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Title: Developmental Biology and Phenology of the Walnut Husk Fly, *Rhagoletis completa* Cresson, (Diptera: Tephritidae) in the Willamette Valley of Oregon.

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Developmental biology and phenology of the walnut husk fly (WHF), *Rhagoletis completa* Cresson, (Diptera: Tephritidae) were investigated. Preoviposition, egg, and larval development increased with increasing temperature, development was fastest at 28°C, but started to decline beyond this temperature. Egg deposition by mature females and postdiapause pupal development increased with increasing temperature up to 24°C, but dropped thereafter. Using a linear and nonlinear modelling approach, the lower thresholds were estimated to be 6.6, 5.4, 2.9, and 5°C for preoviposition, egg, larval and pupal stages, respectively. The upper developmental thresholds were 34°C for preoviposition, egg and larval stages, and 30°C for pupal stage.

The WHF adults began to emerge in ground emergence cages as early as June 29, with an average time of emergence of July 10. Peak fly emergence occurred between July 20 and August 5. A consistent temporal relationship

was noticed between first emergence and first oviposition. The average preoviposition period was three weeks. A mean egg hatch of 98% and larval survival of 80% was observed. Fruit infestation levels reached over 95%. Seasonal development of the WHF was influenced by the prevailing temperatures and husk development.

In unsprayed walnut trees, first flies appeared in aerial traps in early July (July 1 through 17), with an average emergence date of July 9. Seasonal peak varied from August 10 through September 4. In commercial walnut orchards, the first flies were detected in aerial traps from July 13 through August 5. Dissections of field collected females indicated that flies were capable of egg laying 12 days after emergence. There was only one generation in the Willamette Valley.

A more accurate prediction of various biological and population events can be made using a physiological time scale as opposed to calendar dates. Using surface temperature and a 5°C developmental threshold, first flies in aerial traps were detected at an average of 1060 thermal units (TU), first oviposition averaged 1512 TU, 10% fly capture averaged 1661 TU and 50% fly capture averaged 1912 TU. A temperature dependent-developmental rate phenology model is developed and described. Validation of the model was checked by coefficient of variation (CV). The model was found to be highly efficient in predicting fly activity levels.

DEVELOPMENTAL BIOLOGY AND PHENOLOGY OF THE WALNUT HUSK FLY, *RHAGOLETIS COMPLETA* CRESSON (DIPTERA: TEPHRITIDAE) IN THE WILLAMETTE VALLEY OF OREGON

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Walnut (*Juglans* spp.) is known for the nuts and timber it produces. Persian walnut, *Juglans regia L.*, is believed to have originated near the Caspian Sea in Iran. After thousands of years of natural selection and adaptation, the present day thin shelled walnuts came into existence. Varietal selection and breeding programs the past 100 years have resulted in the development of the current varieties. All walnut species produce edible nuts, however, the Persian walnut, *J. regia* is the most developed horticulturally and widely cultivated. Persian walnuts are grown in North, Central and South America, Europe, Asia, U.S.S.R., and to a limited extent in Oceania and North Africa (Grimo 1981, Ryugo 1988, McGranaban and Leslie 1991). France, Italy, Turkey, China, India, and the United States are well known for their commercial production (Ramos et al. 1984)

In the United States, nearly all the commercial walnut production is now concentrated in the interior valleys of California. Oregon reached a peak of about

12,000 hectare in 1949 and declined slowly to about 1,200 hectare due to various production and marketing constraints (Forde 1981). Currently, approximately 800 hectare of walnuts are found in the state (AliNiazee, personal communication). Many homeowners are still planting new trees (Anonymous 1983).

All varieties of Persian walnuts as well as the native black walnut are suitable hosts for walnut husk fly (WHF), *Rhagoletis completa* Cresson (Diptera: Tephritidae) (Boyce 1934, Riedl et al. 1979, Anonymous 1982). 'Franquette' is the most popular walnut variety grown in Oregon and Washington. Varieties such as 'Franquette', 'Mayette', 'Eureka', and 'Payne' are highly susceptible to WHF attacks, whereas 'Placentia', a variety with a harder husk, is comparatively less susceptible (Boyce 1934).

More than 25 arthropods may cause injury to walnuts (Riedl et al. 1979, Anonymous 1982). Six insects and one mite pest are responsible for walnut injury in the Pacific northwest. The WHF is the key arthropod pest in the Pacific Northwest (Anonymous 1983, 1993).

The WHF is native to southwestern North America and is found in many states. It is quite prevalent in California, Oregon, and Washington (Boyce 1934; Bush 1966; Retan 1980; AliNiazee and Fisher 1985). Initially it was recorded from a walnut orchard at Chino in southern

California in 1925 (Michelbacher and Ortega, 1958) and has since spread throughout that state. The founders of the California population may have originated from western Texas (Berlocher 1976).

The first record of the fly in Oregon was in 1963 (Bush 1966, Berlocher 1984a). An increasing number of flies started to appear in Oregon orchards toward the end of 1960's. At present the insect is well distributed in all commercial orchards and in many backyard trees. It is a serious pest of walnuts in most commercial walnut-growing districts of Oregon (AliNiazee and Fisher 1985). It is considered a serious mid- to late-season pest on many walnut varieties (Riedl et al. 1979, Anonymous 1982, AliNiazee and Fisher 1985).

The infestation of WHF varies from variety to variety. Cultivars with a soft thick hulls are more susceptible to damage (Shelton and Anderson 1990). Early varieties usually escape serious damage (Anonymous 1982). Late varieties can sustain heavy damage impact, as the larvae cause both stained shells and moldy and shrivelled nut meat. Nut maturation of early varieties is more advanced by the time WHF females start to lay eggs, therefore the damage to kernels is not as severe (Riedl et al. 1979).

Although, the WHF is a key pest of walnuts, it is

also an occasional pest on peaches and nectarines. Boyce (1934) found infested peaches in the vicinity of walnut orchards, and a peach infesting race was found in Washington (AliNiazee, personal communication). Boyce (1934) reported that all *Juglans* species were attacked, but the degree of damage depended on walnut husk hardness in relation to adult emergence. In heavily infested orchards nearly 100% of the nuts can be infested (Riedl and Hoying 1980).

The biology of WHF is similar to that for other fruit infesting *Rhagoletis* species (Boller and Prokopy 1976, AliNiazee 1988). A detailed account of the life history of this pest was described by Boyce (1934) from California. Adult flies usually emerge from overwintering pupae from early July through October (AliNiazee and Fisher 1985). Emergence and mating correspond with the maturing of the husk. After mating the female penetrates the nut husk with her ovipositor depositing several eggs in oviposition cavities. Upon hatching, the larvae tunnel through the husk as they feed. Feeding activities and metabolic products soon turn the green husk into a black, slimy mass. Early researchers believed that this feeding activity was detrimental to the nutmeat formation and quality (Boyce 1934, Michelbacher and Ortega 1958), however, Gibson and Kearby (1977) have shown that this

type of damage was not that serious. Larval feeding generally causes premature nut drop thus reducing the harvestable crop. The larvae generally undergo two molts. At the end of the third instar, larvae leave the blackened husk to enter the soil, where the larval cuticle is shed and hardens to form a puparium, within which pupation takes place (Boyce 1934). The winter is spent in this stage in soil under walnut trees. Adult emergence occurs the following summer; however, a substantial number may not emerge until the second or third season. Boyce (1931) showed that this insect is capable of extending its diapause period for as long as four years.

Chemical control is the most common method of suppressing WHF. A few organophosphate and synthetic pyrethroids insecticides are registered for this use (AliNiazee and Fisher 1985, Anonymous 1993). Biological control has not been effective in WHF control. Boyce (1934) found this fly remarkably free from natural enemies in southern California. However, a few generalist predators, such as spiders, carabids, anthocorids, chrysopid larvae, and ants were reported to prey upon different life stages of the WHF.

For effective chemical control adult fly emergence must be monitored. The timing of insecticide applications against WHF has been based on calendar date or by

monitoring fly activity using dry ammonium carbonate traps, bait pan traps and Pherocon AM traps (Barnes and Ortega 1958, Barnes and Osborne 1958, Gibson and Kearby 1978, Riedl and Hoying 1980, AliNiazee and Fisher 1985). Aerial traps are good indicators of population trends and fly development. Insecticides are usually applied 10 days after traps show the first marked increase in fly catches (Joos et al. 1974). This practice has not always been satisfactory and can give variable results depending on walnut variety. By using trapping data only, treatments are usually recommended when fly catches show a sharp or steady increase over a 3-day period (AliNiazee and Fisher 1985). However, this timing can be inaccurate due to improper servicing of traps. Riedl and Hoying (1980) reported that for timing insecticides, the use of trap catches only may be unreliable because their relationship to onset of oviposition is variable. They also mentioned that timing of insecticide applications can be improved if based on monitoring and routine inspection of nuts for oviposition scars.

Currently, control of WHF is most often achieved in western Oregon by applying insecticidal sprays twice during the month of August. Historically, Malathion bait sprays have been successful against fruit flies including WHF (Barnes and Ortega 1959, Barnes et al. 1978, Hislop

et al. 1981, Mohammed and AliNiazee 1989). Experimentally, systemic insecticides applied to control young larvae have been effective (Nickel and Wong 1966). Growers may apply insecticides on a calendar basis against adults to prevent egg laying. Bait pans containing glycine-sodium hydroxide solution have been to used to monitor adult flies (Barnes and Ortega 1958), as have sticky food carton traps containing ammonium carbonate (Barnes and Osborne 1958) and similar to ones developed by Frick (1952) for the western cherry fruit fly, *Rhagoletis indifferens* (Curran). Fluorescent yellow sticky rectangles originally developed for apple maggot (Prokopy 1975) proved more effective for WHF than previous monitoring methods and were easier to handle in the field as well (Riedl and Hoying 1980).

Relatively little information is available on the environmental biology of the WHF, although detailed field studies were conducted by Boyce (1934). Adult monitoring studies were conducted by Barnes and Ortega (1958), Barnes and Osborne (1958), Gibson and Kearby (1978), Riedl and Hoying (1980), and Riedl et al. (1989).

Successful chemical control WHF is dependent upon precise timing of an insecticide application to coincide with WHF emergence and egg deposition. Riedl et al. (1979) indicated that the development of a management model is essential for effective control.

The purpose of this study was to develop an understanding of the developmental biology of the WHF, particularly in relation to temperature, and to predict the occurrence of various life history events in the field. This knowledge can improve the management of WHF in Oregon.

CHAPTER II

EFFECT OF TEMPERATURE ON DEVELOPMENT OF THE WALNUT HUSK FLY, *RHAGOLETIS COMPLETA* CRESSON (DIPTERA: TEPHRITIDAE) UNDER CONTROLLED LABORATORY CONDITIONS

ABSTRACT

The developmental rates of various stages (preoviposition, egg, larval, and pupal) of the walnut husk fly (WHF), *Rhagoletis completa* Cresson were determined in the laboratory at seven different constant temperatures: 8, 12, 16, 20, 24, 28, and 32±1°C, relative humidity 80±10%, photoperiod 16:8 [L:D]. Preoviposition rate was most rapid at 28°C (9.9±0.7 days) (x±SD) and slowest at 12°C (26.4±1.1 days). About 83% of the females deposited eggs at 20 and 24°C and only 25% oviposited at 32°C. Females laid the highest number of eggs at 24°C and the lowest at 8°C. Egg development was fastest at 28°C (54.8±0.5 hrs) and slowest at 8°C (389.3±2.4 hrs). Greater than 90% egg hatch was observed at temperatures between 12 and 32°C. Eclosion decreased to 73% at 8°C. Larval development was fastest at 28°C (19.5±0.2 days). Over 65% pupation was recorded at 20 and 24°C, but decreased to 14.7% at 32°C and 11.7% at 8°C. Pupal development was most rapid at 24°C (53.5±0.5 days) and slowest at 8°C (162.2±2 days). Emergence was greater than 70% between 16 and 24°C but decreased to 19.5% at 8°C.

Based on a linear model of the temperature-development rate relationship, the lower developmental thresholds were determined to be 6.6, 5.3, 2.9, and 5°C

for preoviposition, egg, larval, and pupal stages, respectively. Based on a non-linear model of the temperature-development rate relationship, the upper developmental thresholds were 34°C for preoviposition, egg, and larval stages and 30°C for pupal stage.

INTRODUCTION

Like other insects, the developmental rates of *Rhagoletis* flies are dependent on a number of environmental factors including temperature (Kamal 1954, Reid and Laing 1976, Baker & Miller 1978, Stark and AliNiazee 1982 and Van Kirk and AliNiazee 1981, 1982), food (Kamal 1954), humidity (Trottier and Townshend 1979), rainfall (Smith and Jones 1991), and photoperiod (AliNiazee 1988).

Kamal (1954) studied the influence of constant temperature on preoviposition and oviposition of the western cherry fruit fly, *Rhagoletis indifferens* Curran and reported 26.6°C (80°F) as the optimum temperature for egg development and deposition. Neilson et al. (1981) reported the effects of constant and variable temperature conditions on the preoviposition and oviposition periods of the apple maggot, *R. pomonella*. Many researchers have studied the effects of temperature on postdiapause development of *Rhagoletis* species (Stark and AliNiazee 1982, Van Kirk and AliNiazee 1981, Boller 1964, Jubb and Cox 1974, Maxwell and Parsons 1969, Reid and Laing 1976, Reissig et al. 1979), and used data derived from these studies to construct phenological models.

Little is known about the influence of constant

temperatures on development of various life stages of the walnut husk fly (WHF), *Rhagoletis completa* Cresson. Also no data exist on the developmental thresholds for various life stages of this insect. Since this type of information is essential to develop a better understanding of developmental biology and phenology, it was considered an important component of my investigations. I report here the results of a laboratory study dealing with the effect of temperature on developmental rates of various life stages of the WHF.

MATERIALS AND METHODS

Insects required for this study were obtained as follows: infested nuts were collected during September and October of 1990 from abandoned backyard trees in Corvallis, Oregon. For pupation these nuts were maintained at room temperature in trays containing vermiculite. Pupae were sifted and kept at 3°C for four months to fulfill diapause development requirements (AliNiazee, personal communication). These pupae were used for all studies reported here unless otherwise indicated.

To establish the relationship between temperature and developmental rates, the time required for 50% of individuals to complete the development of a particular stage was determined at a series of constant temperatures. The effect of the following constant temperatures (±1°C) on developmental rates of the WHF was determined: 8, 12, 16, 20, 24, 28, and 32°C. A 16:8 (L:D) photoperiod and relative humidity of 80±10% were used in all treatments. The relative humidity was maintained with different quantities of tap water in plastic trays except for the 24 and 32°C treatments where it was maintained by saturated salt solutions of sodium chloride and sodium nitrate, respectively (Solomon 1951). A thermohygrograph (White Box, Inc., Stanford, CT) was used to monitor temperature

and humidity in each growth chamber.

Temperature and developmental rate approach linearity at intermediate temperatures (Shelford 1930) and curvilinear over a wide temperature range (Davidson 1944). Data obtained from the temperature range in this study were used to develop a nonlinear model estimating lower and upper developmental thresholds and a linear model (only at intermediate temperature ranges) for estimating lower developmental thresholds.

Either mean or median times can be used to calculate the rate of development. Messenger and Flitter (1958) argued in favor of using median time on the grounds that it is less affected by abnormal values than mean times. Percent development per day was calculated by the formula, 1/number of days for 50% development x 100. Percent development per day for intermediate ranges of temperatures was plotted against temperature of incubation for various life stages. Linear regression analysis (Neter et al. 1989) was used to calculate developmental thresholds by X-intercept method (Arnold 1959). The X-intercept method has been used by many other investigators including Chiang and Sisson (1968), Eckenrode and Chapman (1972), Litsinger and Apple (1973), Reid and Laing (1976), Obrycki and Tauber (1978), Reissig et al. (1979), Van Kirk and AliNiazee (1981), and Liu et al. (1982) to determine

the lower developmental threshold for a number of insect species.

To fit a non-linear model to the entire range of temperature, an exponential curve was fitted to developmental rates at the low to intermediate temperature ranges, and a quadratic curve was fitted to developmental rates at intermediate to high temperature ranges. Data were analyzed by ANOVA and means were separated by Duncan's multiple range test (P=0.05).

Adult longevity: Adults were kept at seven different constant temperatures (8, 12, 16, 20, 24, 28, and 32°C), 80±10% relative humidity, 16:8 (L:D) photoperiod in Pervical (model E 30 B) growth chambers. Newly emerged (<24 hrs) flies (10 males and 10 females) were confined in clear plastic cages (18.5x13x11 cm) (Tri-State Plastics, Dixon, NY). One cage was placed in each growth chamber. A standard meridic diet consisting of a mixture of yeast hydrolysate, fructose (Nutritional Biochemicals Co., Cleveland, Ohio) and distilled water at a ratio 4:7:10, respectively, as described by Tsiropoulos (1978), was provided to adults. Diet in liquid form and distilled water were offered on sterile absorbent cotton balls to flies at all times. Flies were checked daily and mortality was recorded for male and female until the death of the last fly at each temperature.

At each temperature treatment, male and female longevity was compared but no significant difference ($p=0.05$) was noticed. Therefore, the male and female data were combined and analyzed.

Preoviposition: Walnut twigs of the 'Franquette' variety, bearing one nut each, were used. An effort was made to select nuts of uniform size during the course of the entire experiment. They were taken from a single unsprayed tree of 'Franquette' variety. The twigs were cut 15 cm below the nuts and placed in small container with water. Ten centimeter of the twigs were cut off and the remaining portion bearing the nuts was inserted into a water filled clear plastic 35 ml cup (Jetware Plastica Industries Inc., Hatfield, Pennsylvania) through a hole in lid. The absorbent tissue paper was tightly wrapped around the stem to support it in an upright position. The tissue paper also served to prevent the flies from becoming trapped in the water. This method maintained walnuts in a susceptible and fresh condition for a period of 12 to 14 days. However, nuts were changed weekly to maintain favorable conditions for oviposition.

Walnuts were placed in clear plastic cages (18.5x13x11 cm) (Tri-State Plastics, Dixon, NY), one unit to each cage. A pair of flies less than 24 hrs old were released in each cage. A standard meridic diet as

described earlier and distilled water were provided to flies. These cages (12 boxes in each temperature treatment) were placed in growth chambers maintained at 8, 12, 16, 20, 24, 28, or 32°C. Food and water were provided daily, and boxes were checked daily. If a male fly died it was replaced with another male from a stock of same age. If the female fly died, the replicate was discarded. Checking for oviposition began on the fifth day for flies maintained at 24, 28, and 32°C, on the seventh day for flies at 16 and 20°C and on the tenth day for flies at 8 and 12°C. Once oviposition began, number of days after which oviposition occurred, location of oviposition puncture, and number of eggs in each puncture were recorded. At the end of 35th day, the live females were dissected to record the presence or absence of matured eggs in the ovaries.

Oviposition: Flies were reared from field-collected pupae. Adults were maintained in wood-frame cages (35x25x40 cm) in a rearing room at a temperature of 24+1°C, relative humidity of 80±10%, and 16:8 (L:D) photoperiod. An adult diet (as described earlier) and water was provided to flies.

One male and female pair, 16-19 day-old was introduced into each of the 56 individual confinement plastic cages (18.5x13x11cm). Susceptible host material

was supplied by placing a cup of water containing a twig with one walnut in each cage. One mature and mated female and one male was introduced in each cage. All nuts used in this study were obtained from a single tree of 'Franquette' variety which had been continuously attacked by the WHF for several years. The eight cages were placed in each growth chamber maintained at constant temperatures described earlier and permitted a 48 hrs oviposition access period. Oviposition puncture location, number of oviposition punctures, eggs in each cavity were recorded.

