pear seedlings held at 20° ± 1°C under a 16:8 h L:D photoperiod. A new colony was established with wild insects every two or three generations to minimize any possible behavioural change that might be induced by genetic shifts within the laboratory colony. Teneral adults were obtained daily from the colonies, separated, grouped by sex and held on pear seedlings. Two age classes were used: 6 d old psylla, which are reported to be sexually receptive (Burts and Fisher 1967), and 10 d old psyllids.

A stimulus, whether an insect or an extract, was placed on a moist filter paper disk under mesh screen in an end

chamber of the olfactometer. Extracts were transferred by syringe onto a glass cover slip and the pentane solvent allowed to evaporate before placing the cover slip under a screen. The other chamber contained an alternative stimulus or was left as an unbaited or solvent control. The test insects were released into the center chamber as described above.

Live psyllids, whether used as a stimulus source or a test insect, were replaced after a single use by fresh specimens of the same status. Each experiment, unless otherwise noted, was replicated 18 times at 20° ± 1°C, utilizing three olfactometers simultaneously. The following experiments tested the responsiveness of male winter form psylla: 1) unbaited control vs unbaited control, 2) one winter form female vs unbaited control, 3) 10 p.eq. winter form female extract vs pentane control, 4) one winter form female vs one 10 d old summer form female. Response of female winter form psyllids to 10 p.eq. winter form male extract vs pentane control was also evaluated.

Two age classes of summer form psylla were tested. The following experiments were conducted: 6-d old male psylla response to females vs unbaited control and 6-d old female response to males vs unbaited control. Ten day old male psylla response to: 1) 1 female vs unbaited control 2) 2 females vs unbaited control 3) 5 females vs unbaited

control, 4) 10-d male vs 10-d female, 5) 10-d female vs 6-d female, 6) 10 p.eq female vs 10 p.eq. male, 7) 10 p.eq. winter form female vs pentane control. Ten day old female response was tested in the following choice tests: 1) 10-d female vs 10-d male, and 2) male vs unbaited control.

3.3. Results and Discussion

Response of Winter form Pear Psylla to Host Odours. The miniaturized static air olfactometer proved satisfactory for the evaluation of pear psylla response to semiochemicals. Winter form females responded positively to the odour of hidden 'Anjou' pear fruit buds (Table 21). There were more visits to the chamber containing the buds than to the control chamber, and greater durations and proportions of time spent in the experimental chamber.

These results indicate that the static air olfactometer could be used to test the behavioural responses of pear psylla to olfactory stimuli. Moreover, the positive responses to the hidden 'Anjou' pear bud support the hypothesis that kairomonal cues are indeed involved in this insect's ability to find its host.

Should the active kairomones be isolated and identified they could be used as stimuli in traps designed to monitor the survival and abundance in overwintered populations of winter form psylla.

Table 21 Response of 14 female winter-form P. pyricola to Anjou pear fruit buds in a two-choice static air olfactometer.

	Response ($\bar{x}$ ± S. E.)		
Stimulus	Number of visits	Duration of response (sec)	Proportional response (%)
Anjou fruit bud	5.7 ± 0.83	275.1 ± 40.24	72.9 ± 4.9
Unbaited control	3.4 ± 0.49	83.6 ± 11.66	27.8 ± 4.8
P level (t-test)	0.0199	0.0004	0.0001

Chemically-mediated Communication Between the Sexes

Winter form psylla. Male winter form pear psylla were attracted to winter form females or extracts thereof (Fig. 22, Exps. 2,3). The response was greater to the 10-fold stronger extract stimuli (Exp. 3) than to the females themselves (Exp. 2) as shown in a difference in numbers of visits between the experimental and control stimuli and a longer duration in the baited chamber. Equal responses to the two unbaited chambers indicated no directional bias in the apparatus (Fig. 22, Exp. 1). Response by males to female extracts suggests that chemical communication plays a major role in mate location in nature. Winter form males distinguished only in the proportional response between reproductively active winter form and summer form females, (Fig. 22, Exp. 4), suggesting a similar or identical pheromone structure in both female seasonal forms.

Female winter form psylla were not attracted to extracts of their winter form males (Fig. 22, Exp. 5). In fact, the data on duration of visits suggest that the male extract may have repelled the females.

