Larval movement and its potential impact on the management of the obliquebanded leafroller (Lepidoptera: Tortricidae)

DE Waldstein,[1] WH Reissig, JP Nyrop

Department of Entomology, Cornell University, New York State Agricultural Experiment Station, Geneva, New York, United States 14456

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Abstract—The rate at which obliquebanded leafroller, *Choristoneura rosaceana* (Harris), larvae vacated feeding sites in apple, *Malus domestica* Borkhauser (Rosaceae), trees was determined by monitoring infested terminal foliage under field conditions. The overwintering and summer generations of *C. rosaceana* were monitored in two orchards in 1997 and 1998. Larvae vacated terminal feeding sites relatively frequently because 50% of the sites during the overwintering and summer generations were vacant 34 ± 6°d (threshold = 6°C) and 53 ± 10°d, respectively, after sites had been marked. Vacancy rates increased from the beginning to the end of the summer generation in 1997 but remained relatively constant throughout the summer generation in 1998. The differences between the 2 years were probably because of less precipitation and lower availability of actively growing terminal foliage at the end of the summer in 1997 than in 1998. Differences in larval development did not seem to contribute to differences in vacancy rate. Recolonization of growing terminals was also studied in the field by removing *C. rosaceana* larvae from terminals only (1997) and the entire tree (1998). In 1997 and 1998, larval recolonization of terminals and trees occurred, because 6–8 d after larvae were removed populations in removal and adjacent control trees were not significantly different. Frequent larval movement to actively growing terminal foliage with sublethal insecticide residues may increase larval survival and could slow resistance development by providing a refuge for susceptible insects.

Waldstein DE, Reissig WH, Nyrop JP. 2001. Déplacements des larves et impact de ces mouvements sur la gestion de la Tordeuse à bandes obliques (Lepidoptera : Tortricidae). *The Canadian Entomologist* **133** : 687–696.

Résumé—La vitesse à laquelle les larves de la Tordeuse à bandes obliques, *Choristoneura rosaceana* (Harris), quittent leur site d'alimentation a été mesurée en nature par examen des pousses terminales de pommiers, *Malus domestica* Borkhauser (Rosaceae). Les générations d'hiver et d'été de *C. rosaceana* ont été suivies dans deux vergers en 1997 et 1998. Les larves quittent les pousses terminales relativement souvent, puisque 50 % des sites de la génération d'hiver et de la génération d'été étaient libres, respectivement 34 ± 6°jour (seuil = 6°C) et 53 ± 10°jour après le marquage des sites. Les taux de retrait ont augmenté du début à la fin de la génération d'été de 1997, mais sont restés relativement constants chez la génération d'été de 1998. Ces différences entre les 2 années semblent attribuables à des précipitations moins abondantes et à la disponibilité des pousses terminales en croissance active moins grande à la fin de l'été 1997 qu'en 1998. Les différences de taux de retrait ne semblent pas être reliées à des différences dans le développement larvaire. La recolonisation des pousses terminales en croissance a aussi été étudiée en nature par le retrait de larves de *C. rosaceana* des pousses terminales seules en 1997 et des arbres entiers en 1998. Il s'est fait de la recolonisation par les larves en 1997 et en

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[1] Author to whom all correspondence should be sent at the following address: B18 Food Safety and Toxicology Building, Michigan State University, East Lansing, Michigan, United States 48824-1302 (E-mail: waldste1@msu.edu).

1998, aussi bien sur les arbres entiers que sur les pousses terminales, puisque, 6–8 jours après le retrait des larves, les populations de larves des arbres expérimentaux ne différaient pas de celles d'arbres témoins adjacents. Les déplacements larvaires fréquents vers des pousses terminales en croissance porteuses de résidus d'insecticide sous le seuil létal peuvent augmenter la survie des larves et peuvent aussi ralentir le développement de la résistance en procirant un refuge aux insectes sensibles.