Egg development: A stock of 20 pairs of flies was maintained at 24°C to obtain eggs for an incubation study. A week after oviposition was observed in the field, fresh nuts were provided to these flies for oviposition. Eggs less than 24 hrs old were collected by dissecting the husk. Forty eggs were placed on moist filter paper in one petri dish of 9-cm-diam with a fine camel hair brush. Each petri dish was covered and sealed with Scotch tape. Five petri dishes (a total of 200 eggs) were then placed in cardboard containers to keep them darkened, and five petri dishes were placed at temperatures of 8, 12, 16, 20, 24, 28, or 32°C in growth chambers for incubation. Eggs were examined twice daily under a binocular microscope to determine hatch for eight days after first hatch. Filter papers were moistened as needed. Number of eggs hatched

and unhatched were recorded. Unhatched eggs usually remained firm whereas hatched eggs collapsed. Occasionally unhatched eggs collapsed, to determine whether these eggs had hatched, egg shells were immersed in water on the eighth day and the presence or absence of exit hole were determined (Neilson 1969). Among the unhatched eggs, the number of infertile and fertile eggs in which the developing embryo had died was recorded. The infertile eggs usually retained a pearly-white color, and became semitransparent at both ends and contents become watery (Boyce 1934).

Larval development: The nuts obtained from a single tree of 'Franquette' which were inserted in 35 ml plastic cups containing water, were used for the larval development study. The eggs were incubated at 24°C and 25 neonate larvae transferred in each walnut inside husk in artificial holes with a fine camel hair brush. A total of 300 larvae were reared at each temperature treatment. The method of handling nuts maintained them in fresh and susceptible condition for 12-14 days, however, nuts were replaced weekly. The host material was carefully dissected under a binocular microscope to locate the feeding larvae. The first instar were difficult to detect, but when they molted it was relatively easy to detect them. The larvae were transferred weekly into fresh nuts inside the husk.

When the mature larvae came out of the husk for pupation, they were provided with moist vermiculite for pupation in 35 ml plastic cups. At each temperature, newly formed pupae were picked with a small soft-tipped forceps and placed in 35 ml plastic cups.

At the end of this experiment (i.e., on 55th day), three samples of 10 pupae each from various temperature treatments were collected and weighed. The effect of different rearing temperatures was checked by plotting average weight (gms) against treatments and evaluating the treatment impact. The life span of different instars was checked by removing 10 larvae from husks daily to study their development at the different temperatures. The percent larvae in first, second, and third instars was recorded through pupation. The duration for median maturity was considered as the time required to complete a particular instar.

When larvae reached maturity, they congregated in the area of broken-down husk tissue, and came out through the entrance holes/punctures which were made to insert larvae in the husk. Depending on the temperatures, several days difference was noticed between the first larvae and the last larvae to emerge from the husk.

Postdiapause pupal development: The pupae used in this study were incubated at 3°C for 7 months, and then

moved to different temperature treatments to determine the postdiapause developmental rates. Two hundred chilled puparia were placed in four 35 ml plastic cup (50 per container). Four containers (each with 50 pupae) were placed at each of the following temperatures: 8, 12, 16, 20, 24, 28, and 32°C. Pupae were checked daily for adult emergence, the flies were sexed and recorded on emergence. The experiment was terminated one month after the last fly emerged at each temperature treatment. At 32°C, where no flies emerged, the pupae were removed from the chamber after 3 months. A representative sample of pupae was dissected to determine whether flies were alive or dead inside the puparium.

RESULTS AND DISCUSSION

Adult longevity: Adult longevity determined under laboratory conditions is given in Table II-1. The mean adult life span of newly (< 24 hrs) emerged flies varied from treatment to treatment. The longest mean life span (77.05±6.5 days, x±SD) was noticed at 16°C and the shortest life span (17.3±0.8 days) at 32°C. Both the low and high temperatures were detrimental whereas the median temperatures ranges from 16 to 24°C were optimum for adult longevity.

Boyce (1934) reported that a few flies lived for 85 days under field conditions. However, the weather conditions were not well defined in his experiments. In my experiment, the longest life span was 112 days at 16°C, which is the longest life span ever reported for this insect. The mean life span under most favorable laboratory conditions was 77 days at 16°C. Boyce (1934) also reported that virgin females lived an average of 35 days and one lived for 85 days. Tsiropoulos (1981) terminated experiments with adult husk flies after 80 days (temperature= 25±2°C, relative humidity= 51-61%, and photoperiod= 16:8 [L:D]) and reported that some flies lived this long. My data establish that husk flies live longer than that previously reported.

Table II-1. Life span of adult *Rhagoletis completa* exposed to different constant temperature treatments.

TEMPERATURE (°C)	NO OF DAYS ADULT LIVED			
	MEAN		STANDARD DEVIATION	RANGE
8	30.1	b	2.5	8-45
12	49.6	c	3.2	19-69
16	77.0	d	6.5	28-112
20	65.8	d	6.1	23-109
24	64.6	d	5.5	21-103
28	37.8	bc	1.8	18-49
32	17.3	a	0.8	11-23

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

Preoviposition: The mean preoviposition periods at various constant temperature treatments is presented in Table II-2. In general, the higher the temperature, the shorter the preoviposition period. The duration of preoviposition development decreased linearly with a temperature range of 12-28°C, and dropped at 32°C treatment. My data indicates a preoviposition period of 11 to 17 days and 9 to 14 days at 20±1°C and 24±1°C, respectively. Neilson et al. (1981) reported a preoviposition period of 5 to 11 days for apple maggot under constant (22±1°C) laboratory conditions. My data suggests that female husk flies have a longer preoviposition period than female apple maggot flies and possibly the western cherry fruit flies, *Rhagoletis indifferens* (Frick et al. 1954, Prokopy 1968).

The developmental rates are presented in Table II-2. A linear regression model was developed using temperature (8-24°C) and developmental rates, and is presented in Figure II-1a. A highly positive linear relationship (R^2 =0.96) was evident between the two factors ($P<0.05$). The lower developmental threshold and regression equation are given in Table II-11.

The non-linear model [exponential (8-16°C), quadratic (20-32°C)] of the relationship between the entire range of temperatures and developmental rates is presented in

Table II-2. Preoviposition period of newly emerged *Rhagoletis completa* females exposed to various constant temperature treatments.

TEMP (°C)	NO OF DAYS TO IST OVIPOSITION				DEVELOPMENTAL RATE
	MEAN		SD	RANGE	(100/Y)
8	0.0				0.0000
12	26.4	e	1.1	23-32	4.0000
16	19.5	d	1.2	14-25	5.0000
20	13.1	bc	0.6	11-17	7.6923
24	11.0	ab	0.4	09-14	9.0909
28	9.9	a	0.7	07-12	10.0000
32	14.3	c	0.9	13-16	7.1429

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

Figure II-2a. The adequacy of this approach to describe the observed relationship is indicated by R^2 of 0.97 for the exponential function and R^2 of 0.89 for the quadratic function. This approach was earlier used by Stark and AliNiazee (1982) to describe the postdiapause development rate of the western cherry fruit fly, *Rhagoletis indifferens*. The lower and upper developmental threshold and regression equation relating developmental time to temperature are given in Table II-12.

Developmental thresholds for the preoviposition of *Rhagoletis* species has not been previously determined. However, various thresholds have been arbitrarily tested and used. AliNiazee (1979) suggested a threshold of 5°C for *R. indifferens* preoviposition period. Laing and Heraty (1984) also estimated degree-day requirement for newly emerged females of the apple maggot, *Rhagoletis pomonella* had mature eggs above a threshold of 8.7 and 6.4°C.

Others researchers have reported the lower thresholds for the female preoviposition periods of certain other pest tephritid species including *Dacus* and *Ceratitis* under constant temperature conditions. Keck (1951) determined the preoviposition period of female *D. cucurbitae* under constant temperatures. No eggs were deposited at or below 12.8°C. A lower developmental threshold of 10.4°C was used to estimate a thermal constant for preoviposition period

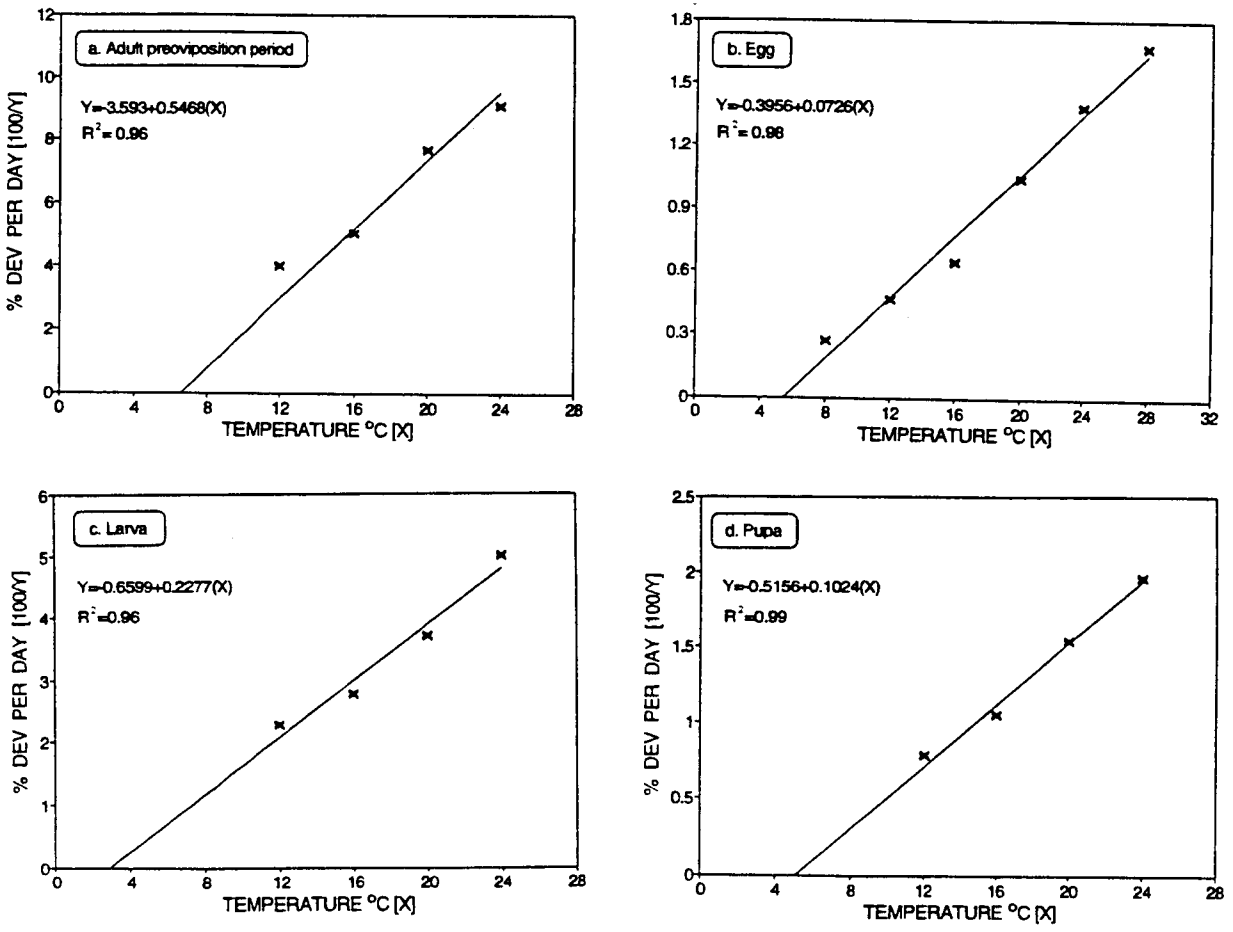

Figure II-1. Effect of constant temperature on developmental rates of different life stages of *Rhagoletis completa*.

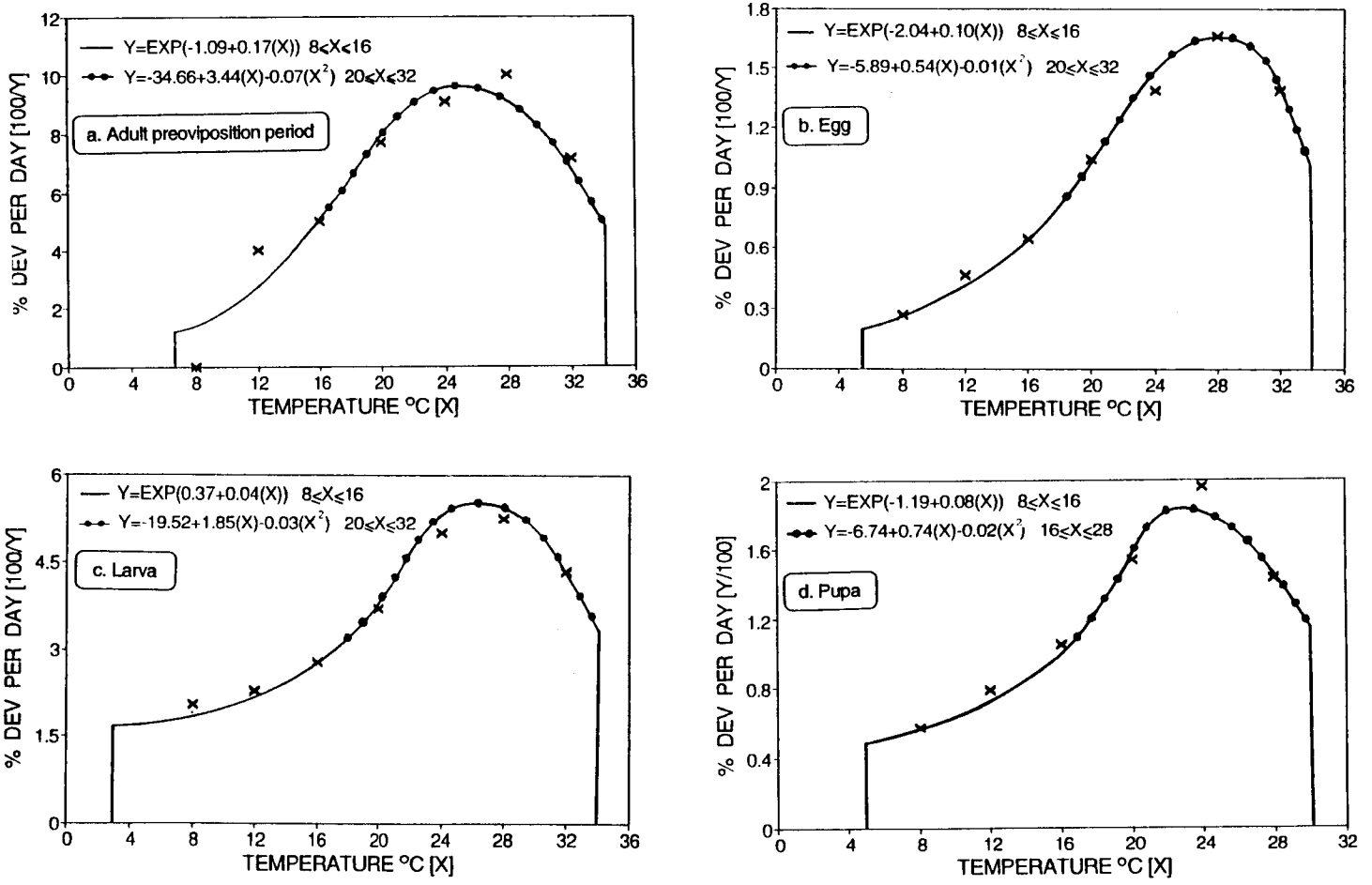

Figure II-2. Developmental rate function of different life stages of *Rhagoletis completa*.

of this insect. Okumura et al. (1981) used a lower developmental threshold of 12.08°C to calculate the thermal constant for the female preoviposition period of *D. cucurbitae*. Saeki et al. (1980) estimated the thermal constant above a threshold of 15.13°C for the female preoviposition period of *D. dorsalis,* and Tassan et al. (1983) used a thermal constant of 44.2°C above a threshold of 16.6°C for the preoviposition of *Ceratitis capitata* in California. Based on my study, a lower developmental threshold of 6.6°C is suggested for the preoviposition of *R. completa* in Oregon (Table II-11 & II-12). I believe that this threshold allows flexibility based on the severity of climatic conditions.

Temperature had no significant effect on number of eggs in the first oviposition clutch ($P>0.05$) (Table II-3). Nearly 83% of females oviposited at 20 and 24°C, 75% at 16°C, 58% at 12°C and only 25% at 32°C through 35th day. About 8% of the females died before 35 days without laying any eggs at 16, 20, and 24°C; 33%, 25%, 50%, and 75% of the females died at 28, 12, 8, and 32°C treatments, respectively, before 35 days. No oviposition was noticed in about 16% of the females at 12 and 16°C, and about 8% didn't oviposit at 20, 24, and 28°C, even though at the end of 35th day fully matured eggs were found in all live female ovaries. At 8°C, the flies did not oviposit at all.

Table II-3. Eggs deposited in first oviposition clutch by newly emerged *Rhagoletis completa* females at different constant temperature treatments.

TEMP (°C)	NO. OF EGGS MEAN		SD	RANGE	% FEMALES UP TO 35TH DAY OVIPOSITED	NOT OVIPOSITED	DIED
8	0.0				0.0	41.7	58.3
12	14.1	a	3.3	06-28	58.3	16.7	25.0
16	22.2	ab	2.3	09-33	75.0	16.7	08.3
20	23.2	ab	2.6	12-37	83.3	08.3	08.3
24	27.9	b	3.7	08-47	83.3	08.3	08.3
28	22.0	ab	5.4	03-46	58.3	08.3	33.3
32	17.0	ab	2.1	13-20	25.0	00.0	75.0

Means followed by same letters are not significantly different (Duncan's multiple range test), P>0.05.

However, mature eggs were found in ovaries of 40% of the live females. Boyce (1934) also reported many females never laid any eggs in spite of the presence of fully matured eggs in ovaries.

Confined conditions may have some effect on the normal development of the eggs, although it is not well understood in *R. completa*. In the melon fly, food types had a marked influence on the development of eggs (Back and Pemberton 1917). The females require a complex diet, including vitamins and amino acids to produce eggs (Tsiropoulos 1978, Tsiropoulos & Hagen 1987). It is also possible that the absence of certain frequencies of the solar light spectrum along with the absence of certain nutritional elements may have adversely affected the flies resulting in reduction of oviposition and decreased developmental rates.

Boyce (1934) reported that adult flies have a preoviposition period of 10 to 20 days under undefined laboratory conditions. In the current study, the mean preoviposition period ranged from 9.4 day at 28°C to 26.4 days at 12°C. However, the range was even wider i.e., at 28°C females oviposited as early as 7 days and at 12°C as late as 32 days after emergence. Neilson et al. (1981) reported the preoviposition period of 5 to 11 days at constant temperatures (22±1°C) and 6 to 15 days at

variable temperature conditions for *R. pomonella* adults. The preoviposition period for females of *R. indifferens* increased with decreasing temperatures and varied from 7-12 days (Kamal 1954).