During periods of fluctuating barometric pressure, activity level, but not stimulus choice, of test insects was often suppressed, typically reflected in few visits, short stays in stimuli chambers and a general reluctance to move.

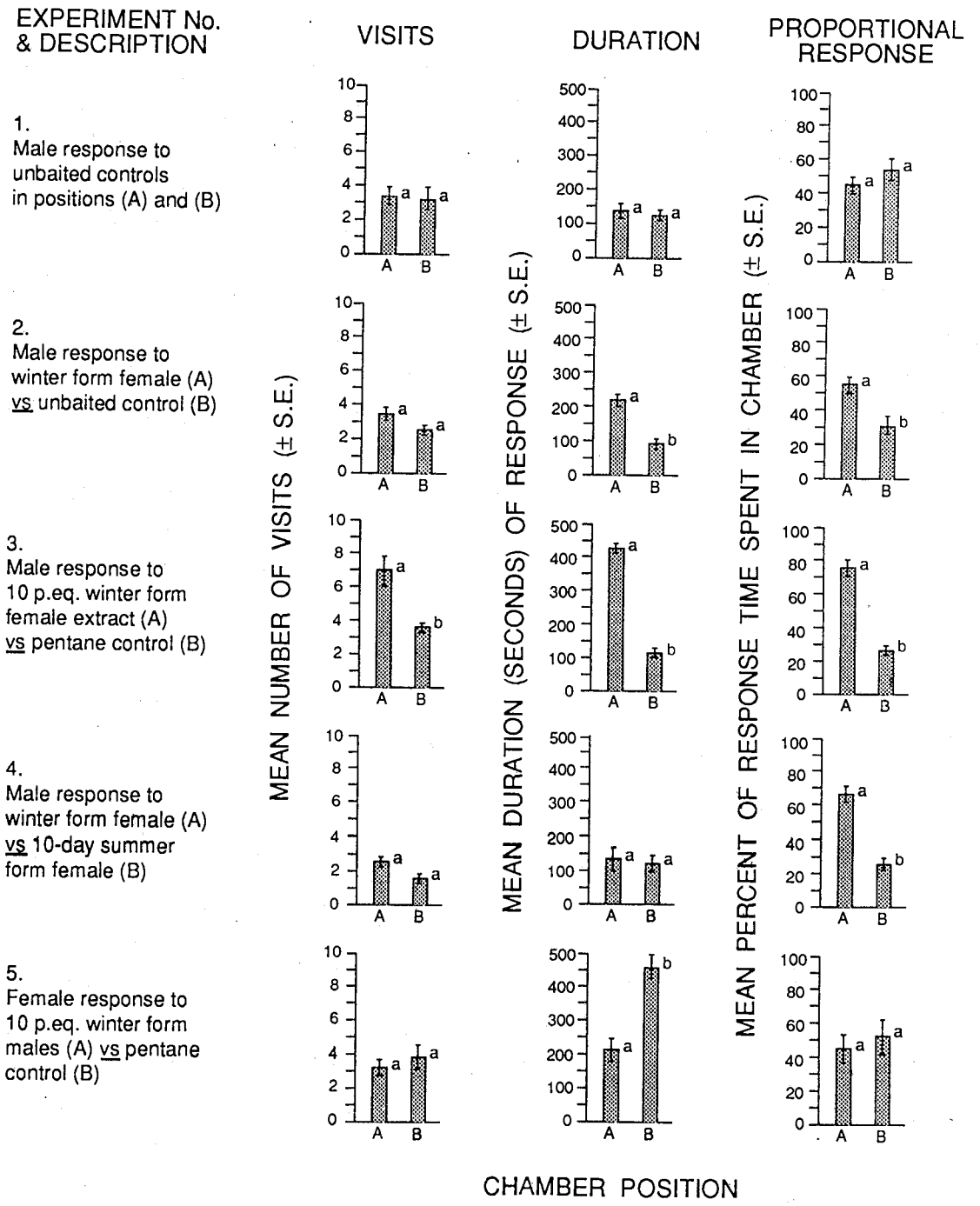
ductively-active winter form

li presented in a two-choice

insects per experiment.