[Traduit par la Rédaction]

Introduction

The obliquebanded leafroller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae), is an important pest of apples, *Malus domestica* Borkhauser (Rosaceae), in Canada and the United States. Throughout most of its range, the obliquebanded leafroller is bivoltine and overwinters as a second or third instar (Chapman and Lienk 1971). Although *C. rosaceana* is primarily a foliage feeder, it also damages fruit (Chapman *et al.* 1968; Chapman and Lienk 1971). This tortricid has become a serious pest of apples in commercial orchards mainly because of resistance to multiple insecticides (Reissig *et al.* 1986; Carrière *et al.* 1996; Lawson *et al.* 1997; Smirle *et al.* 1998; Waldstein *et al.* 1999). In addition to insecticide resistance, the larval movement of *C. rosaceana* may play a role in its pest status. Because larvae are commonly observed feeding in actively growing terminal foliage (Chapman and Lienk 1971), the percentage of terminals infested by *C. rosaceana* larvae is used to determine the need for insecticide applications (Agnello *et al.* 1993). The propensity to feed on terminals may increase the difficulty of controlling this orchard pest. Insecticide residues on terminals are subject to environmental degradation and may also decrease from leaf expansion and production of new foliage throughout the typical 2-week spray interval. Mortality of *C. rosaceana* neonates to chlorpyrifos, esfenvalerate, or tebufenozide on terminal apple foliage collected from commercial orchards 10 d after these insecticides were applied was <15% (Waldstein and Reissig 2001). The frequency of movement of larvae from terminal feeding sites may influence the length of exposure to insecticides. If larvae move frequently to new terminal sites with sublethal residues, they may survive insecticide exposures during the spray season. If, however, larvae remain in the same location for extended periods of time and are exposed to a high dose, they will be less likely to survive insecticide applications. Movement of larvae to actively dividing terminals with sublethal residues may be particularly important for insecticides that require long exposures to be maximally effective. Larvae that move more frequently than the minimum exposure time necessary for an insecticide to cause lethality may survive insecticide treatments.

Although the dispersal of *C. rosaceana* neonates after they hatch from egg masses has been thoroughly examined on multiple hosts (Carrière 1992; Hunter and McNeil 1997), less is known about the movement behavior of post-neonate larvae once they have established enclosed feeding sites. Because the movement of larvae from terminal feeding sites may influence control measures, the first objective of this study was to determine the vacancy rate of *C. rosaceana* larvae from enclosed feeding sites. In the second study, larval movement within and between apple trees was studied by removing *C. rosaceana* larvae from feeding sites to determine if recolonization would occur.

Methods

Field vacancy rates

The frequency of larval movement was determined by labeling feeding sites in terminal apple foliage and revisiting these sites to determine if larvae were present. The second half of the overwintering (larvae that have been through diapause) and the summer generations were monitored in 1997 and 1998. In 1997, the overwintering and summer generations were monitored from 11 to 26 June and 9 July to 3 September, respectively. In 1998, the overwintering and summer generations were monitored from 12 to 26 May and 2 July to 4 August, respectively. Sites were marked by tying colored flagging tape to branches proximal to the site and tying string to the petiole of the leaf or leaves where the larvae resided. Flagging tape was numbered to differentiate sites. Sites were checked every 1–7 d, and 22–409 new sites were added with different colored flagging tape each date the study was conducted. Hand lenses were used when necessary so that larvae in feeding sites could be located without opening leafroller shelters. One to 13 feeding sites per tree were marked in ≥50 trees per orchard and obliquebanded leafroller generation. The study with the overwintering generation of 1997 was conducted in the Trickler experimental orchard (42°54′11′′N, 77°1′45′′W) with ‘Delicious’ and ‘McIntosh’ trees. The Trickler experimental orchard is maintained in a manner similar to that of a commercial orchard except that no insecticides for the control of obliquebanded leafroller were used during the study. The study with the summer generation of 1997 was conducted in the Station Creek experimental orchard (42°52′25′′N, 77°0′32′′W) with ‘Cortland’ trees. This experimental orchard receives fungicide applications but typically no insecticide applications. No insecticides for the control of obliquebanded leafroller were applied in the Station Creek orchard during the study. Reentry restrictions because of repeated fungicide applications for an apple scab, *Venturia inaequalis* Cooke (Venturiaceae), outbreak prohibited us from using the Trickler experimental orchard for the summer generation in 1997. Both orchards are located within 5 km of Geneva, New York. In 1998, the study was conducted for the overwintering and summer generations in both orchards on the same cultivars (*i.e.*, ‘Delicious’, ‘McIntosh’, and ‘Cortland’). A total of 292–692 sites were monitored for each orchard, generation, and year.