Oviposition: The oviposition activity increased with increasing temperatures (Table II-4) to 24°C but declined at 28 and 32°C. The female flies made significantly more ($P<0.05$) punctures and deposited a higher number of eggs at 24°C conversely, at 8°C they made fewer punctures and deposited the lowest number of eggs. About 30 eggs per nut per female were also highest at 24°C, 20 eggs at 20°C, 11 eggs at 28°C, 5 eggs at 16°C, 3 eggs at 32°C, 1 egg at 12°C, and 0.6 egg at 8°C.

Egg development: The mean time required for egg development at different temperatures is presented in Table II-5. The rate of egg development increased with increasing temperature up to 28°C but decreased at 32°C (Table II-5). A linear model of the relationship between temperature and developmental rates was developed and given in Figure II-1b. A highly positive linear relationship was observed between increasing temperatures at the medium range (8-28°C) and egg developmental rate $R^2 = 0.098$ ($P<0.05$). The lower developmental threshold and regression equation are given in Table II-11.

The nonlinear model [exponential (8-16°C), quadratic

Table II-4. Oviposition by *Rhagoletis completa* females at different constant temperature treatments in the laboratory.

TEMP (°C)	PUNCTURE/10 NUTS MEAN		PUNCTURE/10 NUTS STANDARD DEVIATION	EGGS/NUT/FEMALE MEAN		EGGS/NUT/FEMALE STANDARD DEVIATION
8	1.2	a	0.12	0.6	a	0.62
12	2.5	ab	0.16	1.4	a	1.12
16	5.0	abc	0.19	5.4	a	2.53
20	7.5	cd	0.16	20.4	bc	7.68
24	10.0	d	0.00	30.4	c	4.23
28	6.2	bcd	0.18	11.2	ab	4.51
32	2.5	ab	0.16	3.7	a	2.57

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

(20-32°C)] of the relationship between all temperature and developmental rates is presented in Figure II-2b. The adequacy of this approach to describe the relationship is indicated by R^2 =0.98 for exponential function and R^2 =0.93 for quadratic function.

The lower and upper thresholds and regression equation are presented in Table II-12. The current study yielded a lower threshold of 5.3°C for *R. completa* egg development. For other tephritid flies, Fletcher and Kapatos (1983) estimated a threshold of 6.3°C for eggs of *Dacus oleae*, Delrio et al. (1986) reported a lower developmental threshold of 11.1°C for eggs of *Ceratitis capitata*. My study indicated that the upper threshold for egg development is 34°C (Table II-12).

Egg hatch at 8°C treatment is significantly ($P<0.05$) lower than egg hatch at other temperatures (Table II-6). About 70% of the eggs hatched at 8°C, while approximately 95% of the eggs hatched in the other temperatures. About 25% of the embryos died before eclosion at 8°C. Up to 2% of the eggs were found infertile at different temperatures, and infertility did not increase or decrease with increasing temperatures.

Larval development: The mean time required for larval development at various temperatures given in Table II-7. The developmental time decreased with increasing

Table II-5. Developmental rates of *Rhagoletis completa* eggs exposed to different constant temperature treatments.

TEMP (°C)	NO OF HOURS TO EGG HATCH MEAN		SD	RANGE	DEVELOPMENTAL RATE (100/Y)
8	389.3	f	2.4	372-504	0.2688
12	222.6	e	0.7	216-264	0.4630
16	149.8	d	0.7	132-168	0.6410
20	93.8	c	0.5	84-108	1.0417
24	70.4	b	0.4	60-84	1.3889
28	54.8	a	0.5	48-72	1.6667
32	68.4	b	0.7	48-84	1.3889

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

Table II-6. Eclosion of *Rhagoletis completa* at different constant temperature treatments in the laboratory.

	HATCHED			UNHATCHED	
TEMP (°C)	% MEAN HATCHED		SD	% EMBRYO DIED	%INFERTILE
8	73.5	a	1.5	25.0	1.5
12	96.5	b	1.0	1.0	2.5
16	95.5	b	0.5	1.5	2.0
20	95.5	b	0.9	2.0	2.5
24	95.5	b	0.5	2.5	2.0
28	96.0	b	0.6	3.0	1.0
32	94.0	b	1.2	4.0	1.0

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

temperature from 8 to 28°C and increased at 32°C. Development was slowest at lower temperatures, and optimum at intermediate temperatures.

The developmental rates for the entire larval stage are given in Table II-7. The relationship between intermediate temperature ranges (12-24°C) and developmental rates is presented in Figure II-1c. A highly positive correlation was observed between incremental temperature increase and developmental rates R^2 =0.96 ($P<0.05$). Increasing temperature resulted in predictable increases in development. The X-intercept method was used to determine developmental thresholds, the thresholds and regression equations are given in Table II-11.

The non-linear model [exponential (8-16°C), quadratic (20-32°C)] of the relationship between the entire temperature range and developmental rate is presented in Figure II-2c. The adequacy of this approach to describe the observed relationship is supported by the R^2 value of 0.97 for the exponential function and R^2 of 0.99 for quadratic function. The lower and upper developmental thresholds and regression equations are given in Table II-12. A general developmental threshold of 2.9°C was determined for larvae of the WHF.

The intra-larval survivorship and developmental times from neonate larvae to pupal formation are given in Table

Table II-7. Developmental rates of *Rhagoletis completa* larvae exposed to different constant temperature treatments.

TEMP (°C)	NO OF DAYS TO LARVAL DEVELOPMENT MEAN		SD	RANGE	DEVELOPMENTAL RATE (100/Y)
8	48.9	g	0.3	44-53	2.0408
12	43.9	f	0.3	37-51	2.2727
16	35.9	e	0.2	28-43	2.7778
20	26.9	d	0.2	20-34	3.7037
24	20.4	b	0.2	16-26	5.0000
28	19.5	a	0.2	16-25	5.2632
32	22.2	c	0.2	17-27	4.3478

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

II-8. Mortality varied across temperatures. The highest mortality was recorded at 8°C and mortality started to decrease as the temperature increased to optimum ranges; increased mortality was also noticed at 28°C and 32°C treatments.

Relatively few larvae completed the third the instar at 8°C. Maximum numbers reached the third instar at 24 and 28°C. The greatest pupal mortality was also recorded at the extreme temperatures (8 and 32°C). The lowest mortality was recorded at 24 and 28°C. These data indicate that at 32°C development is delayed and mortality increases. Over 65% pupation was observed at 20 and 24°C treatments. However, pupation decreased to 14% at 32°C and 11% at 8°C.

Boyce (1934) reported a mean larval development time of 27.9 days at variable laboratory temperatures (mean= 86°F, range= 67-90°F) and 36.8 days at variable field temperatures (mean= 64°F, range= 45-104°F).

The number of days required for different larval instars is given in Table II-9. The total larval period is similar to the mean larval development period (Table II-7) at each temperature. The larvae spent longer time in the third instar followed by second and first instar. Approximately 49% of the total larval time was spent in the third instar, 31% in second instar, and 20% in the

Table II-8. Percentage of *Rhagoletis completa* larvae maturing and pupating at different constant temperature treatments in the laboratory.

TEMP (°C)	INITIAL NUMBER	% LARVAE COMPLETING 3RD INSTAR MEAN		% LARVAE COMPLETING 3RD INSTAR SD	% PUPATION MEAN		% PUPATION SD
8	300	15.7	a	1.2	11.7	a	0.9
12	300	53.3	bc	0.9	49.7	b	0.9
16	300	62.3	c	2.6	54.3	b	2.3
20	300	70.3	d	3.2	65.3	c	2.0
24	300	75.3	d	0.9	66.0	c	3.5
28	300	72.3	d	1.4	56.0	b	1.7
32	300	58.3	b	0.9	14.7	a	1.4

Means followed by different letters are significantly different (Duncan's multiple range test), $P<0.05$.

first instar. At 28°C, the larvae spent 10 days in the third instar, 6 days in the second instar, and 4 days in the first instar with a total larval period of 20 days, while at 16°C the corresponding days were 17, 12, 7, and 36 days.

There was considerable variation in the time required for larvae of the same age to complete an instar. This suggests that they were not behaving normally under artificial conditions. In contrast, the development of larvae of one batch of eggs under field conditions was remarkably uniform.

Boyce (1934) reported that larvae spent a mean of 14.3 days in third instar, 8.3 in second, 5.3 in first at 27.8°C (82°F) in laboratory, while the corresponding values at a mean field temperature 17.7°C (64°F) were 14.1, 13, and 9.7 days. Although these data are more precise, it nevertheless supports the preliminary data of Boyce (1934) from California.

Pupal weights decreased with increasing temperature (Figure II-3). Greatest pupal weight was obtained at 12°C followed by 16, 20, and 24°C. It appears that high temperatures negatively impact pupal weight. It is possible that reduced pupal weight may affect the adult longevity and robustness, although this was not investigated in this study.

Table II-9. Development of *Rhagoletis completa* larval instars at different constant temperature treatments in the laboratory.

TEMP (°C)	TIME SPENT IN DIFFERENT LARVAL INSTARS							
	1ST INSTAR		2ND INSTAR		3RD INSTAR		TOTAL	
	DAYS	% OF TOTAL	DAYS	% OF TOTAL	DAYS	% OF TOTAL	DAYS	% OF TOTAL
8	11	23	16	33	21	44	48	100
12	9	21	15	35	19	44	43	100
16	7	20	12	33	17	47	36	100
20	5	18	8	29	13	53	28	100
24	4	20	6	30	10	50	20	100
28	4	20	6	30	10	50	20	100
32	4	18	7	32	11	50	22	100

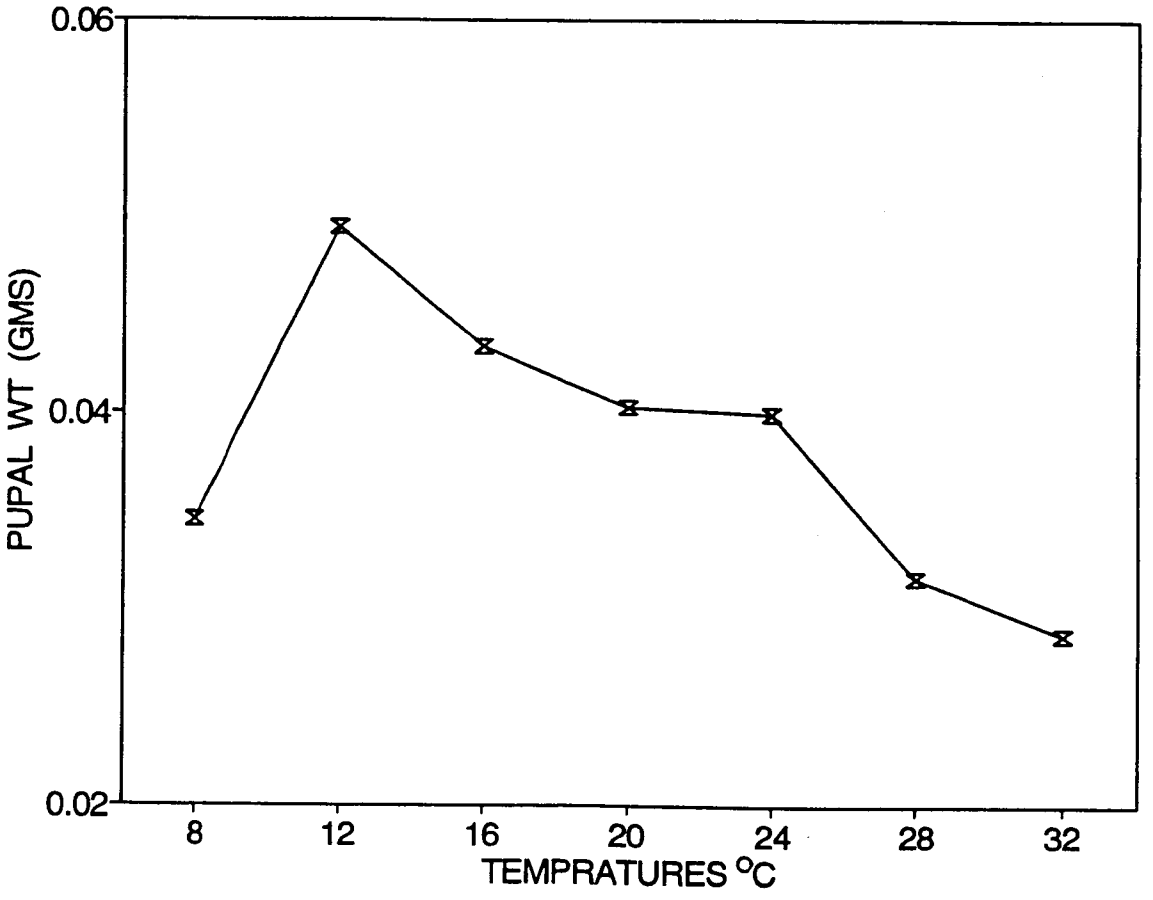

Figure II-3. Pupal weight from larvae of *Rhagoletis completa* raised at different temperatures in the laboratory.

Postdiapause pupal development: The postdiapause developmental rate function (Table II-10) suggests that as temperatures increase, the mean emergence time decreases up to 24°C in a linear fashion. Developmental time was greater at 28°C than 24°C. No development occurred at 32°C. Most rapid development occurred at 24°C. Little development occurred at 8°C. The linearity of the developmental rate observed at intermediate temperature ranges (between 12-24°C) was similar to that observed earlier for other stages including larvae and eggs. The non-linear relationship observed at higher and lower temperatures also was common in the other stages studied.

A linear model depicting the relationship between intermediate temperatures (12-24°C) and developmental rates are presented in Figure II-1d. These data show a highly positive relationship between the incremental increase of temperatures and development rate, R^2 =0.99 ($P<0.05$). The developmental threshold and regression equation are given in Table II-11.

An exponential model for lower temperatures (8-16°C) and a quadratic model for higher temperatures (16-28°C) was developed and fitted to show temperature/ development rate function for the entire range of temperatures tested and is presented in Figure II-2d. The R^2 of 0.99 for the exponential function and R^2 of 0.90 for the quadratic

Table II-10. Postdiapause developmental rates of *Rhagoletis completa* pupae exposed to different constant temperature treatments.

TEMP (°C)	DAYS TO EMERGENCE MEAN		SD	RANGE	% FLIES EMERGED MEAN		SD	DEVELOPMENTAL RATE (100/Y)
8	162.2	e	2.0	146-194	19.5	a	1.0	0.5714
12	124.1	d	1.0	102-165	65.5	b	2.2	0.7874
16	87.7	c	0.7	61-112	70.5	bc	1.7	1.0526
20	67.5	b	0.6	51-84	73.0	bc	5.1	1.5385
24	53.5	a	0.5	34-65	79.0	c	2.1	1.9608
28	68.8	b	0.5	52-86	69.0	bc	5.9	1.4286
32	NO EMERGENCE							

Means followed by same letters are not significantly different (Duncan's multiple range test), $P<0.05$.

function show the adequacy of this approach. The lower and upper developmental thresholds and regression equation are given in Table II-12.

Different developmental thresholds were developed for the different life history stages of WHF. Although, these various thresholds are more meaningful biologically, they are difficult to use in phenology models. Similar difficulties were noted with other insects including fruit flies.

A number of workers have suggested using 5°C for constructing phenology models of *R. indifferens* and *R. cerasi* (AliNiazee 1976, 1979, Boller 1964), while Jubb and Cox (1974) reported a threshold of 4.4°C for *R. fausta* and *R. cingulata*. Maxwell and Parsons (1969) reported 5.5°C threshold for the apple maggot. Reissig et al. (1979) reported 6.4°C threshold for the development of apple maggot pupae, using linear regression. In a detailed study, Van Kirk and AliNiazee (1981) estimated the development threshold for the western cherry fruit fly, and reported that a threshold of 8.3°C was most accurate biologically. Here, I suggest using 5°C as the general threshold for estimating postdiapause development of WHF and also recommend using this threshold for phenology models.

For other species of Tephritidae such as Daciines,

Table II-11. Developmental thresholds for various life stages of *Rhagoletis completa* derived using linear models.

DEVELOPMENTAL STAGE	DEVELOPMENTAL THRESHOLD (°C)	REGRESSION EQUATION	R^2
Adult (Preovip.)	6.6	Y= -3.5930+0.5468(X)	0.96
Egg	5.3	Y= -0.3956+0.0726(X)	0.98
Larva	2.9	Y= -0.6600+0.2277(X)	0.96
Pupa	5.0	Y= -0.5156+0.1024(X)	0.99

Table II-12. Lower and upper development thresholds of various life stages of *Rhagoletis completa* derived using nonlinear models.

DEVELOPMENTAL STAGE	LDT (°C)	UDT (°C)	NONLINEAR MODEL	R^2
Adult (preovip.)	6.6	34	$Y= EXP(-1.090+0.1727(X))$	0.74
			$Y= -34.6333+3.4350(X)-0.0664(X^2)$	0.89
Egg	5.3	34	$Y= EXP(-2.0452+0.1009(X))$	0.98
			$Y= -5.8945+0.5411(X)-0.0098(X^2)$	0.93
Larva	2.9	34	$Y= EXP(0.3749+0.0397(X))$	0.97
			$Y= -19.5255+1.8525(X)-0.0346(X^2)$	0.99
Pupa	5.0	30	$Y= EXP(-1.1936+0.0776(X))$	0.99
			$Y= -6.7388+0.7387(X)-0.0159(X^2)$	0.90

LDT = Lower developmental threshold
UDT = Upper developmental threshold

Fletcher and Kapatos (1983) estimated a lower development threshold of 8°C for pupae of *D. oleae*, and similar thresholds have been reported for Mediterranean and Oriental fruit flies. The lower development threshold estimated here for WHF pupae is similar to those reported in other studies for other *Rhagoletis* species. However, it is lower than the 8.7°C threshold reported for the apple maggot pupae from a Canadian population (Reid and Laing 1976).

Stark and AliNiazee (1982) estimated an upper development threshold of 30°C for the pupal stage of *R. indifferens*, and Reid and Laing (1976) reported an upper threshold of 31°C for apple maggot. Upper developmental thresholds for other *Rhagoletis* flies have not been reported. In the current study, the upper developmental threshold for pupae of the WHF was 30°C using the non-linear approach. Data also suggests that development and survival of WHF decreased as the temperature is increased beyond 24°C and eventually the development stopped and lethal changes were noticed.

REFERENCES

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette Valley of Oregon. Environ. Entomol. 5:397-402.

AliNiazee, M. T. 1979. A computerized phenology model for predicting biological events of *Rhagoletis indifferens* (Diptera: Tephritidae). Can. Entomol. 111: 1101-1109.

AliNiazee, M. T. 1988. Diapause modalities in some *Rhagoletis* species. *In* M. T. AliNiazee [Editor], Ecology and Management of Economically Important Fruit Flies. Agric. Exp. Sta. Oreg. State Univ. Special Report 830.

Arnold, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. Am. Soc. Hort. Sci. 74: 430-445.

Back, E. A. and C. E. Pemberton. 1917. The melon fly in Hawaii. U. S. Dept. Agric. Bull. 491:1-64.

Baker, C. R. B. and G. W. Miller. 1978. The effect of temperature on the post-diapause development of four geographical populations of the European cherry fruit fly (*Rhagoletis cerasi*). Entomol. Exp. Appl. 23: 1-13.

Boller, E. F. 1964. Auftreten der Kirschenfliege (*Rhagoletis cerasi* L.) Und. Pragnose mittels Bodentemperature. Schweiz. Z. Obst. Weinbou. 73: 53-58.

Boyce, A. M. 1934. Bionomics of the walnut husk fly, *Rhagoletis completa*. Hilgardia. 8:363-579.