.ıng a common letter are not

$P > 0.05$, t test SAS Institute 1985.


EXPERIMENT No. & DESCRIPTION
VISITS
DURATION
PROPORTIONAL RESPONSE
1. Male response to unbaited controls in positions (A) and (B)
2. Male response to winter form female (A) vs unbaited control (B)
3. Male response to 10 p.eq. winter form female extract (A) vs pentane control (B)
4. Male response to winter form female (A) vs 10-day summer form female (B)
5. Female response to 10 p.eq. winter form males (A) vs pentane control (B)
MEAN NUMBER OF VISITS (± S.E.)
MEAN DURATION (SECONDS) OF RESPONSE (± S.E.)
MEAN PERCENT OF RESPONSE TIME SPENT IN CHAMBER (± S.E.)
CHAMBER POSITION

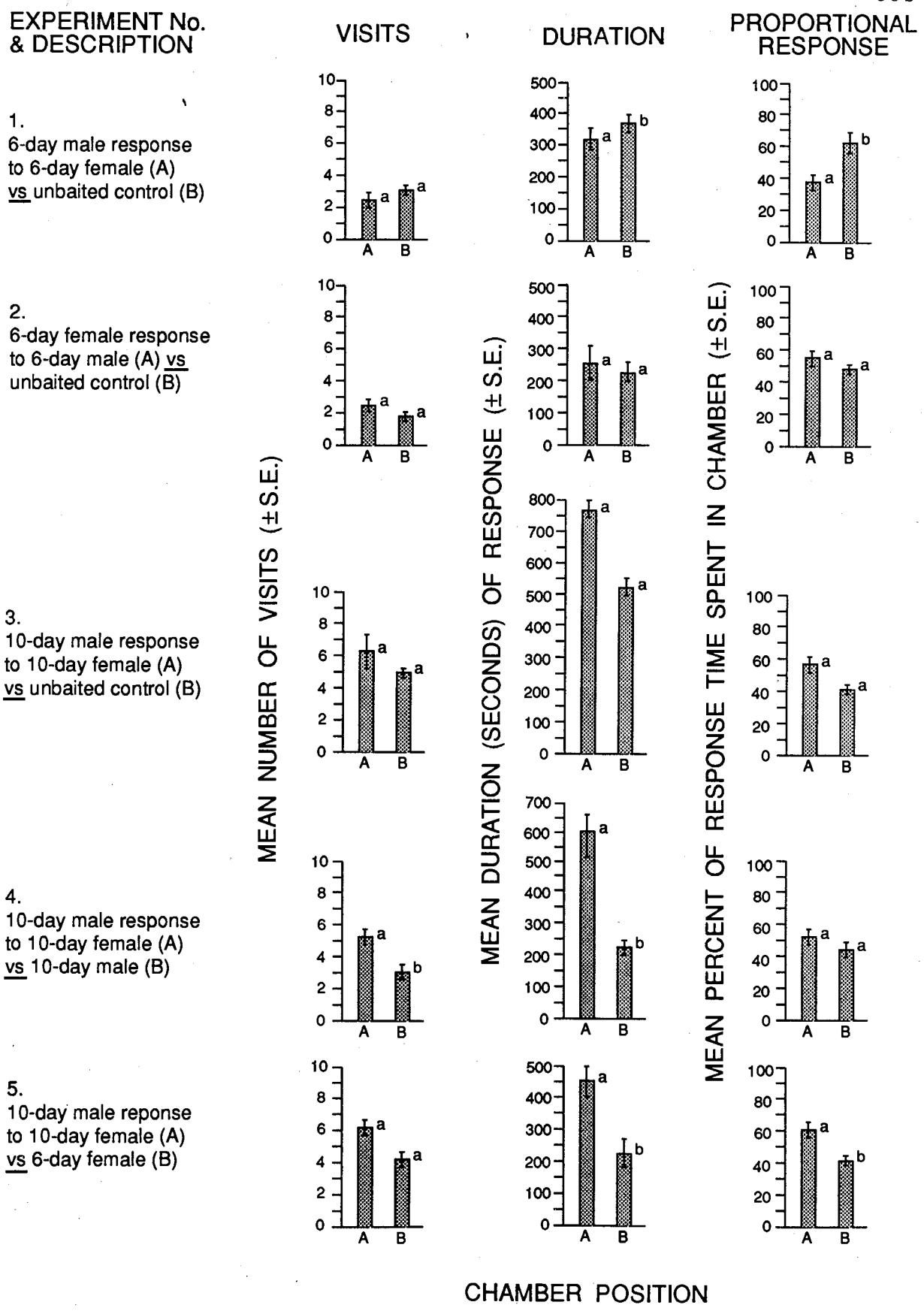
Responsiveness expressed by converting durations of stay to percent of response time spent in each chamber normalized this response between replicates (Fig. 22).