Cumulative percent vacancy was calculated for each day sites were monitored. Larvae that were dead or parasitized were omitted from the calculations. Data from the Trickler orchard were used to determine if differences between the two cultivars (*i.e.*, ‘McIntosh’ and ‘Delicious’) influenced the vacancy rate of *C. rosaceana* larvae. Cultivar differences in vacancy rates were examined in 1997 for the overwintering generation and in 1998 for the summer generation. A χ^2 test was used to analyze the data. Expected values for vacancy were the sum of vacancy rates for larvae in ‘McIntosh’ and ‘Delicious’ foliage at each time interval divided by 2. A logarithmic regression of cumulative percent vacancy and degree-days (threshold = 6°C; $°d_6$) was fitted for each generation, year, and orchard using the following equation:

$$y = m \ln(x) + b$$

where y is the cumulative percent vacancy, x is degree-days, b is the y intercept, and m is the slope. Vacancy rate was determined by calculating the ratio of the percent vacancy at each time sites were monitored to the number of degree-days larvae remained in feeding sites. Vacancy rate was compared with the number of degree-days accumulated after Biofix (*i.e.*, first sustained moth catch) at the first date sites were marked to determine if the ratio varied throughout the summer generation. The higher the vacancy ratio, the more frequently larvae vacated feeding sites. For example, at a vacancy ratio of 1:1, at 50°d after sites were marked 50% of the larvae had vacated feeding sites. Comparisons between number of degree-days and vacancy rate were made for only the summer generation because only the latter portion of the overwintering generation was monitored. Because head capsules and weight measurements could not be made without disturbing larvae and affecting their behavior in feeding sites, pest phenology was indirectly measured using number of degree-days. Because egg hatch of obliquebanded leafroller occurs over a wide range of degree-days (170–550°d after Biofix) and the corresponding larval development occurs over a wide range of degree-days (170 to >900°d after Biofix), there is a considerable range of developmental stages occurring at any particular time in the field during the summer generation (Onstad *et al.* 1985; Gangavalli and Aliniazee 1985). Therefore, number of degree-days was related to pest phenology by using data from Onstad *et al.* (1985, 1986) and Gangavalli and Aliniazee (1985) to determine when the majority of larvae were in a particular stage. Based on these studies, the median larval stage (*i.e.*, majority of larvae occurring in the field) for the 1st through 6th instars corresponds to 328, 385, 441, 527, 598, and 690°d after Biofix, respectively (peak hatch = 250°d; development of all instars = 440°d).

Larval removal

The study was conducted in 1997 and 1998 on 'Delicious' apple trees in the Trickler experimental orchard. Trees were 16 years old, 3.0 m high, and planted 1.6 × 4.5 m apart. In 1997, obliquebanded leafroller terminal infestations were monitored in a total of 11 trees in two rows. Trees in which the terminal infestations of obliquebanded leafrollers were removed every 6–8 d (removal trees, $n = 5$) were adjacent to trees in which terminal infestations were monitored but not removed (control trees, $n = 6$). Larvae at the top of the tree were removed by standing on the lowest scaffold limb of the trees. No insecticides for the control of obliquebanded leafroller were applied during the study. The experimental block was arranged with alternating removal and control trees (Fig. 1).