Chiang, H. C. and V. Sisson. 1968. Temperature relationships of the development of northern corn rootworm eggs. J. Econ. Entomol. 61: 1406-10.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13:26-38.

Delrio, G., B. Conti, and A. Crovetti. 1986. Effect of abiotic factors on *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) I. Egg development under constant temperatures. In R. Cavalloro [Editor], Fruit Flies of Economic Importance 84. Balkema, Rotterdam, pp. 131-141.

Eckenrode, C. J., and R. K. Chapman. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Ann. Entomol. Soc. Am. 65: 151-156.

Fletcher, B. S. and E. T. Kapatos. 1983. An evaluation of different temperature-dependent rate models for predicting the phenology of the olive fly, *Dacus oleae*. *In* R. Cavalloro (Editor), Fruit Flies of Economics Importance. Balkema, Rotterdam, 321-329 pp.

Frick, K. E., H. G. Simkover, and H. S. Telford. 1954. Bionomics of the cherry fruit flies in eastern Washington. Tech. Bull. Wash. Agric. Expt. Stn. No. 13.

Jones, V. P., D. W. Davis, S. L. Smith, and D. B. Allred. 1989. Phenology of the apple maggot associated with cherry and hawthorn in Utah. J. Econ. Entomol. 82: 788-792.

Jubb, G. L. Jr., and J. A. Cox. 1974. Seasonal emergence of two cherry fruit fly species in Eric County, Pennsylvania: a 25-year summary. J. Econ. Entomol. 67: 613-615.

Kamal, A. S. 1954. Ecological and nutritional studies on the cherry fruit fly. J. Econ. Entomol. 47: 959-65.

Keck, C. B. 1951. Effect of temperature on development and activity of the melon fly. J. Econ. Entomol. 44: 1001-1003.

Laing, J. E. and J. M. Heraty. 1984. The use of degree-days to predict emergence of the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae) in Ontario. The Canadian Entomologist. 116: 1123-1129.

Litsinger, J. A. and J. W. Apple. 1973. Thermal requirements for embryonic and larval development of the alfalfa weevil in Wisconsin. J. Econ. Entomol. 66: 309-311.

Liu, H. J., F. L. McEwen, and G. Ritcey. 1982. Forecasting Events in the Life Cycle of the Onion Maggot, *Hylemya antiqua* (Diptera: Anthomyiidae): Application to Control Schemes. Environ. Entomol. 11: 751-755.

Maxwell, C. W. and. C. Parsons. 1969. Relationships between hour-degree F soil temperature summations and apple maggot adult emergence. J. Econ. Entomol. 62: 1310-1313.

Neilson, W. T. A. 1969. Rearing larvae of the apple maggot on an artificial Medium. J. Econ. Entomol. 62: 1028-1031.

Neilson, W. T. A., A. D. Knowlton, and K. B. McRae. 1981. Preoviposition and oviposition periods of the apple maggot, *Rhagoletis pomonella* [Diptera: Tephritidae]. Can. Entomol. 113: 1061-67.

Neter, J., W. Wasserman, and M. H. Kutner, 1989. Applied linear regression models. Richard D. Irwin, Inc. pp. 667.

Obrycki, J. J. and M. J.Tauber. 1978. Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasites *Perilitus coccenillae* (Hymenoptera: Braconidae). Can. Entomol. 110: 407-412.

Okumura, M., T. Ide, and S. Takagi. 1981. Studies of the effect of temperature on the development of the melon fly, *Dacus cucurbitae* Coq. Res. Bull. Plant Protection Service Japan. 17: 51-56.

Prokopy, R. J. 1968. Influence of photoperiod, temperature and food on initiation of diapause in the apple maggot. Can. Entomol. 100: 318-329.

Reid, J. A. K. and J. E. Laing. 1976. Developmental threshold and degree-days to adult emergence for overwintering pupae of the apple maggot, *Rhagoletis pomonella* (Walsh) collected in Ontario. Proc. Entomol. Soc. Ontario. 107: 19-22.

Reissig, W. H., J. Barnard, R. W. Weires, E. H. Glass, and R. W. Dean. 1979. Prediction of the apple maggot fly emergence from thermal unit accumulation. Environ. Entomol. 8: 51-54.

Saeki, S., M. Katayama, and M. Okumura. 1980. Effect of temperature upon the development of the Oriental fruit fly and its possible distribution in the mainland of Japan. Res. Bull. Plant Protection Service Japan. 16: 73-76.

Shelford, V. E. 1930. Phenology and one of its modern descendants. Q. Rev. Biol. 5: 207-216.

Smith, S. L., and V. P. Jones. 1991. Alteration of apple maggot (Diptera: Tephritidae) emergence by cold period duration and rain. Environ. Entomol. 20: 44-47.

Solomon, M. E. 1951. Control of humidity with potassium hydroxide, sulfuric acid, or other solutions. Bull. Entomol. Res. 42: 543-54.

Stark, S. B. and M. T. AliNiazee. 1982. Model of postdiapause development in the western cherry fruit fly. Environ. Entomol. 11: 471-474.

Tassan, R. L., K. S. Hagen, A. Cheng, T. K. Palmer, G. Feliciano, and T. L. Blough. 1983. Mediterranean fruit fly life cycle estimations for the California eradication program. *In* R. Cavalloro (Editor), Fruit Flies of Economic Importance. Balkema, Rotterdam, pp. 564-570.

Trottier, R. and J. L. Townshend. 1979. Influence of soil moisture on apple maggot emergence, *Rhagoletis pomonella* (Diptera: Tephritidae). Can. Entomol. 111: 975-976.

Tsiropoulos, G. J. 1978. Holidic diets and nutritional requirements for survival and reproduction of the walnut husk fly. J. Insect Physiol. 24, 239-242.

Tsiropoulos, G. J. 1981. Effects of antibiotics incorporated into defined adult diets on survival and reproduction of the walnut husk fly, *Rhagoletis completa* Cresson (Diptera: Tephritidae). Z. ang. Entomol. 91:100-106.

Tsiropoulos, G. J. and K. S. Hagen. 1987. Effects of nutritional deficiencies, produced by antimetabolites, on reproduction of *Rhagoletis completa* Cresson (Diptera: Tephritidae). Z. Ang. Entomol. 103: 351-354.

Van Kirk, J. R. and M. T. AliNiazee. 1981. Determining low-temperature threshold for pupal development in the western cherry fruit fly for use in phenology models. Environ. Entomol. 10: 968-971.

Van Kirk, J. R. and M. T. AliNiazee. 1982. Diapause development in the western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae). Z. Angew. Entomol. 93: 440-45.

CHAPTER III

SEASONAL PHENOLOGY OF THE WALNUT HUSK FLY, *RHAGOLETIS COMPLETA*, CRESSON (DIPTERA: TEPHRITIDAE) IN THE WILLAMETTE VALLEY, OREGON

ABSTRACT

The seasonal phenology of the walnut husk fly (WHF), *Rhagoletis completa* Cresson was studied in the Willamette Valley of Oregon during a 3-year period (1990-1992). Adult emergence observed in ground emergence cages varied greatly from year to year. Initial emergence ranged from June 29 to July 17, and last emergence occurred as early as August 17 or as late as September 11. Peak fly emergence occurred between the third week of July and the first week of August. Females dominated before emergence peaks and males afterward. The period of adult emergence ranged from 50-56 days with an average of 53. The temporal relationship between first appearance of flies in the ground emergence cages and the first oviposition was consistent during the 3-year study. The interval between first female observed in an emergence cage and oviposition varied from 20 to 22 days. Peak oviposition period was in the second and third week of August. Mean egg hatch and larval survival was 98%, and 80%, respectively. Infestations reached over 95% in unsprayed backyard trees. Mature larvae first exited from husks beginning the fourth week of August through mid September. Larvae penetrated the soil and pupated within 1 to 3 inches deep in the soil. Pupae remained in the soil for over 7 months and

were found from the end of August. Earliest fly emergence occurred at the end of June.

INTRODUCTION

Many studies dealing with life histories of *Rhagoletis* spp. have been under taken over the years (Illingworth 1912, Boyce 1934, Ries 1934, Lathrop and Dirks 1945, Frick et al. 1954, Dean and chapman 1973, AliNiazee 1976,, Gibson and Kearby 1978, AliNiazee and Westcott 1987, Jones et al. 1989 & 1991). Boyce (1934) and Michelbacher and Ortega (1958) conducted a detailed study on the biology of walnut husk fly, *Rhagoletis completa* Cresson in southern California. Gibson and Kearby (1978) determined the life history of the walnut husk fly in Missouri with special emphasis on adult trapping techniques. Riedl and Hoying (1980) conducted a study on seasonal emergence, flight activity, and oviposition of the WHF from northern California and found no consistent relationship between fly catch in Pherocon AM traps and oviposition.

Management of any pest species is dependent on the ability to accurately predict its seasonal phenology. AliNiazee (1988) emphasized the importance of seasonal phenology in developing meaningful IPM programs for other tephritid pests including the apple maggot, *Rhagoletis pomonella* (Walsh) and the western cherry fruit fly, *Rhagoletis indifferens* Curran. Relatively little is known

about the seasonal phenology of the WHF in Oregon. The objective of this study was to describe the phenology and seasonal development of the WHF under Willamette Valley conditions.

MATERIALS AND METHODS

Ground emergence: Emergence of the fly was monitored under unsprayed backyard trees by placing ground-emergence cages at various locations (one in each quadrant) under walnut trees. The cages were made of pyramid shape of wooden frames covered with heavy duty cloth. The bottom dimension was 0.91x0.91 m sq. with a top opening of 3.8 cm as described by AliNiazee (1974). A glass jar was glued at the top of each cage to collect emerging flies. A plastic mesh cone was placed in the top opening of each cage inside the jar. This allowed the flies to enter into the jar, but prevented them from re-entering the cage. The cages (16 in 1991 and 8 in 1992) were set in place one month before the expected date of emergence and monitored daily for the emergence of the first fly and then three times (Mon. Wed. Fri.) a week for the emergence of the subsequent flies. The flies were collected, sexed and recorded at each date. The emergence cages were kept in place throughout the season.

Seasonal nut growth: The 'Franquette' variety was chosen for this study because of its predominance in Oregon. Seasonal patterns of nut growth were monitored weekly during a 3-year period (1990-1992). Length and width of 10 nuts randomly selected were measured with a

Plastic Vernier Type 6914 (SPI 2425 S. Eastern Ave., Los angeles, CA) measuring device. The area/size of the nuts was calculated by multiplying the length and width of nuts. Mean nut size was plotted against sampling dates to depict nut growth.

Preoviposition, oviposition, and larval development: During the study period, a week after the first fly emerged, attempts were made to observe the first oviposition by daily sampling 100 nuts collected 1-3 meters above ground (low canopy area) at three locations covering all side of trees. The trees needed for this study were selected near Corvallis. When the first egg puncture was found, the number of nuts sampled was reduced to 10 nuts. The preoviposition period was calculated as the number of days from first female capture in ground emergence cages and aerial traps to the first egg puncture found in the field (Neilson et al. 1981).

The husk tissue of 10 randomly collected walnuts from nine trees was carefully dissected under a binocular microscope twice (Mon. and Fri.) a week. Data were collected regarding the location of egg puncture, number of egg punctures in each nut, and number of eggs in each cavity. The eggs, egg shells, unhatched eggs and larvae were counted and recorded. Larvae were preserved in 70% ethanol and glycerol for later classification as to first,

second, or third instar based on descriptions given earlier (Boyce 1934).

The location of the egg cavities in a given nut was determined. Cavities located in the husk tissue in the anterior one-third of the nut were considered in the stem region those found in the distal one-third were classified as in the calyx region. When they located in between these two areas they were classified being in the center.

Egg hatch duration in the field was considered the interval from detection of the first oviposition scar to detection of first instar. Larval life span was considered the interval between detection of first instar and detection of first mature larvae in water traps which are described below.

When the first mature larvae began to emerge from the husk to enter soil for pupation was determined by water pan traps. With the appearance of third instars, plastic trays were placed under the tree canopy. Each tray consisted of a high sided rectangular plastic container (50x35x15 cm) with water filled to a depth of 2 cm. Twelve of these trays were placed at random distances from the trunk beneath three trees at three locations in Corvallis, to collect larvae as they dropped to the ground. The larvae that fell into the water, drowned and were easily detected when the trays were examined. These traps were

placed under infested trees 2 weeks prior to the expected date of larval emergence and checked daily until the first larvae were found. As soon as larvae were found in the water traps, wood-trays (0.9x0.9x15 cm) with 2 cm layer of vermiculite and soil (50:50) to trap larvae for the parasitism study, were placed underneath the infested trees to collect falling larvae. To collect pupae, the pupation medium was sifted three times a week. Number of pupae were recorded and placed in individual 35 ml plastic cups (Jetware Plastica Industries Inc., Hatfield, Pennsylvania).

Pupal phenology and activity of natural enemies: Soon after field infestation, 20 nuts from unsprayed backyard trees in Corvallis, and 20 nuts from two commercial walnut orchards in Junction City were picked weekly, and were placed on 2 cm vermiculite in labelled rectangular plastic containers (18.5x13x11 cm) (Tri-State Plastics, Dixon, NY) to allow pupae to exit the husk and pupate in vermiculite. Puparia were then sifted from vermiculite at frequent intervals and placed in separately 35 ml plastic cups. Pupae were placed at 20±1°C for about 1 month to check for any adult emergence or parasite(s) development. Pupae were later moved to a cold room (3±0.5°C) and left for 4 months (AliNiazee, personal communication), to fulfil the diapause requirements. These pupae were kept at 24±1°C,

80±10% relative humidity, and 16:8 [L:D] photoperiod to permit emergence of flies and parasitoids. Data were recorded daily for a period of 4 months.

Vertical distribution of diapausing pupae in soil: In the first week of November 1991, a study was undertaken to determine the vertical distribution of pupae in soil. The study was done in a similar way as described by AliNiazee (1974) for the western cherry fruit fly, *R. indifferens* in Oregon and Gibson and Kearby (1978) on the walnut husk fly, *R. completa* in Missouri. In this study, 30 cm sq. by 15 cm deep soil samples were dug under a heavily infested tree. Each sample was divided into 2.5 cm deep section for examination. Sample sites were marked with a 30 cm sq. wooden frame. The top 2.5 cm soil and litter were removed and placed in a plastic bag. The second 2.5 cm layer of soil was placed in another bag and so on, to a depth of 15 cm. One backyard tree which was infested the preceding season was selected. Four samples sites (one from each quadrant) were randomly chosen for this study. After the samples were collected, pupae were sorted by washing and floatation (AliNiazee 1974). Each 2.5 cm sample was placed in a large pale which was then filled with water. The sample was stirred with a stick to float pupae. The pale water was first poured through 0.6 cm mesh screen and then through a standard 18 mesh screen. The material on the

bottom of this screen was washed. The washing left the husk fly pupae with some debris and small arthropods. The pupae were sorted from each sample, counted and recorded.

RESULTS AND DISCUSSION

During 1991, fly emergence in ground emergence cages began on July 17 and gradually increased until the seasonal peak was reached on August 5, and then decreased gradually. The last fly of the season emerged on September 11. However, the continuous emergence ended on August 16 and then only one fly emerged on September 11. Total emergence duration was 56 days. Data (Table III-1, Figure III-1a&b) representing the seasonal emergence resembled a normal frequency polygon.

A total of 164 flies emerged in 16 ground emergence cages, with a sex ratio of approximately 48 males: 52 females. However, the season long sex ratio of emerging flies was close to 1:1. Female flies were generally more abundant during the early season but the male flies were more prevalent in the later part of the season.

The time and rate of emergence from cages located in various quadrants of trees were compared in 1991 (Table III-2, Figure III-2&3). Differences were noticed in emergence rates of flies in different quadrants underneath tree. The emergence was most rapid in the south quadrant, followed by the east, the west and the north. There was a wide difference in emergence duration, flies emerged for 51 days in the east quadrant but only for 12 days in the

Table III-1. Seasonal patterns of ground emergence of *Rhagoletis completa* under field conditions of the Willamette Valley, OR, 1991-92.

YEAR	NO. OF CAGES	FLY EMERGENCE			EMERGENCE DURATION	FLIES EMERGED	FLIES/ TRAP
		FIRST	PEAK	LAST			
1991	16	7/17	8/05	9/11	56 DAYS	156	10
1992	8	6/29	7/20	8/17	50 DAYS	80	10

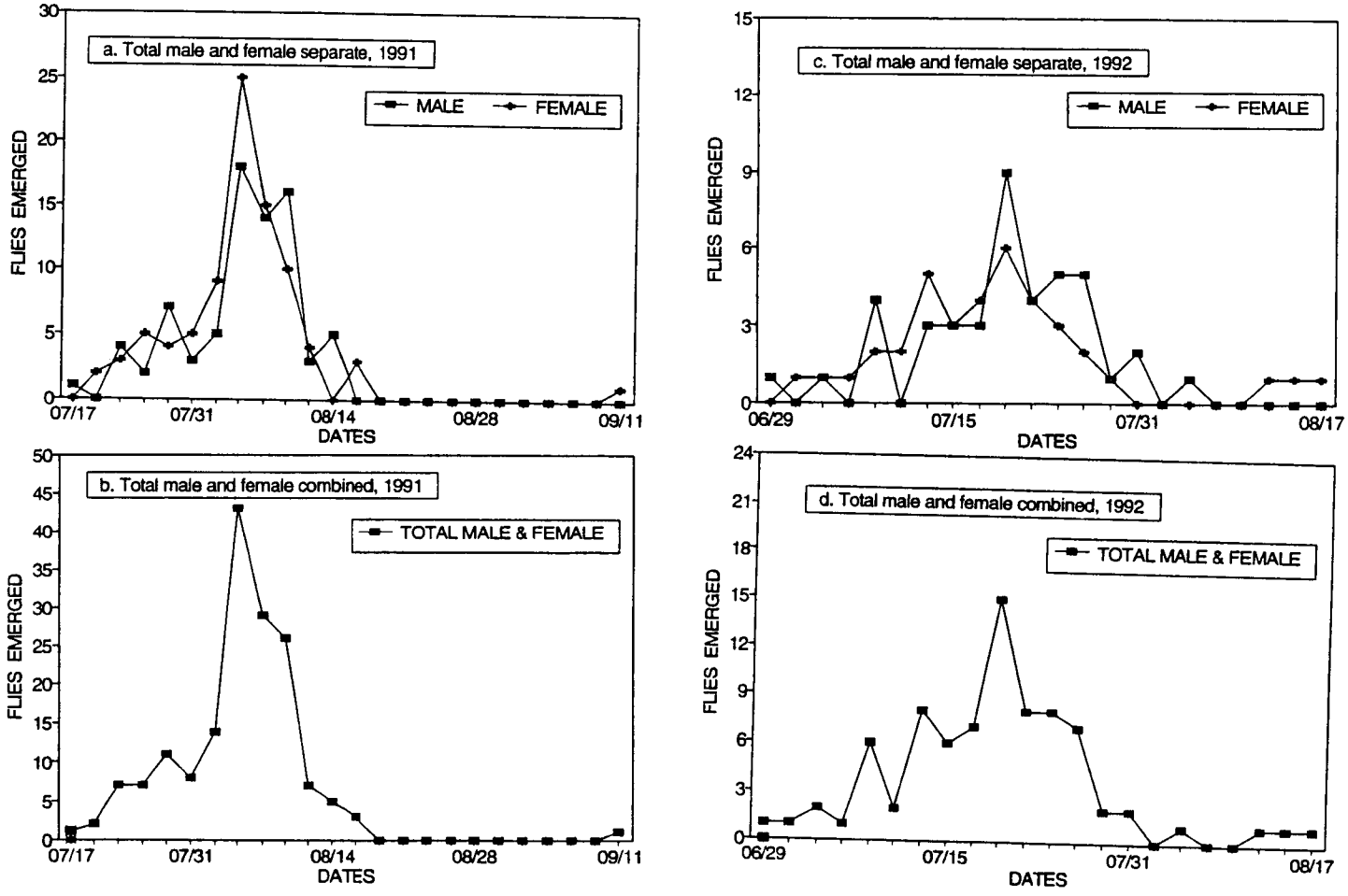

Figure III-1. Seasonal patterns of emergence of *Rhagoletis completa* (male and female separate and combined) recorded in ground emergence cages, in the Willamette Valley, OR [abandoned walnut trees].

north quadrant, for 47 days in the west and 23 days in the south.