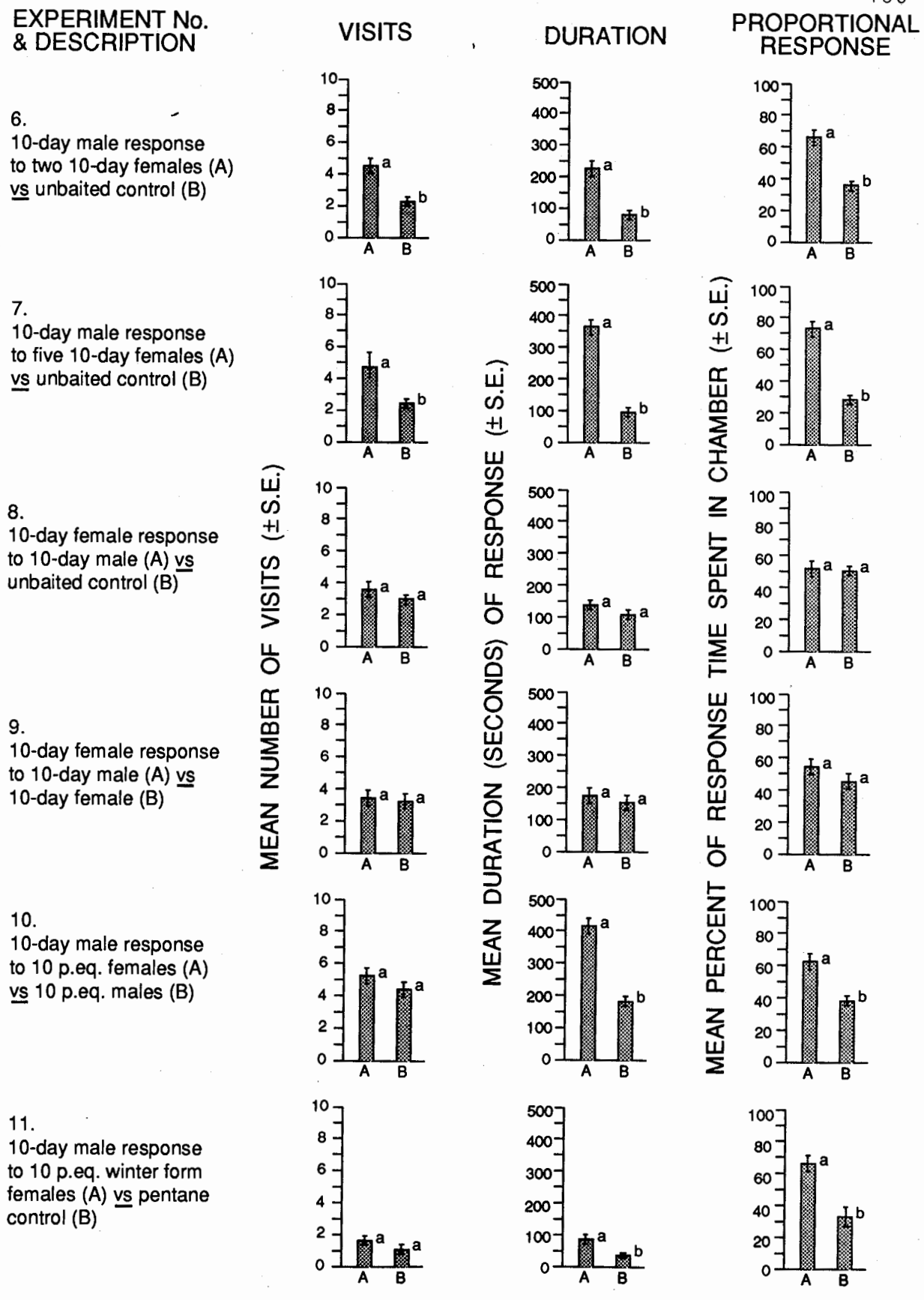
In most instances the proportional results agreed with those on visits and duration of response. However, they did disclose a significant positive bias by males for the winter form over summer form females. Similarly, the perceived repellancy of crushed male psyllids did not hold true when assessed by the percent of time spent in each chamber.