In 1998, the study was repeated in the same orchard in a total of nine trees in one row (four removal trees and five control trees). In 1998, the study was similar to that in 1997, except that all larvae at terminal and spur leaf sites were monitored and removed to determine if obliquebanded leafroller larvae from control trees would repopulate removal trees. In 1997, the study was started 374°d_6 after the first moth catch from the overwintering generation (15 July) and ended 206°d_6 after the first moth catch from the summer generation (18 August). In 1998, the study was started 621°d_6 after the first moth catch from the overwintering generation (14 July) and ended 127°d_6 after the first moth catch from the summer generation (4 August). The study lasted 3–5 weeks to ensure that larvae from only one generation were monitored. The total duration of the study was 3–5 weeks. Because there was correlation among dates, a repeated measures analysis of variance (ANOVA) was conducted for each year on the mean number of live and total (live and dead) larvae per tree (Abacus Concepts 1991). The Greenhouse-Geisser and Hunyh-Feldt estimates of epsilon were used to adjust P values because of the correlation of observations at each date. Both estimates were used because Greenhouse-Geisser tends to understimate epsilon and Hunyh-Feldt typically overestimates epsilon (Abacus Concepts 1991). Data were normalized prior to analysis using a natural logarithm of $n + 1$ transformation.

Results

Field vacancy rates

In 1997, 50% of the sites were vacant 35 and 32°d_6 after feeding sites were marked during the overwintering and summer generations, respectively (Table 1). Ninety percent of the sites were vacant after 179 and 142°d_6, respectively. In 1998, 50% of the sites were vacant 23 and 43°d_6 after feeding sites were marked during the overwintering generation in the Trickler and Station Creek orchards, respectively.

T	T	T	T	T	T	T	T	T	T, etc.
R	C	R	C	C*	T	T	T	T	T, etc.
R	C	R	C	R	C	T	T	T	T, etc.
T	T	T	T	T	T	T	T	T	T, etc.

FIGURE 1. Diagram of the plot arrangement for the *Choristoneura rosaceana* larval removal study in Trickler orchard in 1997. R, trees from which larvae were removed; C, control trees (no larvae removed); T, trees outside the study block; C*, tree added because of the accidental removal of three larvae from the adjacent control tree.

Ninety percent of the sites were vacant after 108 and 152°d_6, respectively. For the summer generation during the same year, 50% of the sites were vacant 63 and 62°d_6 after feeding sites were marked in the Trickler and Station Creek orchards, respectively. Ninety percent of the sites were vacant after 181 and 190°d_6, respectively. There were no significant differences in the vacancy rates for larvae on the 'McIntosh' and 'Delicious' trees for either the overwintering or the summer generations ($P > 0.05$). For the summer generation in 1997, larval vacancy rates at 700°d after Biofix (median instar = 6th) were nearly double the rates at 300°d after Biofix (median instar = 1st) (Fig. 2). In 1998, however, vacancy rates remained relatively constant throughout the summer generation (Figs. 3, 4).

Larval removal

In 1997 and 1998, a similar number of larvae were found in removal and control trees at each date (Table 2). In 1997, from 21 July to 12 August, there were 3.6–5.6 total larvae per tree in terminals on removal trees and 3.2–6.0 total larvae per tree in terminals on control trees. In 1998, from 14 July to 4 August, there were 2.0–13.0 larvae per tree on removal trees and 4.2–9.4 larvae per tree on control trees. There was no significant effect of treatment (*i.e.*, removal and control) or date on the number of total or live larvae on apple trees in 1997 and 1998 (Table 3). There were no significant date × treatment interactions in 1997 or in 1998 with total larvae (Table 3). With *P* values adjusted for correlation among dates using the Hunyh-Feldt estimate of epsilon, there was a significant date × treatment interaction of live larvae in 1998 (Table 3). With *P* values adjusted for correlation among dates using the Greenhouse-Geisser estimate of epsilon, however, there was no significant date × treatment interaction.