There appeared to be no difference in the sex ratio (male to female) on a seasonal basis among the different quadrants. The sex ratio was 47.6% male to 52.4% female in the east quadrant, 50% male to 50% female in the west quadrant, 43.2% male to 56.8% female in the north quadrant, and 48.9% male to 51.1% female in the south quadrant.

During 1992, emergence began on June 29, the seasonal peak was reached on July 20 and closed on August 17 (Table III-1, Figure III-1c&d). The total emergence duration was 50 days. A total of 80 flies emerged in eight ground emergence cages. The sex ratio was 52.5% males to 47.5% females. Again, the sex ratio was nearly 1:1 on a seasonal basis. Females were more abundant than males during the early part of the season, while the reverse was apparent in the later portion.

The general shape of the emergence curve (Figure III-1c&d) differed from that of the previous year; it appeared to be a polymodel, which was probably caused by the climatic conditions prevailing during the season. There is no indication of a second generation.

Fly emergence in various quadrants of trees is presented in Table III-2 and Figure III-4 & 5. East

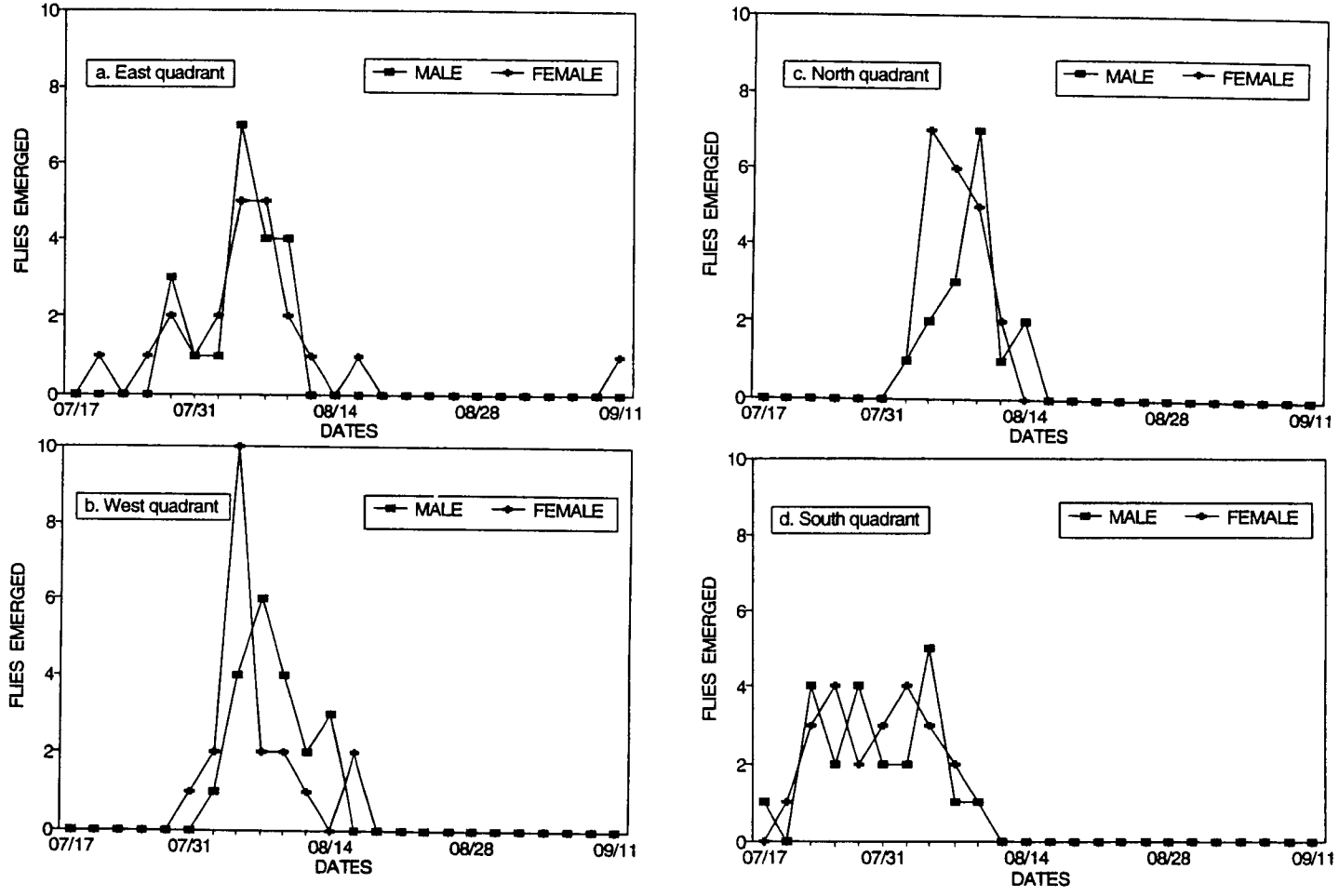

Figure III-2. Seasonal patterns of ground emergence of *Rhagoletis completa* (male and female separate) in different quadrants under walnut trees in the Willamette Valley, OR [abandoned walnut trees].

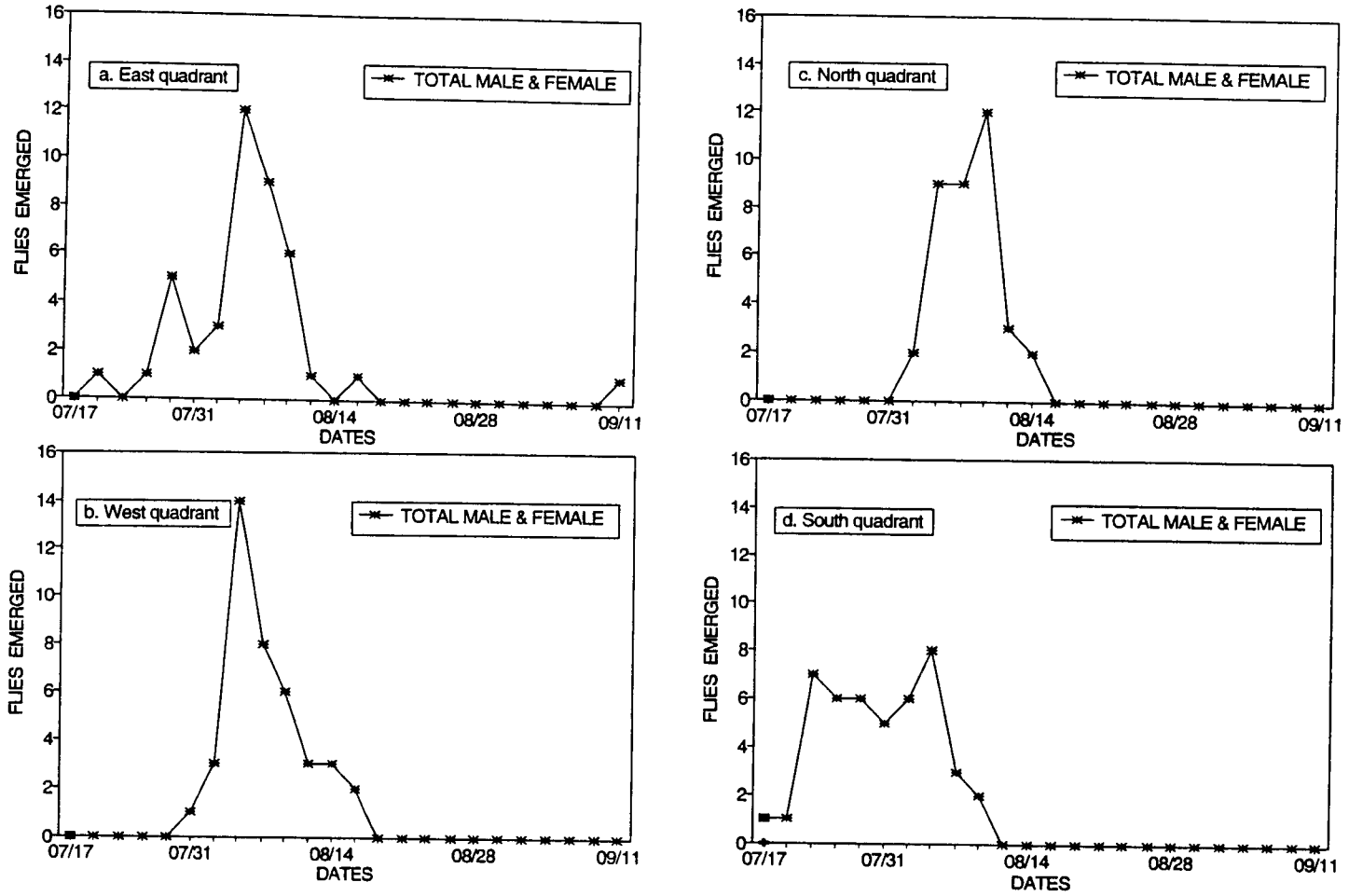

Figure III-3. Seasonal patterns of ground emergence of *Rhagoletis completa* (male and female combined) in different quadrants under walnut trees in the Willamette Valley, OR [abandoned walnut trees].

quadrants had the earliest emergence followed by south, west, and north quadrants. The sex ratio was 57.1% male to 42.9% female in the east quadrant, 55.6% male to 44.4% female in the west quadrant, 45% male to 55% female in the north quadrant, and 52.4% male to 47.6% female in the south quadrant. The emergence lasted for 45 days in the east followed by 40 days in the north, 31 days in south, and 16 days in the west quadrants. This indicates differential developmental rates in different quadrants reflecting differential accumulation of heat units. Similar trends, although not as pronounced were also observed during the 1991 season.

Boyce (1934) using ground emergence cages reported a similar difference in time and rate of emergence of flies from cages placed on different sides of trees. The emergence of flies was most rapid from the west side, followed by south and north. In the north quadrant, first flies always emerged later than those of from other quadrants. Jubb and Cox (1974) reported that *Rhagoletis fausta* and *R. cingulata* flies always emerged several days earlier from ground emergence cages in the south quadrant than those in the north quadrant.

Based on ground emergence cage and aerial trap catch data, Gibson and Kearby (1978) reported that WHF adults began to emerge in mid-July, with a seasonal peak near

Table III-2. Seasonal patterns of *Rhagoletis completa* ground emergence in different quadrants beneath a tree under field conditions of the Willamette Valley, OR 1991-92.

YEAR	QUADRANT	FLY EMERGENCE			EMERGENCE DURATION	% FLY EMERGED
		FIRST	PEAK	LAST		
1991	EAST	7/22	8/05	9/11	51	25.6
	WEST	7/31	8/05	8/16	47	24.4
	NORTH	8/02	8/09	8/14	12	22.6
	SOUTH	7/17	8/05	8/09	23	27.4
1992	EAST	6/29	7/20	8/12	45	26.2
	WEST	7/08	7/15	7/24	16	22.5
	NORTH	7/08	7/27	8/17	40	25.0
	SOUTH	7/01	7/20	7/31	31	26.3

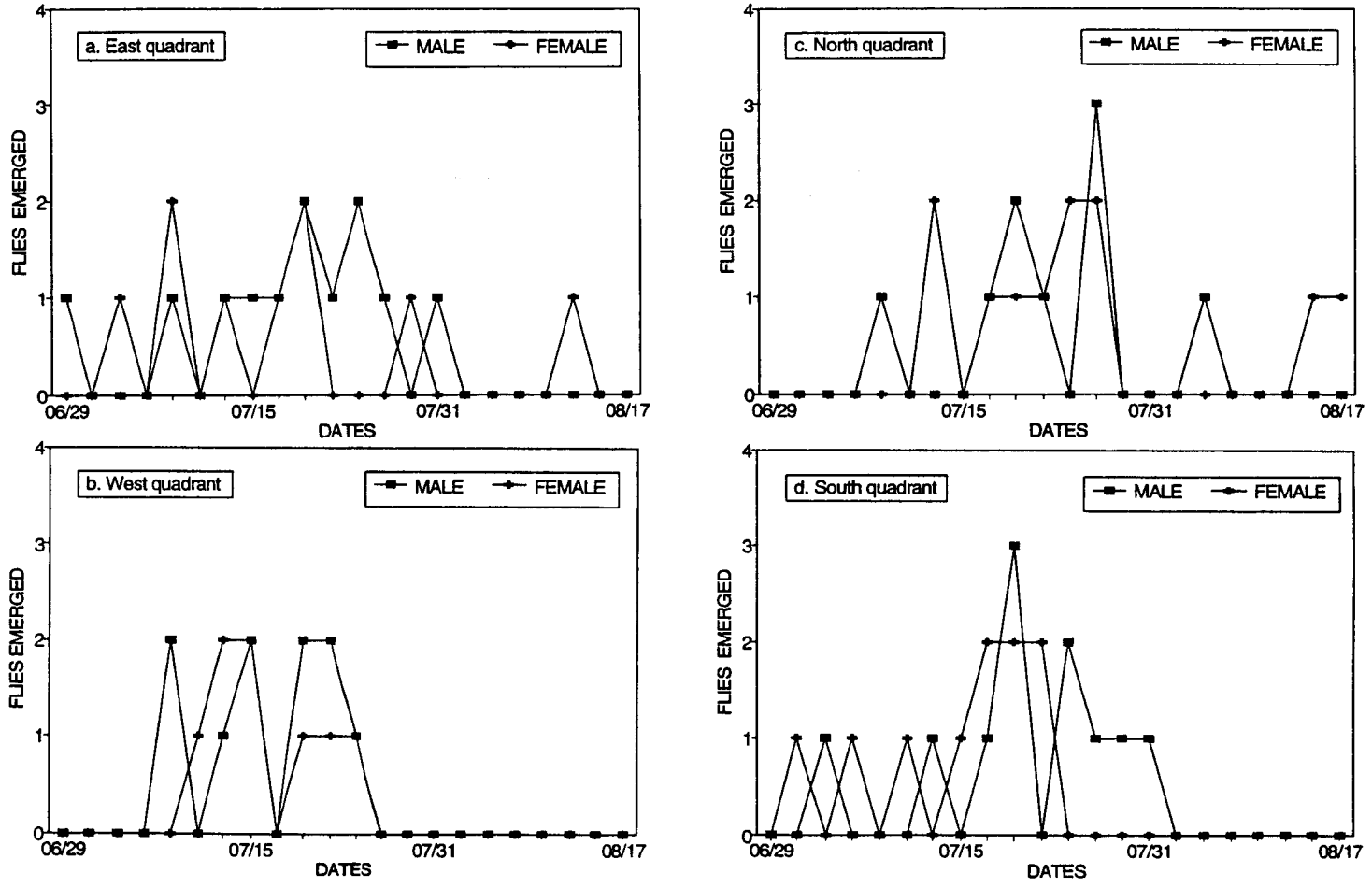

Figure III-4. Seasonal patterns of ground emergence of *Rhagoletis completa* (male and female separate) in different quadrants under walnut trees in the Willamette Valley, OR [abandoned walnut trees].

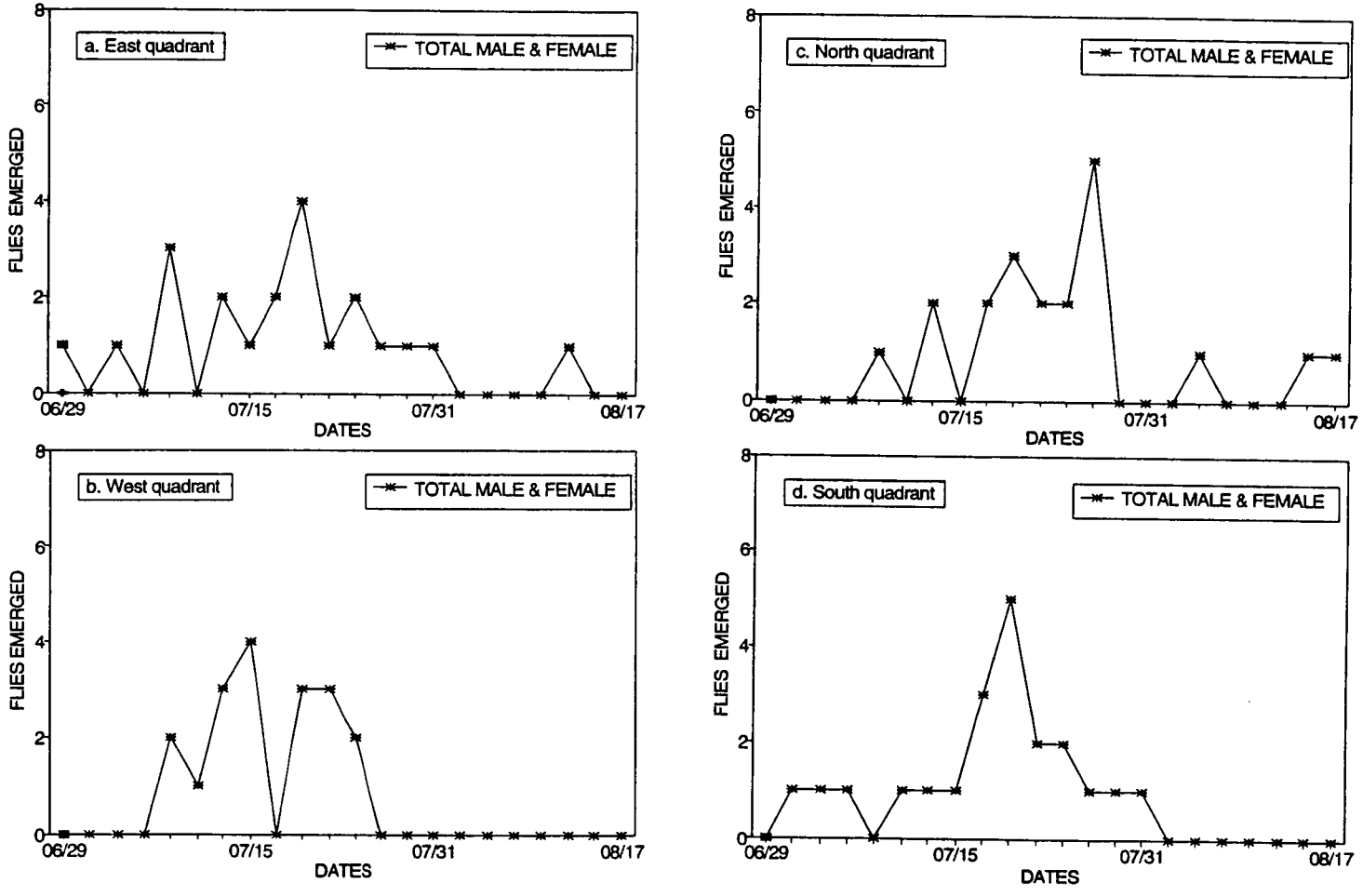

Figure III-5. Seasonal patterns of ground emergence of *Rhagoletis completa* (male and female combined) in different quadrants under walnut trees in the Willamette Valley, OR [abandoned walnut trees].

mid-September and terminated in mid-October in Missouri. Riedl and Hoying (1980) reported adult fly emergence began in late June and the main emergence period was in July and nearly all flies emerged by early August in northern California. My study established that first emergence occurred as early as June 29, with peak emergence third week of July and first week of August. The time difference for first fly emergence among different regions has puzzled *Rhagoletis* researchers. It has been speculated that different geographical populations differ in their developmental thresholds as well as the heat units required. The microclimatic conditions pupae experience including such factors as soil type, ground cover, host plant density, etc. may have a direct bearing on the time of emergence.