Summer form psylla. Ten-d-old summer form males were positively attracted to 10 d-old females and their extracts, confirming the results with the winter form psylla (Fig. 23, Exp. 3-7). The apparent inability of males to locate 10-d females in Exp. 3 may have been due to the intermittent emission of pheromone or its low quantity. However, responses to 2 or 5 10-d females were significant (Exp. 6,7). Males were able to distinguish between 10-d females and 10-d males (Exp. 4), between 10-d and 6-d females (Exp. 5), and between female extracts and male extracts (Exp. 10).
fig 23a

Based on number of visits six-d-old males could not locate females of the same age (Exp. 1); however, when the stimulus female was released from beneath the screen, the two psyllids made physical contact and mated. One hypothesis is that despite the fact that the psyllids were

Figure 23 Response of reproductively-active summer form psylla to olfactory stimuli presented in a two-choice static air olfactometer, 18 test insects per experiment. Bars within each subgraph sharing a common letter are not significantly different $P > 0.05$, t test SAS Institute 1985.


EXPERIMENT No. & DESCRIPTION
VISITS
DURATION
PROPORTIONAL RESPONSE
1. 6-day male response to 6-day female (A) vs unbaited control (B)
2. 6-day female response to 6-day male (A) vs unbaited control (B)
3. 10-day male response to 10-day female (A) vs unbaited control (B)
4. 10-day male response to 10-day female (A) vs 10-day male (B)
5. 10-day male reponse to 10-day female (A) vs 6-day female (B)
MEAN NUMBER OF VISITS (±S.E.)
MEAN DURATION (SECONDS) OF RESPONSE (±S.E.)
MEAN PERCENT OF RESPONSE TIME SPENT IN CHAMBER (±S.E.)
CHAMBER POSITION
A
B
a
b


EXPERIMENT No. & DESCRIPTION
VISITS
DURATION
PROPORTIONAL RESPONSE
6. 10-day male response to two 10-day females (A) vs unbaited control (B)
7. 10-day male response to five 10-day females (A) vs unbaited control (B)
8. 10-day female response to 10-day male (A) vs unbaited control (B)
9. 10-day female response to 10-day male (A) vs 10-day female (B)
10. 10-day male response to 10 p.eq. females (A) vs 10 p.eq. males (B)
11. 10-day male response to 10 p.eq. winter form females (A) vs pentane control (B)
MEAN NUMBER OF VISITS (±S.E.)
MEAN DURATION (SECONDS) OF RESPONSE (±S.E.)
MEAN PERCENT OF RESPONSE TIME SPENT IN CHAMBER (±S.E.)
CHAMBER POSITION
A
B

old enough to mate (Burts and Fisher 1967), the chemical stimulus from the virgin 6-d-old female was still weak, and was undetectable to the inexperienced male. A complementary hypothesis is that a chemotactic response is involved in mate-acceptance. Groups of males (but not females) held together in a petri dish engaged in a pseudo-mating act lasting 3 - 5 sec. (personal observation). Once it was apparently determined by abdominal probing that the partner was not a female, the individuals parted. However, if a male probes a receptive female, he will remain with her (Cook 1963), suggesting that chemotactic recognition has occurred. There was no attraction of females to males for either age class of female (Fig. 23, Exp. 2, 8 and 9).

Summer form males responded positively to crushed extract of winter form females (Fig. 23, Exp 11), however both number of visits and duration of stay were noticeably reduced in comparison with other experiments involving 10-d summer form females. Possibly summer form males can distinguish between winter and summer form females, and chose the latter. As a reproductive strategy this would be beneficial because males would be inclined to seek out summer form females; spermatazoa would not be wasted on matings with winter form females, which would be in reproductive decline when occurring coincidentally with the summer form females.