Discussion

Neither the overwintering nor the summer generations of obliquebanded leafroller larvae remained in individual growing terminals for extended periods of time. Larvae that were removed from sites by predation may have influenced the vacancy rate of obliquebanded leafroller larvae. Because insecticides are not commonly used in the Station Creek orchard but are in the Trickler orchard, we would expect predation to be a larger factor in the Trickler orchard. It is unlikely predation had a major influence on vacancy rates, however, because vacancy rates were similar in both orchards. Parasitism and other sources of mortality did not affect vacancy rates, because parasitized and dead larvae were not included when estimating vacancy rates. The total percentage of dead larvae from the overwintering and summer generations in 1997 was 1.0% (0.7% parasitized) and 14.9% (2.8% parasitized), respectively. General mortality and parasitism rates in 1998 were similar to those in 1997.

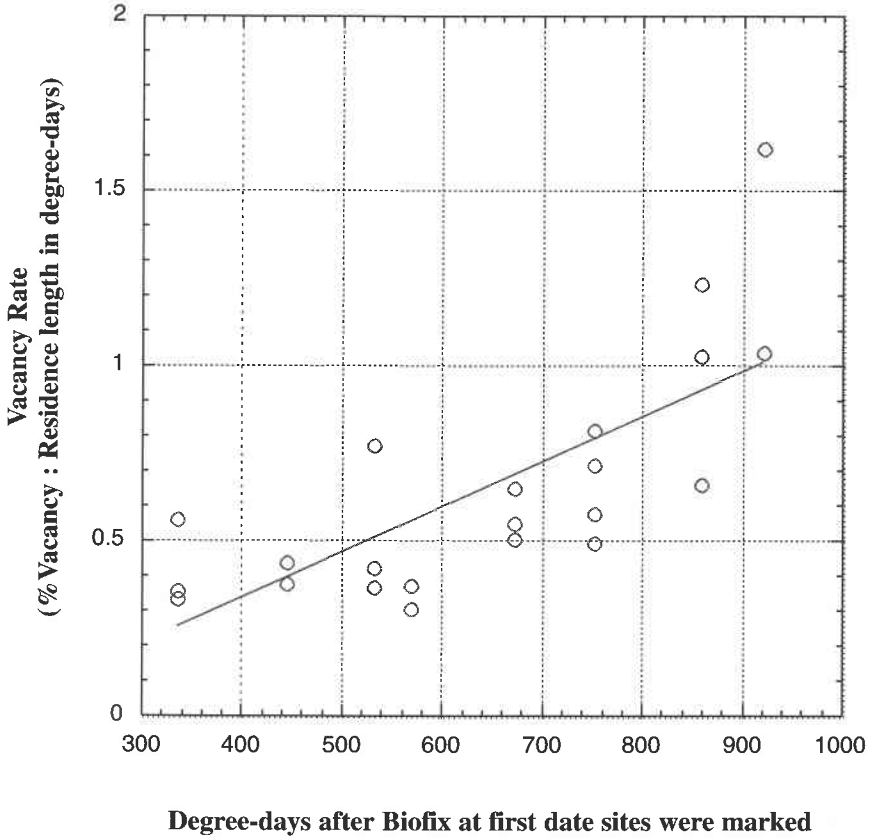

Figure 2. Comparison of vacancy rate [ratio of percent vacancy to residence length in degree-days (threshold = 6°C)] of *Choristoneura rosaceana* larvae to degree-days accumulated after Biofix at first date sites were marked in the Station Creek orchard for the summer generation in 1997.

Table 1. Logarithmic regression of cumulative percent vacancy of *Choristoneura rosaceana* larvae and degree-days (threshold = 6°C) in 1997 and 1998.

Orchard	Generation*	Slope	*y* intercept	R^2
		1997		
Trickler	OW	24.62	–37.79	0.51
Station Creek	S	27.10	–44.29	0.58
		1998		
Trickler	OW	25.45	–29.18	0.85
Trickler	S	38.07	–107.97	0.92
Station Creek	OW	31.82	–69.89	0.97
Station Creek	S	35.65	–97.00	0.93

* OW, overwintering; S, summer.