Although, the emergence timing and pattern may differ from quadrant to quadrant, the total number of flies in each quadrant did not differ and no distinct pattern was noticed in my study. For instance in 1991, 25.6% of the total flies were found in the east quadrant, 24.3% in west, 22.5% in north, and 27.4% in south. During 1992, the corresponding percentages were 26.2%, 22.5%, 25%, and 26.2% for east, west, north and south quadrants, respectively.

The old French late varieties (i.e. 'Franquette') are

dormant from December until March. Leafing started the third week of April during 1990, the fourth week of April during 1991, and the first week of April during 1992. Following pollination, the nuts went through an active growth period, and about 15 to 16 weeks after pollination both nut and hull had completely sized (Figure III-6).

Under Willamette Valley conditions, the nuts reached full size about 2341 mm sq. on August 13 in 1990, 2351 mm sq. on August 19 in 1991, and 2380 mm sq. on August 3 in 1992. The first oviposition was noticed when the nut size reached 2231 mm sq. during 1990, 2243 mm sq. in 1991, and 2275 mm sq. during 1992 with a mean of 2250±23 (X±SD) mm sq. Based on these data, I suggest that in addition to adult emergence and detection in traps, a close examination of nut size will be helpful in determining possible infestation dates and treatment schedules. It appears that the husk became soft enough at this growth stage, and females were able to penetrate their ovipositor easily into the husk to lay eggs. Boyce (1934) established husk hardiness as the key factor which determined varietal susceptibility. His data showed that 'Franquette' had a harder husks, and became susceptible only during the later part of the season. Some early varieties become susceptible early in the season. Riedl and Hoying (1980) reported that oviposition began about 10-14 days after the

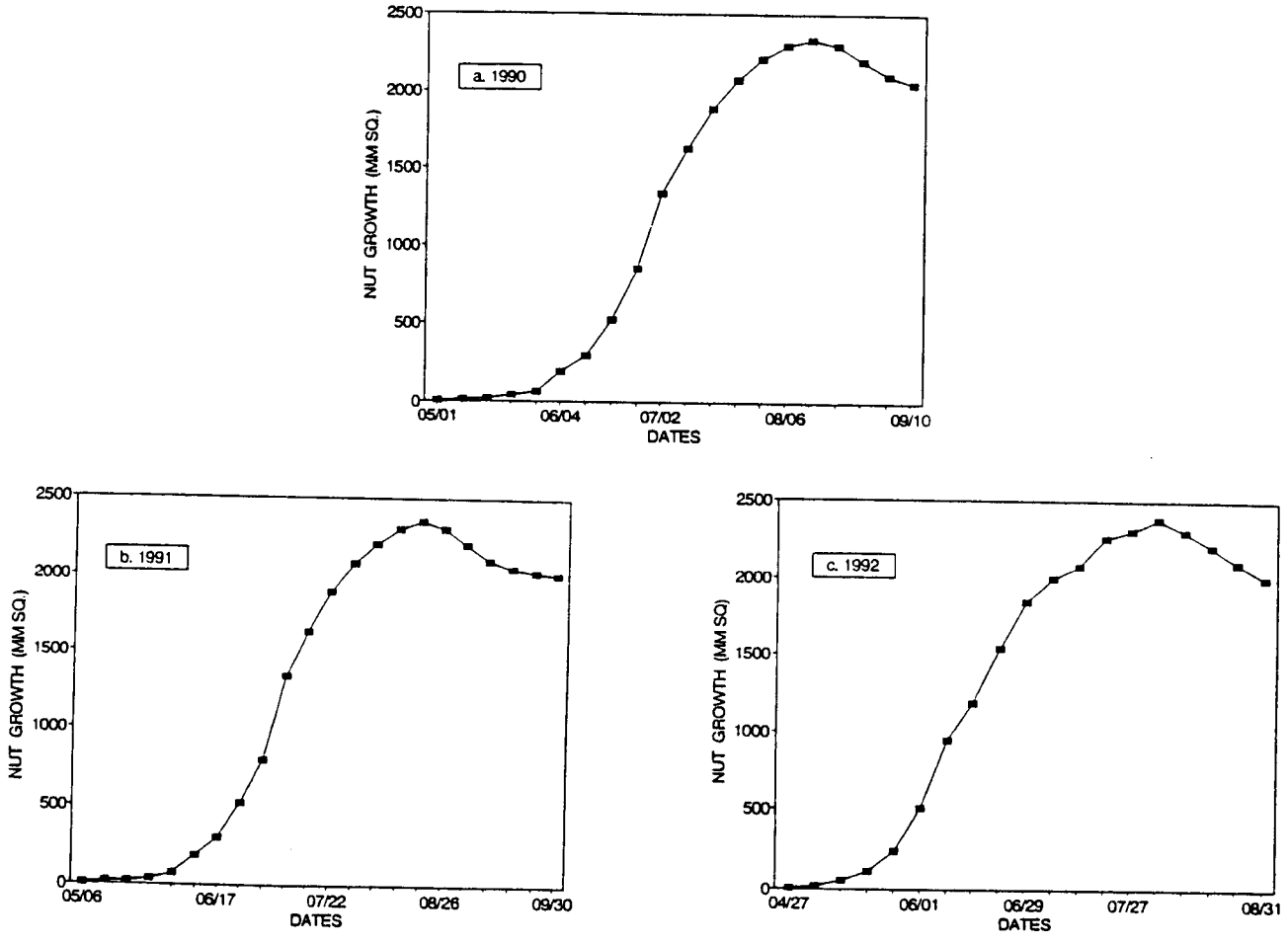

Figure III-6. Seasonal patterns of nut growth of a late variety ('Franquette') in the Willamette Valley, OR 1990-92.

first flies were caught in aerial traps in mixed variety (early and late including 'Franquette' variety) orchards at two study sites, but at a third site the lag time between the first fly catch in aerial traps and oviposition was 4 weeks in 'Franquette' variety. Little is known about the role of physical and chemical cues responsible for varietal susceptibility.

Under field conditions, the female dissections showed that flies were capable of laying eggs on July 23 during 1990, on July 29 during 1991, and on July 13 during 1992 (Table III-4). The preoviposition period was 20, 22, and 22 days during 1990, 1991, and 1992, respectively (Table III-3). Thus, there is a lag time of 8-10 days between appearance of sexually mature females in the traps and first oviposition. Even after females attained sexual maturity, gravid females could not oviposit in walnuts, which were apparently too hard. Since husk hardness decreases with maturity oviposition increases substantially during late season. Data further show that in 'Franquette' variety when nuts attain a minimum size of 2231 mm sq. the husk is soft enough for females to penetrate their ovipositors to lay eggs. Infestation of fruits by tephritid flies is frequently influenced by the degree of fruit ripeness (Boyce 1934, Dean and Chapman 1973, Stoffolano and Yin 1987). Unripe fruits appear to be

Table III-3. Preoviposition and oviposition periods of *Rhagoletis completa* under field conditions of the Willamette Valley, OR 1991-92.

YEAR	FIRST CATCH IN PHEROCON AM TRAP: FEMALE	FIRST CATCH IN PHEROCON AM TRAP: MATURE FEMALE	NUT SIZE AT IST OVIPOSITION (MM SQ.)	OVIPOSITION: FIRST	OVIPOSITION: PEAK	OVIPOSITION: LAST
1990	7/11	7/23	2231	7/31	8/24	8/31
1991	7/17	7/29	2243	8/08	8/31	9/09
1992	7/01	7/13	2274	7/22	8/14	8/21

Mature female= where at least terminal oocytes have reached full size.

Table III-4. Preoviposition, egg hatch, and larval development duration of *Rhagoletis completa* under field conditions of the Willamette Valley, OR 1990-92.

	FIRST OCCURRENCE				
YEAR	FEMALE CAPTURE	MATURE FEMALE	OVIPOSITION OBSERVED	LARVAL INSTAR	LARVAL EXIT FROM HUSK
1990	7/11	7/23	7/31	8/10	9/10
1991	7/17	7/29	8/08	8/16	9/13
1992	7/01	7/13	7/22	7/27	8/25

too hard for successful penetration by the female ovipositors (Pritchard 1969, Averill and Prokopy 1989), and consequently, no infestation is found in immature fruit.

The difference in time of first fly emergence and first oviposition in various *Rhagoletis* species has been less understood. Ovaries in female *Rhagoletis pomonella* mature within 9-10 days after emergence (Dean 1935) and first oviposition can be found soon thereafter (Illingworth 1912). However, if host or environmental conditions are not favorable, it may take longer. Neilson (1978) and Neilson et al. (1981) reported a 2-3 week preoviposition period in the apple maggot. Messina and Jones (1990) reported that the discrepancy was even greater, with nearly 45 days between the capture of the first sexually mature female fly and the first oviposition in this insect.

In *Rhagoletis indifferens*, Messina et al. (1991) found that oviposition in tart cherries did not occur for about 7-11 days after sexually mature flies were caught in the traps and was closely related to fruit maturity as measured by the mean penetration resistance of the fruit skin.

Boyce (1934) reported female husk flies become fully mature and capable of laying eggs 10-20 days after

emergence, while AliNiazee and Fisher (1985) mentioned that females usually begin mating and laying eggs 1-2 weeks after emergence. Riedl and Hoying (1980) reported a preoviposition period of 10-28 days in walnut husk fly. My study suggests that the preoviposition period is not variable for 'Franquette' variety. It appears that, after attaining sexual maturity, gravid females would not oviposit in walnuts which were too hard. This factor along with certain physical and chemical stimuli probably contribute to the variability in time required for the appearance of first stings.

In my experiments during 1990, oviposition began on July 31, gradually increased until August 24 when the seasonal peak was reached, then decreased and terminated on August 31 (Figure III-7a, Table III-3&5). The total ovipositional period was 1 month. In 1991, the oviposition began on August 8, reached a seasonal peak on August 31, and terminated on September 9 (Figure III-7b, Table III-3&5), with a total oviposition period of 1 month. In 1992, the oviposition began on July 22 gradually increased and reached a seasonal peak on August 14, then decreased and terminated on August 21 (Figure III-7c, Table III-3), again with a total oviposition period of about a month.

During the entire period of study, the oviposition duration was about 1 month. Over-ripe and/ or

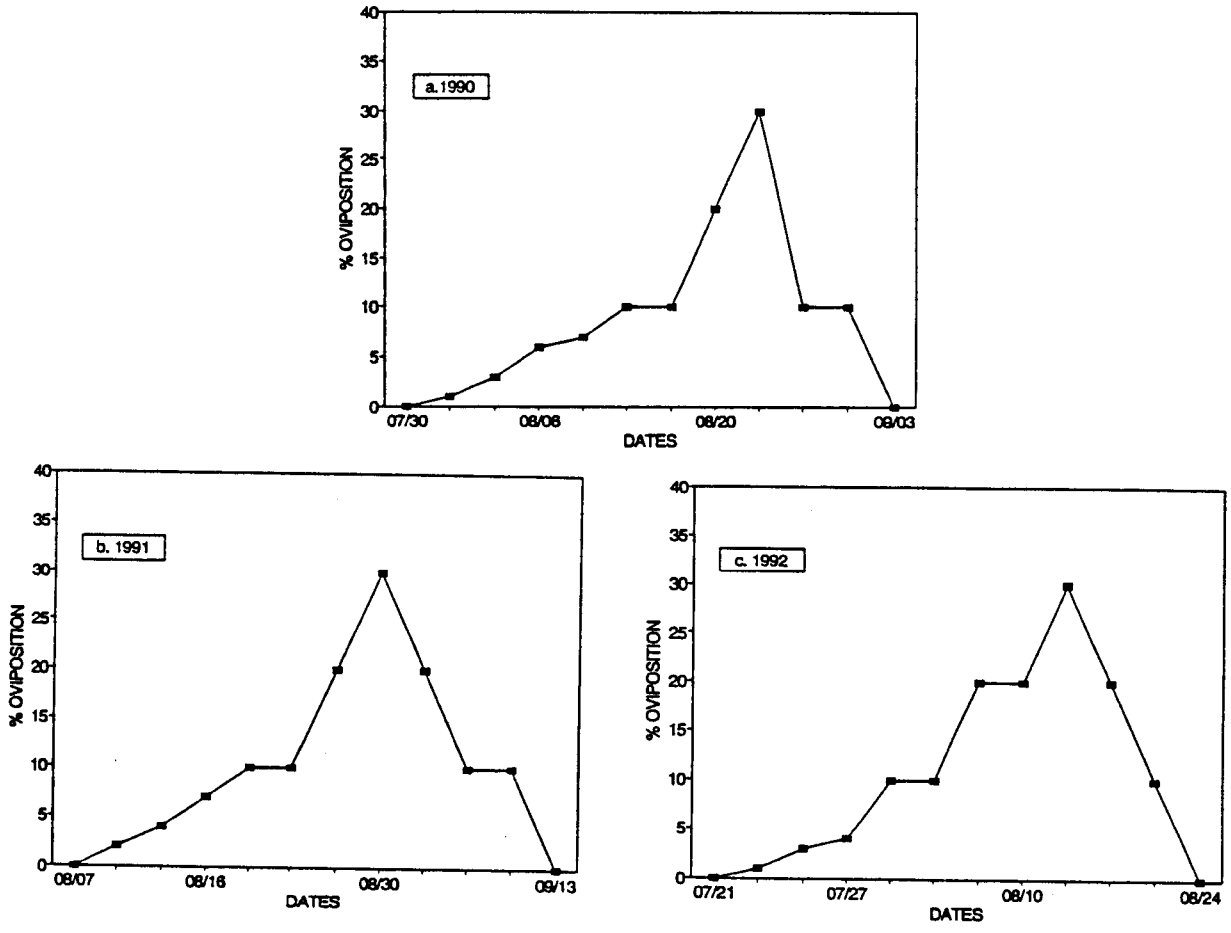

Figure III-7. Seasonal patterns of oviposition of *Rhagoletis completa* in the Willamette Valley, OR [abandoned walnut trees].

deteriorating fruits mainly due to larval activities make fruit less suitable for oviposition and this may have affected the egg laying (Prokopy and Boller 1971, Smith 1984, Girolami et al. 1986). In addition, the presence or absence of oviposition deterring pheromone (Cirio 1972) may have also influenced the oviposition.

The larval development pattern is presented in Figure III-8. In 1990, the first instar was found on August 10, the number gradually increased and reached a seasonal peak from August 27 through September 3 and terminated on August 31. The second instar were found on August 17, gradually increased to a seasonal peak on August 31 through September 7 then decreased and terminated on September 14. The third instar were found on August 27, gradually increased and by September 17 all larvae transformed into third instar (Figure III-8a).

In 1991, the first instar appeared on August 16 gradually increased until a seasonal peak was reached on September 6 and then decreased and terminated on September 13. The second instar appeared on August 23, reached a seasonal peak September 9 through September 13, and then decreased and terminated on September 23. The third instar first appeared on August 31, increased until all larvae transformed into third instar on September 27 (Figure III-8b)

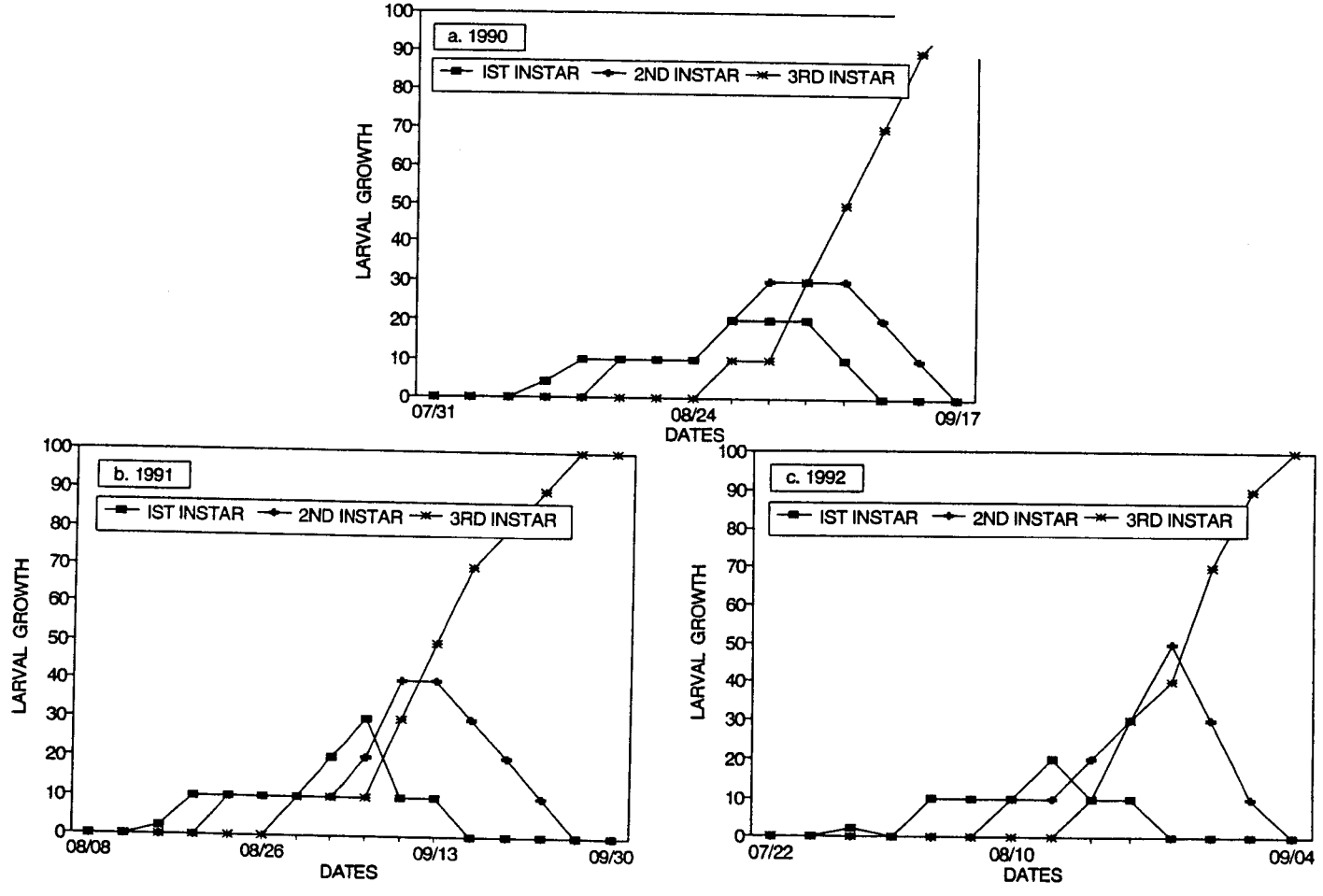

Figure III-8. Seasonal patterns of larval growth of *Rhagoletis completa* in the Willamette Valley, OR [abandoned walnut trees].