The percentages of response time that the test insects spent in each chamber agreed in general with the data on numbers of visits and duration of time spent. There was a gradual increase from 58 to 68 to 70% of the time that 10-d males spent with each 1, 2 or 5, 10-d females, respectively (Fig. 23), suggesting an increasing response to pheromone concentration.

My results demonstrated that P. pyricola females attract and probably excite males with a sex pheromone that apparently works at short range. Further research should be undertaken to identify this newly discovered pheromone.

Homopteran pheromones per se have not received the same magnitude of attention that those of other orders, e.g. Lepidoptera, have encountered. A noteworthy exception is the work on aphid alarm pheromones (Nault and Phelan 1984). Nault et al. (1973) demonstrated that chemoreceptors for these pheromones are present in antennal segments; the compounds are exuded from the cornicle, are effective from a distance of 1-3 cm, and last for several minutes.

Chemical-based sexual communication among homopterans has been demonstrated in the San Jose Scale, Quadraspidiotus perniciosus (Comstock), California red scale, Aonidiella aurantii (Maskell) (Roelofs et al 1978), the citrus mealybug, Planococcus citri (Risso) (Bierl-Leonhardt et al. 1981) and the aphid Schizaphis borealis Tambs-Lyche

(Pettersson 1970). Undoubtedly, sex pheromones for other homoptera species will be discovered as research efforts are focused on them.

Because the sex pheromone of the pear psylla apparently operates at short range, it's most likely practical application may be as a bioirritant used to increase the activity of males, and therefore increase their rate of contact with chemical or microbial insecticides. However, it is also possible that effective disruption of mating could be achieved through broadcast application of the pheromone.

CONCLUSIONS

The principal theme prompting this research was the need for an improved monitoring system for detecting and assessing populations of two significant tree fruit pests, Campylomma verbasci, the mullein bug and Psylla pyricola, the pear psylla. The results suggest that the need is near to being met for C. verbasci.

Biological studies on this insect should lead to a greater understanding of fecundity, hatching, and development, and will allow laboratory rearing of populations for future studies. Because of these as well as past biological studies, it was possible to conduct detailed research on developmental thresholds for eggs and to construct degree-day models that calculated accumulated physiological time. These models predicted hatching of overwintering eggs with accuracy equal to or greater than current predictive intervals for limb-tap sampling. These models are now ready for operational testing and could be accepted for use in the Okanagan Valley within 1-2 years.

Collaborative research has resulted in the isolation and identification of the first known sex pheromone in the Miridae. Results using live-caged females suggest that the synthetic pheromone may have utility in predicting potentially damaging populations at least six months before they occur in the spring.

The existence of a sex pheromone was discovered in Psylla pyricola, the first demonstration of a sex pheromone-based communication in the Psyllidae. The apparent short range nature of the pheromone suggests that it may have more use as a bioirritant used in combination with chemical pesticides than it would have as a monitoring tool. However, the response by pear psylla in the laboratory to the odour of pear buds may indicate that a host volatile could eventually be developed as a monitoring tool for this species.