Carrière (1992) demonstrated higher dispersal rates on apple foliage for larvae <2 h old than for larvae that were 24 h old. It is unlikely the differences observed in 1997 were the result of different vacancy rates of early and late instars, because a similar trend was not observed in 1998. Although vacancy rates increased threefold from the

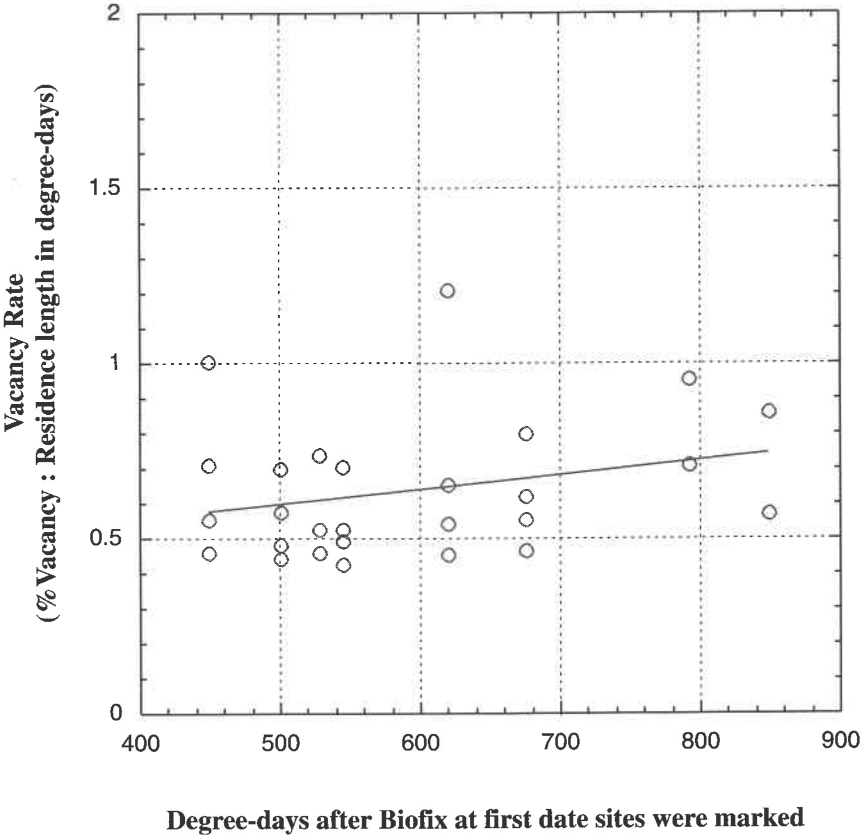

FIGURE 3. Comparison of vacancy rate of *Choristoneura rosaceana* larvae to degree-days accumulated after Biofix at first date sites were marked in the Station Creek orchard for the summer generation in 1998.

beginning to the end of the summer generation in 1997, they remained relatively constant throughout the summer generation in 1998. The availability of terminal foliage may have an influence on larval vacancy rates. During July and August of 1997, precipitation was abnormally low. Total precipitation in those 2 months was 74 mm in 1997 and 161 mm in the more typical year of 1998. The amount of actively growing terminal foliage was substantially less at the end than the beginning of the summer generation in 1997. This lack of terminal foliage availability may have contributed to the increased movement of larvae during the summer of 1997. In 1998, larvae from the summer generation remained in terminal feeding sites longer than overwintering larvae. This also may be related to foliage availability, because more foliage was available to larvae during the summer months than in the spring when trees were less developed. Hunter and McNeil (1997) demonstrated a higher rate of *C. rosaceana* neonate dispersal from paper birch, *Betula papyrifera* Marshall (Betulaceae), and black ash, *Fraxinus nigra* Marsh (Oleaceae), than from chokecherry, *Prunus virginiana* L. (Rosaceae), a more suitable host based on nutrient quality and decreased time for larval development. Onstad *et al.* (1986) showed that larvae which fed on young apple foliage developed more quickly than those which fed on old foliage, indicating that young foliage is more suitable than old foliage for larval development. With 24-h-old *C. rosaceana*, however, Carrière (1992) demonstrated no significant effect of leaf age on larval dispersal rates.