Table III-5. Time and thermal unit required for different biological events of *Rhagoletis completa* under field conditions in the Willamette Valley, OR 1990-92.

BIOLOGICAL EVENTS	YEARS OF STUDY 1990	1991	1992	AVERAGE (DATE)	TIME REQ. BET. EVENTS (DAYS)	AVERAGE TU REQUIRED STARTING MARCH 1	TU REQUIRED TO PROGRESS FROM ONE EVENT TO ANOTHER
EMERGENCE							
A. FIRST	7/11	7/17	7/01	7/09	---	1050	---
B. 10%	8/10	8/19	7/27	8/08	30	1517	467
C. 50%	8/27	9/04	8/12	8/24	16	1751	234
D. 90%	9/05	9/11	8/26	9/03	10	1895	144
E. 100%	10/1	10/9	9/11	9/26	23	2198	303
MATURE FEMALES							
A. FIRST	7/23	7/29	7/13	7/21	12	1234	184
B. PEAK	8/27	9/04	8/10	8/23	32	1736	502
OVIPOSITION							
A. FIRST	7/31	8/08	7/22	8/01	12	1378	144
B. PEAK	8/24	8/31	8/14	8/23	22	1728	350
C. LAST	8/31	9/09	8/21	8/31	8	1841	113
EGG HATCH	8/10	8/16	7/27	8/06	5	1500	
PUPATION	9/10	9/13	8/25	9/04	29	1923	423

In 1992, the first instar began to appear on July 27, increased to a seasonal peak on August 14 and terminated on August 21. The second instar began to show on August 10 reached a seasonal peak on August 24 and disappeared on August 31. The third instar appeared on August 17, increased until all transformed into third instar on September 4 (Figure III-8c).

The seasonal fruit infestation approached 100% on September 14 in 1990, on September 16 in 1991, and August 31 in 1992. The close examination of the Figure III-9 reveals that the infestation rates actually fluctuated between 96-100%. Riedl and Hoying (1980) reported the husk fly infestation level on all varieties reached nearly 100% late in the season. When oviposition was first detected in my study, the infestation levels ranged from 1-2% of the nuts and egg punctures averaged 1.3%. Riedl and Hoying (1980) reported levels of infestation ranging from 0.1-2.8% nuts with egg punctures with an average of 0.8%.

The seasonal patterns when mature larval exits the husks is presented in Figure III-10. In 1991, mature larvae began to exit on September 13, gradually increased to a seasonal peak on October 7, then decreased and terminated on October 30.

Data from this 3-year field study (1990-1992) revealed that an average of 84.5% of the egg cavities were

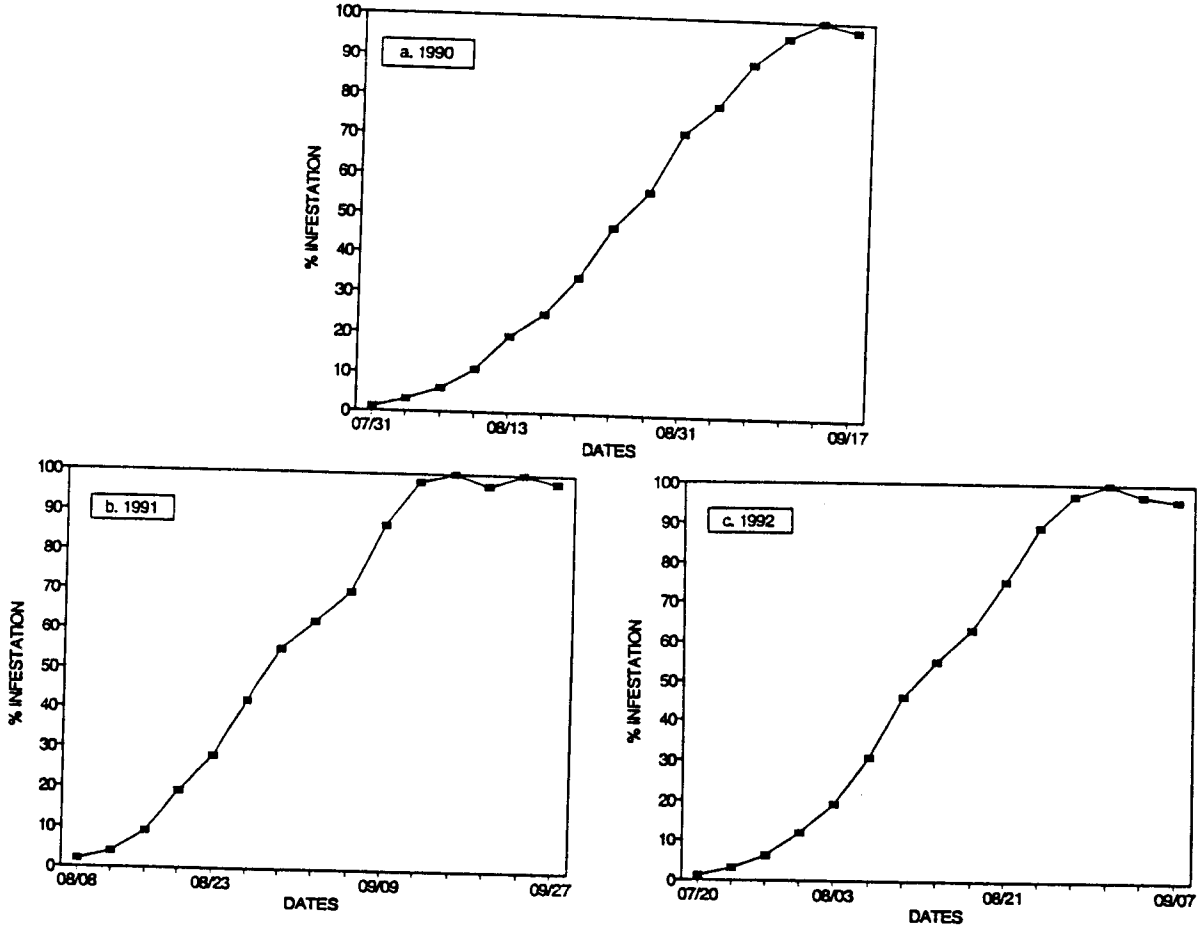

Figure III-9. Seasonal patterns of fruit infestation of *Rhagoletis completa* in the Willamette Valley, OR [abandoned walnut trees].

located in the stem region; 13.5% in the middle region; and 2% in the calyx region (Table III-6). Under laboratory conditions in 1991, the percentages were 66.1, 25.4 and 8.5 for these respective regions. This shows a large difference among different areas, but general similarities between the field and laboratory conditions were evident. In an earlier study Boyce (1934) reported 72% of the egg cavities were located in the stem region, 24% in the middle region and 4% in the calyx region under field conditions, although the differences were not quite as marked in the laboratory.

Number of eggs per cavity and number of cavities per walnut are presented in Table III-7. Female flies oviposited an average of 33.8 eggs per cavity over a three year period. The range of eggs per cavity was 13-73. Only one egg cavity was found in the majority (X= 85.8%) of nuts; two cavities were found in 12.6% nuts, and three cavities in 1.6% nuts. Boyce (1934) reported that the average number of egg per cavity under field conditions was 14.9 and varied from 4-40 eggs per cavity, 76% of the nuts had one cavity, 20% had two cavities and 4% had three cavities.

In my study, a consistently higher egg hatch was observed. Over a 3-year period, the mean percent egg hatch was 98% and the mean percent larval survival was 80%

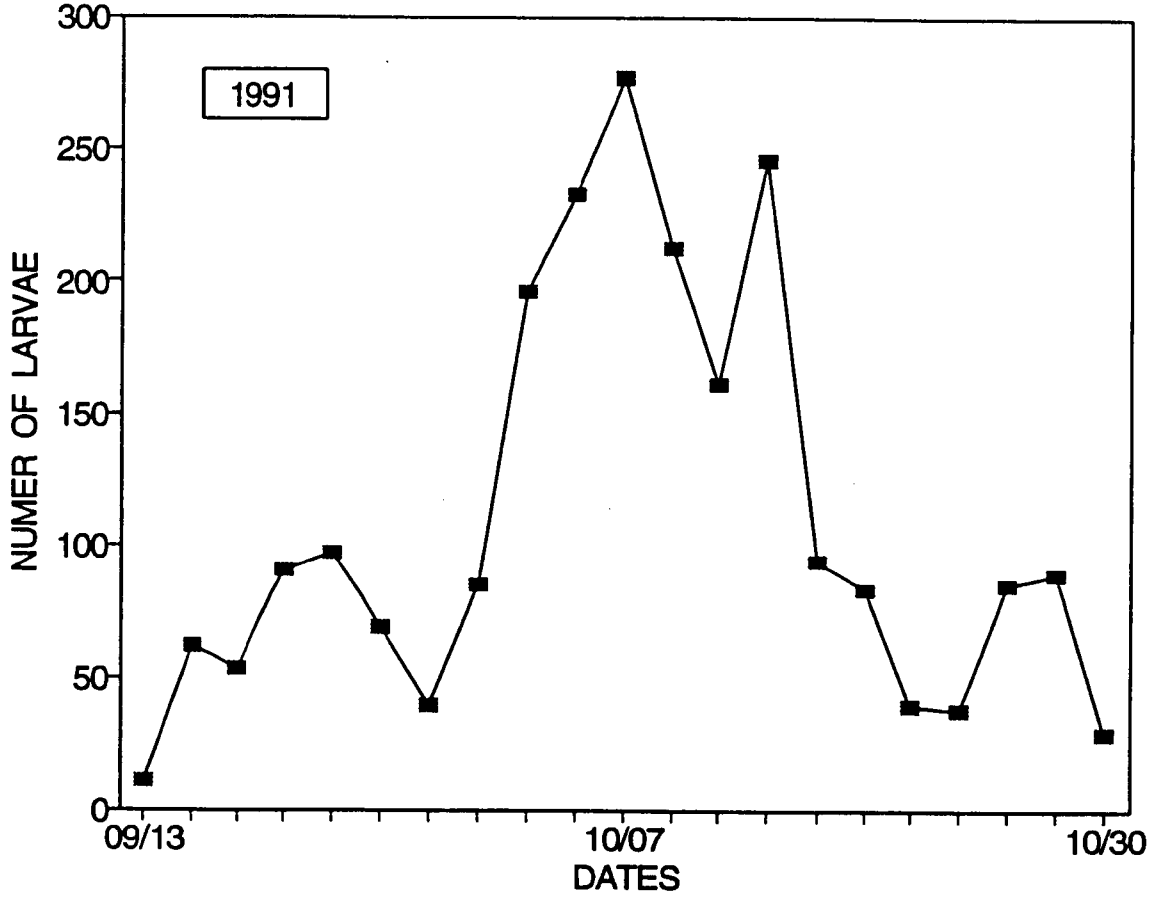

Figure III-10. Seasonal patterns of *Rhagoletis completa* mature larval exit from husk in the Willamette Valley, OR.

Table III-6. Location of *Rhagoletis completa* egg cavities on surface of walnuts under field and laboratory conditions.

YEAR	TOTAL NO. WALNUTS EXAMINED	TOTAL NO. CAVITIES FOUND	% EGG CAVITIES IN EACH REGION STEM	CENTER	CALYX
A. FIELD					
1990	67	75	81.3	16.0	2.7
1991	82	94	89.4	8.5	2.1
1992	71	81	82.7	16.0	1.3
MEAN	73.3	83.3	84.5	13.5	2.0
B. LABORATORY					
1991	76	76	66.1	25.4	8.5

(Table III-8). This appeared to be somewhat higher than the 80% egg hatch and 75% larval survival reported by Boyce (1934).

Under field conditions, larvae were first detected 10 days after first oviposition in 1990, 7 days in 1991, and 4 days in 1992. Since eggs hatch in 5 to 7 days depending on temperature (Jones 1967, Riedl and Hoying 1980, AliNiazee and Fisher 1985), this pattern was expected. The larval life span was 31 days in 1990, 28 days in 1991, and 29 days in 1992 (Table III-4). Boyce (1934) reported 36.8 days for mean larval development under field conditions. However, an appreciable number of larvae may complete their development in 18 to 20 days. The larvae complete their development in 3 to 5 weeks (Jones 1967, Gibson and Kearby 1978, AliNiazee and Fisher 1985).

Out of 362 pupae collected from the wooden trays in Corvallis, a total of 234 flies (64%) emerged, and no parasitoids emerged. A total of 4303 flies (77%) emerged from 5247 pupae collected from Corvallis and Junction City during 1991, and no parasitoids were seen. However, AliNiazee (unpublished) reared an unidentified species of *Coptera* from husk fly pupae collected from Albany, Oregon. It means that limited parasitism of the husk fly pupae may exist at some locations in Oregon. Legner and Goeden (1987) reported an high incidence of WHF larval parasitism

Table III-7. Egg deposition by female *Rhagoletis completa* under field conditions of the Willamette Valley, OR 1990-92.

YEAR	TOTAL CAVITIES EXAMINED	TOTAL EGGS FOUND	EGGS PER CAVITY	EGGS RANGE	% WALNUTS WITH CAVITIES 1	2	3
1990	18	584	32.4	16-60	83.3	16.7	0.0
1991	21	708	33.7	13-73	85.7	9.5	4.8
1992	17	601	35.3	19-58	88.2	11.8	0.0
MEAN	18.7	631	33.8	13-73	85.8	12.6	1.6

Table III-8. Egg hatch and larval survival of *Rhagoletis completa* under field conditions of the Willamette Valley, OR 1990-92.

	EGG		LARVAE	
YEAR	TOTAL CAVITIES EXAMINED	% EGG HATCH	TOTAL CAVITIES EXAMINED	% LARVAL SURVIVAL
1990	47	98.2	16	78.6
1991	64	98.2	24	82.1
1992	44	98.8	16	80.1
MEAN	51.7	98.4	18.7	80.3

in western Texas and southern New Mexico.

The vertical distribution of the diapausing pupae in soil is illustrated in Figure III-11. Nearly 72% of the pupae were found in the top 2.5 cm layer of soil and ground litter. The 5-7.5 cm layer accounted for another 16.7%. Only 11.1% pupae were recovered at a depth of 7.5-12.5 cm and none was found at the depth of 15 cm.

Gibson and Kearby (1978) found 74.5% pupae in the upper 2.54 cm layer and 18% in the 2.54-5.08 cm layer, while Ries (1934) reported pupae of *Rhagoletis suavis* (Loew) overwinter at a depth of 4-7 inches indicating a possible difference in the overwintering behavior of these two species. Also, the soil samples with different cultivation practices might have different overwintering profiles. Jones et al. (1989) reported that *R. pomonella* pupae are generally found at a depth of 2.5 cm below ground. AliNiazee (1974) reported that a majority of diapausing pupae of the western cherry fruit fly, *R. indifferens* overwinter in the soil at a depth of 1-4 inch. My data suggests that, although a very small proportion of the WHF pupae may get down below 10 cm, a majority overwinters in the top 2.5 cm. Again, the cultivation practices including ploughing and discing may interfere with the depth to which the larvae might enter to diapause.

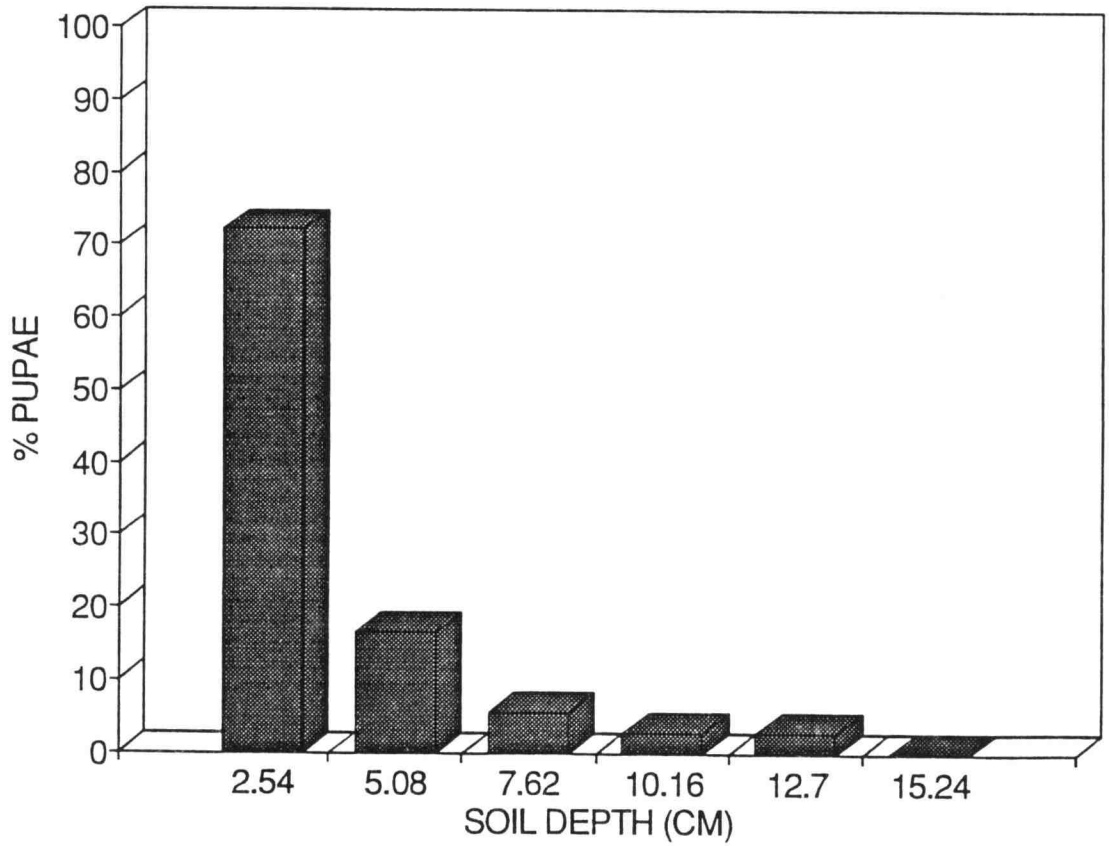

Figure III-11. Vertical distribution of overwintering pupae of *Rhagoletis completa* in the Willamette Valley, OR.

Pupae were found in all four quadrants beneath the tree. No distinct pattern emerged, suggesting no apparent difference among the quadrants. Out of a total of 36 pupae, 10 were found in the east quadrant, 9 in the west, 8 in the north, and 9 in the south.

In summary, this 3-year seasonal phenology study suggests that under Willamette Valley conditions, the WHF began to emerge at the end of June, peaked during the end of July and early August, the emergence continued through middle of September. The flies emerged for an average 53 days. The temporal relationship between emergence and oviposition was consistent in Franquette variety. The average preoviposition period was 3 weeks, and the oviposition period was close to 1 month. The fruit infestation reached over 95% in unsprayed walnut trees. Overwintering pupae appear as early as third week of August, continued for 6 weeks and almost all larvae had exited husks by the end of October.

REFERENCES

AliNiazee, M. T. 1974. The western cherry fruit fly, *Rhagoletis indifferens* (Diptera: Tephritidae) 1. Distribution of the diapausing pupae in the soil. Can. Entomol. 106: 909-12.