FOOTNOTES

1. Manufactured by Albany International Inc., Needham Heights Massachusetts 021940

2. Olson Products Inc., Medina, Ohio

3. Supelco Canada Ltd., Oakville, Ontario

4. J & W Scientific Inc., Folsom, California

5. Fisher Scientific, Ottawa, Ontario

6. Retired entomologist, Agriculture Canada Research Station, Summerland, B.C.

APPENDIX A: FORTRAN DEGREE-DAY PROGRAM FOR MAINFRAME COMPUTER (VAX/VMS)

```
C This program computes heating degree-days by the
C rectangular, triangular, sine and averaging methods, and
C cooling degree-days by the sine method.  The user must
C supply the name of the data file that includes the Julian
C dates and corresponding daily maximum and minimum
C temperatures (degrees Celsius).  This program is based on
C that of Higley et al. 1986  ENVIRON. ENTOMOL. 15:999 -
1016.

  COMMON  /AREA/  TUP,TLO,JULIAN(731),TMAX(731),TMIN(731),
  1               RECT,SINE,TRI,AVG,COOL,I,NDAY
  COMMON  /FNAME/ INFILE
  CHARACTER*1     FF /12/
  CHARACTER*25    INFILE

  TRECT=0.0      ! INITIALIZE CUMULATIVE HEAT UNITS AND CHILL
                 ! UNITS
  TTRI=0.0
  TSINE=0.0
  TCOOL=0.0
  TAVG=0.0

  CALL INPUT     ! INVOKE THE SUBROUTINE FOR INPUT DATA

  NLINE = 75

  DO I=1,NDAY    ! COMPUTE HEAT UNITS AND CHILL UNITS
    CALL DDAY
    TRECT=TRECT+RECT
    TTRI=TTRI+TRI
    TSINE=TSINE+SINE
    TAVG=TAVG+AVG
    TCOOL=TCOOL+COOL
    IF ( NLINE .GT. 62 ) THEN
      WRITE(5,5) FF, JULIAN(1), JULIAN(NDAY), INFILE, TLO,
          TUP
      NLINE = 7
    END IF
    WRITE(5,6) JULIAN(I), I, TRECT, TTRI, TSINE, TAVG, TCOOL
    NLINE = NLINE + 1
5   FORMAT(A1 /
  1      'DEGREE DAY CALCULATIONS FOR JULIAN DAYS', I4, ' TO'
  2      I4, ' FROM DATA FILE ', A25 /
  3      'TEMPERATURE THRESHOLDS:', 2F6.1 //
  4      5X,'JULIAN',5X,'DAY',6X,'TRECT',5X,'TTRI',
  5      6X,'TSINE',5X,'TAVG',6X,'TCOOL' / )
    FORMAT(6X,I4,5X,I4,5F10.1)
  END DO
```

```
      STOP
      END

      SUBROUTINE INPUT

      COMMON  /AREA/  TUP,TLO,JULIAN(731),TMAX(731),TMIN(731),
     1                RECT,SINE,TRI,AVG,COOL,I,NDAY
      COMMON  /FNAME/ INFILE
      CHARACTER*25    INFILE, OUTFILE
    1 FORMAT(A)

      TYPE '('' THE NAME OF YOUR TEMPERATURE FILE IS: '',$)'
      ACCEPT 1,INFILE

      OPEN(UNIT=1,NAME=INFILE,TYPE='OLD',READONLY)

      OUTFILE = INFILE(1:INDEX(INFILE,'.')) // 'RPT'
      OPEN(5,STATUS='NEW',NAME=OUTFILE,CARRIAGECONTROL='LIST')
      TYPE *, ' YOUR REPORT FILE WILL BE ', OUTFILE

      TYPE '('' UPPER TEMPERATURE THRESHOLD: '',$)'
      ACCEPT *,TUP
      TYPE '('' LOWER TEMPERATURE THRESHOLD: '',$)'
      ACCEPT *,TLO
      TYPE '('' FIRST DAY (0 FOR BEGINNING OF FILE): '',$)'
      ACCEPT *, NDAY1
      TYPE '('' LAST DAY (0 FOR END OF FILE): '',$)'
      ACCEPT *, NDAY2
      IF ( NDAY2 .EQ. 0 ) NDAY2 = 9999
      IF ( NDAY1 .EQ. 0 ) GOTO 90
      NDAY1 = NDAY1 - 1
      JDAY = 0
      DO WHILE ( JDAY .LT. NDAY1 )