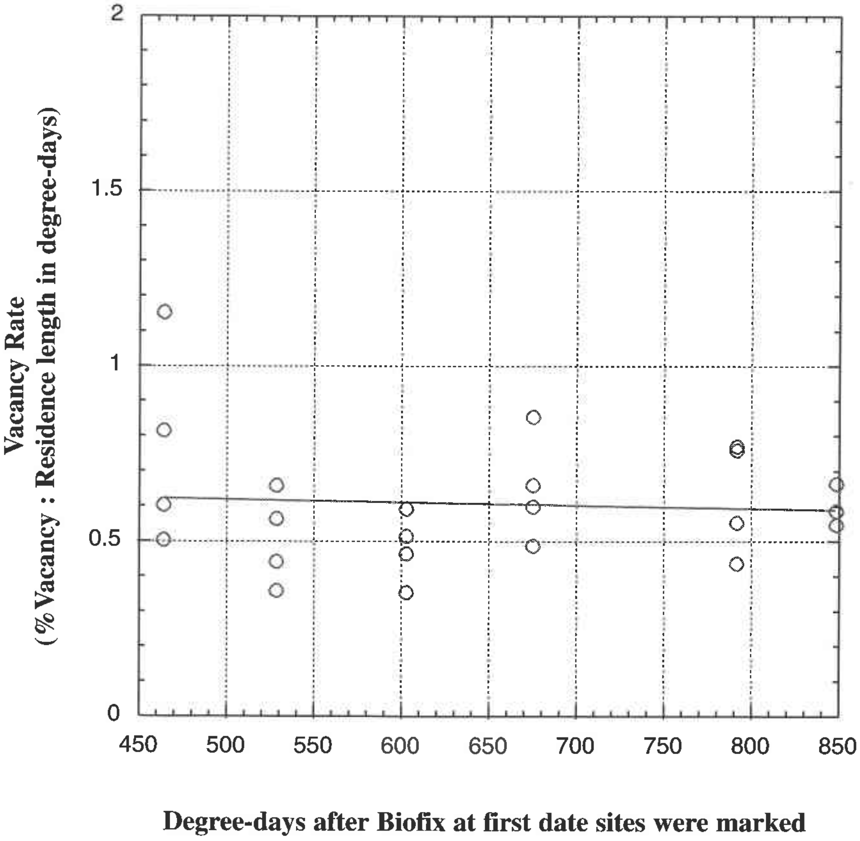

Figure 4. Comparison of vacancy rate of *Choristoneura rosaceana* larvae to degree-days accumulated after Biofix at first date sites were marked in the Trickler orchard for the summer generation in 1997.

In 1997 and 1998, approximately equal numbers of larvae were found on removal and control terminal foliage 6–8 d after larvae were removed from terminals. Egg mass hatch begins 170–250°d_6 and ends 450–550°d_6 after the first moth is caught (Onstad *et al.* 1985). Although larvae from hatching egg masses could have contributed to the population during the study in 1997, it is unlikely that moths would have preferentially laid egg masses on either the removal or control trees. In 1998, the study was started after egg mass hatch was complete (621°d_6) and completed before egg masses from the summer-generation moths hatched (127°d_6). Therefore, because of the timing of the study in 1998, larvae hatching from egg masses should not have influenced the results. Although removal trees were carefully examined for larvae, it is possible that not all larvae were removed; however, it is unlikely this form of experimental error could explain the important increase in the number of larvae in removal trees 1 week after larvae had been removed. Larvae are likely to have colonized the removal trees from an external source (*i.e.*, control trees or trees outside the study plot). Potential avenues for larval movement include foliar contact between control and removal trees, wind blowing larvae hanging from silk threads, or ground locomotion. Dispersal of neonates on silk threads is a dominant form of locomotion (Carrière 1992); however, the distance and probability of wind-blown dispersal *via* this mechanism may decrease at the later instars. A considerable amount of foliar contact between trees existed in the Trickler orchard during the study and may have given larvae a means of recolonizing removal trees.