        READ(1,*,END=999) JDAY
      END DO

   90 I = 1
  100 READ(1,*,END=101) JULIAN(I),TMAX(I),TMIN(I) ! READ
JULIAN
                                                  ! DATES,
        I = I + 1                                 ! DAILY
                                                  ! MAXIMUM
AND
        IF ( JULIAN (I-1) .EQ. NDAY2 ) GOTO 101   ! MINIMUM
                                                  !
TEMPERATURES
        GOTO 100
  101 NDAY = I - 1

        RETURN

  999 TYPE *, ' SORRY, COULDN''T FIND DAY', DAY1
```

```
      STOP
      END

      SUBROUTINE DDAY

      COMMON  /AREA/  TUP,TLO,JULIAN(731),TMAX(731),TMIN(731),
     1                RECT,SINE,TRI,AVG,COOL,I,NDAY
      LOGICAL*1       ACCUM

C     ****** HEATING UNITS BY THE SIMPLE AVERAGE METHOD*****

      AVG = (TMAX(I)+TMIN(I))/2 - TLO

C     ****** HEATING UNITS BY THE RECTANGULAR METHOD*****

      RECT=0.0
      TMIN1=AMAX1(TLO,TMIN(I))
      TMIN1=AMIN1(TUP,TMIN1)
      TMAX1=AMIN1(TUP,TMAX(I))
      IF(TMAX1.GT.TLO) RECT=((TMAX1+TMIN1)/2.0)-TLO

C     ****** HALF-DAY TRIANGLE AND SINE WAVE METHODS*****

      TRI=0.0
      SINE=0.0
      COOL=0.0

      DO J=1,2      ! BEGIN HALF DAY LOOP

      TMIN1=TMIN(I)
      IF(J.EQ.2.AND.I.LT.NDAY) TMIN1=TMIN(I+1)
      TMAX1=TMAX(I)

      A=(TMAX1-TMIN1)/2.0         ! AMPLITUDE FOR THIS HALF DAY
      TBAR=(TMAX1+TMIN1)/2.0      ! MEAN FOR THIS HALF DAY

      IF (TMIN1.GE.TUP.AND.TMAX1.GT.TUP) THEN     ! CASE 1

        HTRI=(TUP-TLO)/2.0
        HSINE=(TUP-TLO)/2.0
        HCOOL=0.0
        ACCUM = .FALSE.

      ELSE IF (TMIN1.LT.TLO.AND.TMAX1.LE.TLO) THEN     ! CASE 2

        HTRI=0.
        HSINE=0.
        HCOOL=(TLO-A)/2.0
        ACCUM = .FALSE.

      ELSE IF (TMIN1.GE.TLO.AND.TMAX1.LE.TUP) THEN     ! CASE 3
```

```
  HTRI=(TBAR-TLO)/2.0
  HSINE=(TBAR-TLO)/2.0
  HCOOL=0.
  ACCUM = .FALSE.

ELSE IF (TMIN1.LT.TLO.AND.TMAX1.LE.TUP) THEN     ! CASE 4

  HTRI=(TMAX1-TLO)**2/((TMAX1-TMIN1)*4.0)
  X1=(TLO-TBAR)/A
  T1=ATAM)X1((1-X1**2)**2))
  T2=1.5708
  ACCUM = .TRUE.

ELSE IF (TMIN1.GE.TLO.AND.TMAX1.GT.TUP) THEN     ! CASE 5

HTRI=((TBAR-TLO)/2.0)-(((TMAX1-TUP)**2)/((TMAX1-
  TMIN1)*4))
X2=(TUP-TBAR)/A
T1=-1.5708
T2=ATAN(X2/((1-X2**2)**2))
ACCUM = .TRUE.

ELSE IF (TMIN1.LT.TLO.AND.TMAX1.GT.TUP) THEN     ! CASE 6

  HTRI=((TMAX1-TLO)**2-(TMAX1-TUP)**2)/((TMAX1-TMIN1)*4)
  X1=(TLO-TBAR)/A
  X2=(TUP-TBAR)/A
  T1=ATAN(X1/((1-X1**2)**2))
  T2=ATAN(X2/((1-X2**2)**2))
  ACCUM = .TRUE.

END IF

IF ( ACCUM ) THEN          ! ACCUMULATION FORMULA CASES 4-6

  HSINE=.159155*((TBAR-TLO)*(T2-T1)+A*
1         (COS(T1)-COS(T2))+(TUP-TLO)*1.5708-T2))
  HCOOL=.159155*((TLO-TBAR)*(T1+1.5708)+A*COS(T1))
END IF

  TRI=TRI+HTRI             ! HALF-DAYS INCREMENTS ARE ADDED
  SINE=SINE+HSINE
  COOL=COOL+HCOOL

END DO          ! END HALF DAY LOOP

RETURN
END
```

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