Table 2. Mean ± SE number of live and live + dead (total) *Choristoneura rosaceana* larvae per tree in removal and control apple trees in 1997 and 1998.

Date	Treatment	No. of live larvae per tree	Total no. of larvae per tree
		1997	
15 July	Removal	1.8±0.7*	1.8±0.7*
	Control	—	—
21 July	Removal	3.6±1.5	3.6±1.5
	Control	4.6±1.0	4.6±1.0
28 July	Removal	5.6±0.9	5.6±0.9
	Control†	6.0±1.9	6.0±1.9
4 August	Removal	4.0±0.6	5.2±0.7
	Control	3.0±0.7	3.2±0.7
12 August	Removal	3.4±0.6	4.0±0.9
	Control	3.7±1.3	4.0±1.2
18 August	Removal	1.0±0.6	1.2±0.7
	Control	3.2±0.7	3.4±0.7
		1998	
14 July	Removal	9.8±1.7	10.3±1.8
	Control	4.8±1.9	4.8±1.9
21 July	Removal	13.0±1.2	16.8±2.9
	Control	9.4±1.4	11.0±1.5
29 July	Removal	4.8±0.9	5.8±1.0
	Control	4.2±1.1	5.6±1.4
4 August	Removal	2.0±2.4	4.0±3.1
	Control	5.4±1.4	6.6±1.4

* Not included in the analysis of variance because no data were collected from control trees.

† Three larvae were accidentally removed from a control tree.

Table 3. Analysis of variance of number of live and live + dead (total) *Choristoneura rosaceana* larvae in apple trees with control and removal treatments in 1997 and 1998.

	1997						1998					
	Live			Total			Live			Total		
		P adjusted			*P* adjusted			*P* adjusted			*P* adjusted	
Source	df	G-G	H-F	df	G-G	H-F	df	G-G	H-F	df	G-G	H-F
Date	4	0.60	0.63	4	0.57	0.59	3	0.58	0.60	1	0.79	0.79
Treatment	1	0.42	0.42	1	0.49	0.49	1	0.31	0.31	3	0.35	0.35
Date × treatment	4	0.17	0.14	4	0.12	0.09	3	0.06	0.03*	3	0.10	0.06

Note: *P* values were adjusted using the Greenhouse-Geiser (G-G) and Hunyh-Feldt (H-F) estimates of epsilon.

* Significant at $P = 0.05$.

The results of the larval removal study support the conclusions from the field vacancy rates study. Larvae do not remain in the same location for extended periods of time.

Larval movement of obliquebanded leafroller may have an influence on the efficacy of insecticide applications if larvae move to foliage with sublethal residues before they receive a lethal dose. Movement of larvae to terminal foliage with sublethal residues may have a greater impact on insecticides like tebufenozide that require longer exposures for high mortality than fast-acting neurotoxins (Waldstein and Reissig 2001).

Larval movement of obliquebanded leafroller may also have an influence on the development of insecticide resistance in commercial apple orchards. If susceptible insects survive insecticide applications by movement to foliage with sublethal residues and successfully mate with resistant individuals, the resistant genotypes and phenotypes (depending on inheritance type of the resistance alleles) will be diluted in the population. This potential dilution of phenotypes in the population, in addition to the decreased selection pressure from new terminal growth acting as an internal refuge from insecticide exposure, could slow resistance development in the obliquebanded leafroller.

Foliage growth in an apple orchard can have an important influence on the population ecology and management of the obliquebanded leafroller. Factors including age of the tree, cultivar, nutrient management, use of growth regulators, and precipitation can affect foliage growth and may indirectly impact larval movement and the effectiveness of control measures directed against *C. rosaceana*.

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