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette Valley of Oregon. Environ. Entomol. 5:397-402.

AliNiazee, M. T. 1988. Diapause modalities in some *Rhagoletis* species. *In* M. T. AliNiazee [Editor], Ecology and Management of Economically Important Fruit Flies. Agric. Exp. Sta. Oreg. State Univ. Special Report 830.

AliNiazee, M. T. and G. Fisher. 1985. The walnut husk fly in Oregon *Rhagoletis completa*, pests of walnuts. Fact sheet, OSU Extension Service, Corvallis, Oregon.

AliNiazee, M. T. and R. L. Westcott. 1987. Flight period and seasonal development of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), in Oregon. Ann. Entomol. Soc. Am. 80(6): 823-827.

Averill, A. L. and R. J. Prokopy. 1989. Distribution patterns on *Rhagoletis pomonella* (Diptera: Tephritidae) eggs in hawthorn. Ann. Entomol. Soc. Am. 82: 38-44.

Boyce, A. M. 1934. Bionomics of the walnut husk fly, *Rhagoletis completa*. Hilgardia. 8:363-579.

Cirio, U. 1972. Osservazioni sul comportamento di ovideposition della *Rhagoletis completa* Cresson (Diptera: Trypetidae) in laboratorio. Atti IX Congresso Nazionale Italiano di Entomologia 1972, pp. 99-117.

Dean, R. W. 1935. Preoviposition period of the apple maggot fly, *Rhagoletis pomonella* (Walsh), in eastern New York. J. Econ. Entomol. 28:504.

Dean, R. W. and P. J. Chapman. 1973. Bionomics of the apple maggot in eastern New York. Search Agric. (Geneva, N. Y.) 3: 1-62.

Frick, K. E., H. G. Simkover, and H. S. Telford. 1954. Bionomics of the cherry fruit flies in eastern Washington. Tech. Bull. Wash. Agric. Expt. Stn. No. 13.

Gibson, K. E. and W. H. Kearby. 1978. Seasonal life history of the walnut husk fly [*Rhagoletis completa*] and husk maggot [*Rhagoletis suavis*] in Missouri. Environ. Entomol. 7: 81-87.

Girolami, V., A. Strappazon, R. Crnjar, A. M. Angioy, P. Pietra, J. G. Stoffalano, Jr., and R. J. Prokopy. 1986. Behavior and sensory physiology of *Rhagoletis pomonella* in relation to oviposition stimulants and deterrents in fruit, pp. 183-190. *In* R. Cavalloro [ed.], Fruit flies of economic importance. Balkema, rotterdam, The Netherlands.

Illingworth, J. F. 1912. A study of the biology of the apple maggot, *Rhagoletis pomonella*, together with an investigation of methods of control. New York (Cornell) Agric. Expt. Stn. Bull. 324.

Jones, S. C. 1967. The walnut husk fly and its control. Nut-Growers-Soc-Oreg-Wash-Proc., 53:59-62.

Jones, V. P., D. G. Alston, J. F. Brunner, D. W. Davis, and M. D. Shelton. 1991. Phenology of the western cherry fruit fly (Diptera: Tephritidae) in Utah and Washington. Ann. Entomol. Soc. Am. 84(5): 488-492.

Jones, V. P., D. W. Davis, S. L. Smith, and D. B. Allred. 1989. Phenology of the apple maggot associated with cherry and hawthorn in Utah. J. Econ. Entomol. 82: 788-792.

Jubb, G. L. Jr. and J. A. Cox. 1974. Seasonal emergence of two cherry fruit fly species in Eric County, Pennsylvania: a 25- year summary. J. Econ. Entomol. 67: 613-615.

Lathrop, F. H. and C. O. Dirks. 1945. Timing the seasonal cycles of insects: the emergence of *Rhagoletis pomonella*. J. Econ. Entomol. 38: 330-334.

Legner, E. F. and R. D. Goeden. 1987. Larval parasitism of *Rhagoletis completa* (Diptera: Tephritidae) on *Juglans microcarpa* (Juglandaceae) in western Texas and southeastern New Mexico.

Messina, F. J., D. G. Alston, and V. P. Jones. 1991. Oviposition by the western cherry fruit fly (Diptera: Tephritidae) in relation to host development. J. Kans. Entomol. 64: 197-208.

Messina, F. J., and V. P. Jones. 1990. Relationship between fruit phenology and infestation by the apple maggot (Diptera: Tephritidae) in Utah. Ann. Entomol. Soc. Am. 83: 742-752.

Michelbacher, A. E. and J. C. Ortega. 1958. A technical study of insects and related pests attacking walnuts. Calif. Agric. Exp. Stn. Bull. 764. 86 pp.

Neilson, W. T. A. 1978. Female apple maggot captures and injury to unsprayed apples. J. Econ. Entomol. 71:755-56.

Neilson, W. T. A., A. D. Knowlton, and K. B. McRae. 1981. Preoviposition and oviposition periods of the apple maggot, *Rhagoletis pomonella* [Diptera: Tephritidae]. Can. Entomol. 113: 1061-67.

Pritchard, G. 1969. The ecology of a natural population of Queensland fruit fly, *Dacus tryoni* II. The distribution of eggs and its relation to behavior. Aust. J. Zool. 17: 293-311.

Prokopy, R. J. and E. F. Boller. 1971. Stimuli eliciting oviposition of European cherry fruit fly, *Rhagoletis cerasi* (Diptera: Tephritidae) into inanimate objects. Entomol. Exp. Appl. 14: 1-14.

Riedl, H. and S. A. Hoying. 1980. Seasonal patterns of emergence, flight activity, and oviposition of the walnut husk fly in northern California. Environ. Entomol. 9:567-571.

Ries, D. T. 1934. Biological studies of the walnut husk fly [*Rhagoletis suavis* Loew]. Mich. Acad. Sci. Arts and Letters. 20: 717-23.

Smith, D. C. 1984. Feeding, mating, and oviposition by *Rhagoletis cingulata* (Diptera: Tephritidae) flies in nature. Ann. Entomol. Soc. Am. 77: 702-704.

Stoffolano, J. G., Jr. and L. R. S. Yin. 1987. Structure and function of the ovipositor and associated sensilla of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae). Int. J. Insect Morphol. Embryol. 16: 41-69.

CHAPTER IV

FLIGHT DYNAMICS OF ADULT WALNUT HUSK FLY, *RHAGOLETIS COMPLETA* CRESSON (DIPTERA: TEPHRITIDAE) IN THE WILLAMETTE VALLEY, OREGON

ABSTRACT

Adult flight dynamics of the walnut husk fly (WHF), *Rhagoletis completa* Cresson, were investigated using Pherocon AM traps (Pherocon Monitoring Kit for *Rhagoletis* species, Trece Incorporated, Salinas, CA) in abandoned backyard trees near Corvallis, Oregon and commercial walnut orchards in Junction City, Oregon for a 3-year period (1990-1992). Seasonal emergence of the WHF varies from year to year. In Corvallis, flies were first detected from July 1 through July 17, but the average time for first fly detection was July 9. The seasonal peaks were observed between August 10 and September 4. The last flies were trapped on September 11 though October 9. In commercial orchards, the first flies were trapped July 13 through August 5, seasonal peaks occurred around August 31 through September 9. The last flies were trapped between September 14 through 30. In terms of the overall flight pattern, no major difference was noticed between the cultivated commercial orchards and abandoned trees. Dissections of females indicated that under field conditions, WHF is capable of egg laying 12 days after emergence. Nevertheless, only one generation per year in the Willamette Valley of Oregon was observed.

INTRODUCTION

Many studies dealing with flight activities of the genus *Rhagoletis* have been conducted over the past several years (Oatman 1964, AliNiazee 1976, AliNiazee 1978, Gibson and Kearby 1978, Riedl and Hoying 1980, AliNiazee and Westcott 1987, Jones et al. 1989, 1991). Relationship of adult apple maggot flight to various environmental conditions also has been studied in detail by Dean and Chapman (1973) who showed that the rainfall had a marked influence on the adult flight patterns in New York.

The walnut husk fly (WHF), *Rhagoletis completa* Cresson, is the most important pest of walnuts throughout North America. Like many other tephritid flies, the flight of this insect is dependent on the availability of food, shelter and oviposition sites. Gibson and Kearby (1978) in Missouri and Riedl and Hoying (1980) in northern California studied the flight activity of WHF by using Pherocon AM traps. A detailed study on the flight dynamics of this insect from the Willamette Valley of Oregon is lacking. The purpose of this study was to investigate the seasonal adult flight patterns of this insect in Oregon and to determine the impact of climatic conditions on the flight patterns.

MATERIALS AND METHODS

Adult flight dynamics in unsprayed backyard trees: In 1990, 1991 and 1992, unsprayed mature backyard trees of 'Franquette' walnut variety with a history of high WHF infestation were selected for this study. Although the Pherocon AM trap was originally developed for the apple maggot, *Rhagoletis pomonella* (Walsh) (Prokopy 1975), it also has been used for the WHF monitoring in earlier studies (Riedl and Hoying 1980) and was recommended for use by AliNiazee and Fisher (1985). Commercially available standard Pherocon AM traps (Pherocon Monitoring Kit for *Rhagoletis* species, Trece Incorporated, Salinas, CA) consisting of a fluorescent yellow card board rectangle (14x23 cm) coated with polybutene adhesive mixed with the chemical bait of ammonium acetate and casein hydrolysate, were hung at a height of 2 m above the ground on bearing trees (Anonymous 1982) at the four compass directions to trap flies as they emerged from the soil. Traps were hung at the outside of the tree canopy, and small branches and leaves were cleared away to increase visibility and prevent leaves from touching the trap surfaces. From the middle of June until the end of October, traps were replaced every 4 weeks (AliNiazee and Fisher 1985) and serviced each time a count was taken. The flight activity

was monitored three times a week, and the flies caught were sexed (Moffitt 1958) and recorded. The flies were removed from traps washed in kerosene oil and females were stored in a solution of 70% ethanol and glycerol in separate vials for each date for ovarian development studies.

Adult flight dynamics in commercial walnut orchards: Two commercial walnut orchards in Junction City, Oregon were selected for a flight activity study. Orchard No. 1 was a 3 hectare walnut planting of the 'Franquette' variety which had been sprayed annually for WHF control. Orchard No. 2 was a five hectare block of trees consisting of mixed varieties, 'Franquette', 'Manregian', 'Mayette', 'Spurgeon', and 'Hartley'. The orchard was not treated for husk fly or any other pests during the study period. Irrigation and nitrogen fertilizer were applied in both orchards. Sheep grazing also was practiced in both orchards. Two AM Pherocon traps were evenly spaced on south side of two trees 2 m above ground in each orchard. The flight activity was monitored once a week during 1991 and 1992 seasons. The flies trapped were sexed and recorded. The females removed from the traps were washed in kerosene oil and stored in 70% ethanol and glycerol to study ovarian development.

Female ovarian development under field conditions: The females collected from Pherocon AM yellow sticky traps were dissected in the laboratory to check for presence or absence of eggs and egg development. The abdomen of females were cut from both lateral sides. The flies were then placed on their backs in a row on the hard paraffin in a container. They were held stationary with the help of insect pins. Water was added to the paraffin container to such a depth that the flies were completely submerged. The internal parts of the flies were exposed by cutting and removing the ventral exoskeleton with the help of a fine scissors and forceps. A fine needle and a forceps were used to remove the digestive system, tracheae, and some muscles. The ovaries which are near the dorsal surface, were then observed under a binocular microscope. On the basis of egg development stage in the ovaries, the flies were grouped into two categories: undeveloped (mature oocytes absent), and developed (with varying degree of ovarian development where at least terminal oocytes have reached full size). The later category included females capable of laying eggs. A profile of female maturation and ovarian development in the field is developed and is presented in this paper.

RESULTS AND DISCUSSION

In 1990, the earliest flies were detected in Pherocon AM traps on July 11, fly catch gradually increased until the seasonal peak was reached on August 27, then gradually decreased and terminated on October 1 (Table IV-1, Figure IV-1a&b). The total fight period was 82 days. The total number of flies caught in four traps was 1823, and the sex ratio was close to 1:1, 47.9% male to 52.1% female on a seasonal basis. In general, the females outnumbered males in the early season and males outnumbered females after mid-season.

In 1991 the flies captured in Pherocon AM traps began on July 17. Fly catch gradually increased until the seasonal peak reached on September 4 and the last capture was on October 9 (Table IV-1, Figure IV-1c&d). The total flight period was 86 days. A total of 3903 flies were trapped in eight traps. The sex ratio was close to 1:1, 49.5% male to 50.5% female on a seasonal basis.

During 1992, the first flies captured began on June 29, the seasonal peak was reached on August 10, and captures terminated on September 11 (Table IV-1, Figure IV-1e&f), with a total flight period of 75 days. The total number of flies caught in eight aerial traps was 3608 . The sex ratio was close to 1:1, 50.4% male to 49.6% female

Table IV-1. Seasonal patterns of *Rhagoletis completa* catches in Pherocon AM traps in abandoned walnut trees, in the Willamette Valley, OR 1990-92.

YEAR	NO. OF AM TRAPS	DATE OF FLY CATCH			TFD	FLIES TRAPPED			FLIES/ TRAP
		FIRST	PEAK	LAST		MALES	FEMALES	TOTAL	
1990	4	7/11	8/27	10/01	82	874	948	1823	456
1991	8	7/17	9/04	10/09	86	1931	1972	3903	488
1992	8	7/01	8/10	09/11	75	1817	1791	3608	451
MEAN		7/09	8/23	09/25	81	1541	1570	3111	465

TFD =Total flight duration

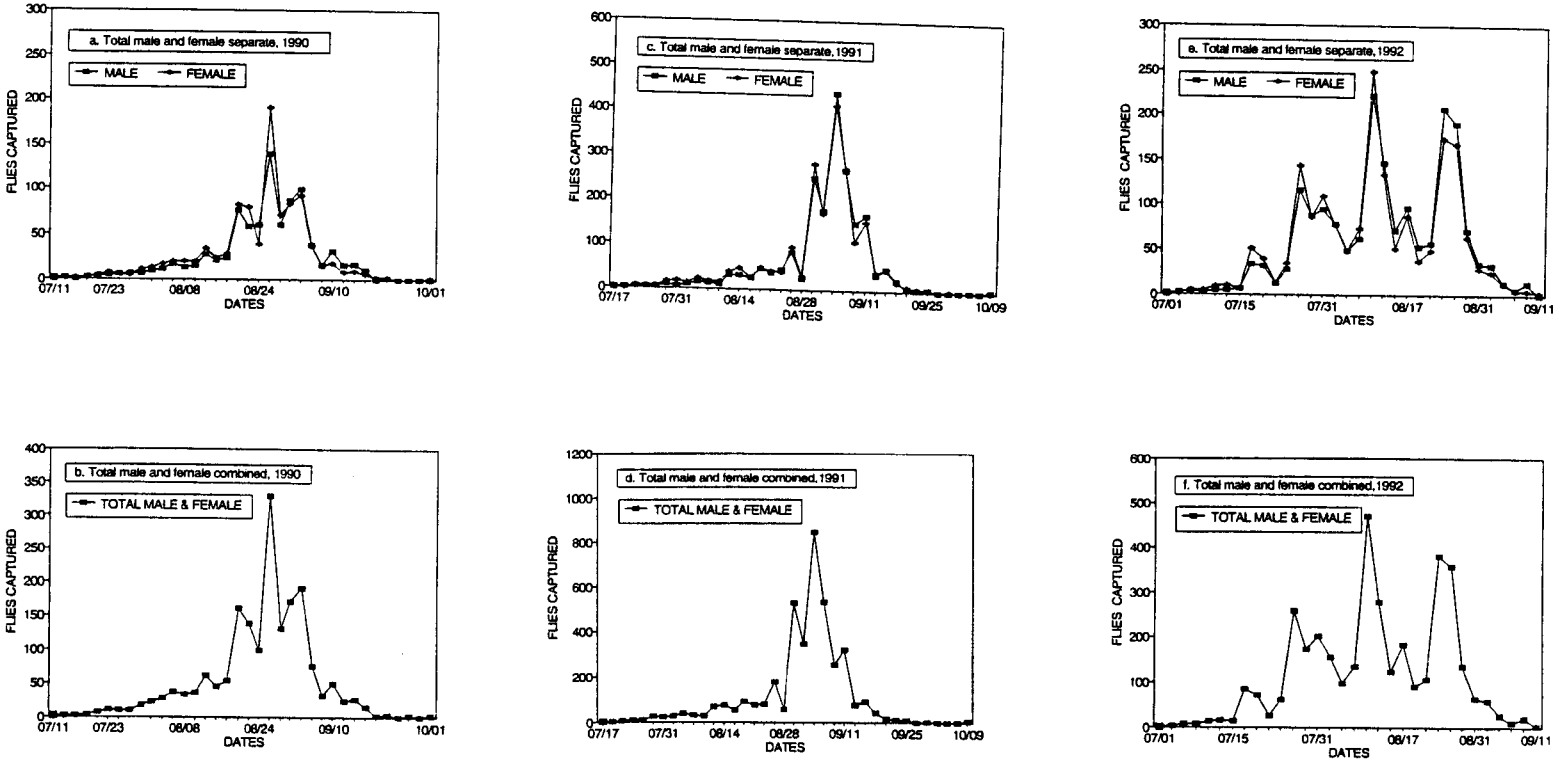

Figure IV-1. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female separate and combined) in the Willamette Valley, OR 1990-92 [abandoned walnut trees].

on a seasonal basis. The average date of first fly catch for the 3-year study period was Julian day 190, the peak catch 235, and last catch was 268. There was a remarkable degree of consistency in the time of fly catch during the three years of study (191±12 Julian day) (x±SD). Also there was good consistency in the number of flies trapped per trap (465±20) (x±SD) showing the high adult population in the field.

The quadrant differences in trap catches were investigated. South quadrants had the earliest capture, followed by east, west, and north quadrants. In 1990, the first flies were captured on July 11 in the south quadrant, followed by July 13 in the east, July 18 in the west and north quadrants. Fly catch gradually increased until a seasonal peak was reached on August 27 in all quadrants, then gradually decreased and terminated on September 21 in all but the north quadrant, where last flies were trapped on October 1 (Table IV-2, Figure IV-2&3).

In 1991, the first fly was trapped in the east quadrants on July 17 followed by July 19 in the north, on July 22 in the east and west quadrants. The fly catch gradually increased until a seasonal peak was reached on September 9 in all quadrants. The fly catches terminated on September 25 in the east, on September 30 in the north

Table IV-2. Quadrant wise seasonal patterns of *Rhagoletis completa* catches in Pherocon AM traps in abandoned walnut trees in the Willamette Valley, OR 1990-92.

YEAR	QUADRANT	DATE OF FLY CATCH			% FLIES TRAPPED
		FIRST	PEAK	LAST	
1990	EAST	7/13	8/27	9/21	25.5
	WEST	7/18	8/27	9/21	24.7
	NORTH	7/18	8/27	10/01	24.5
	SOUTH	7/11	8/27	9/21	25.3
1991	EAST	7/22	9/04	9/25	24.4
	WEST	7/22	9/04	10/09	24.8
	NORTH	7/19	9/04	9/30	25.3
	SOUTH	7/17	9/04	10/09	25.5
1992	EAST	7/03	8/10	9/09	25.8
	WEST	7/01	8/12	9/09	24.8
	NORTH	7/08	8/10	9/11	23.5
	SOUTH	7/03	8/10	9/11	25.9

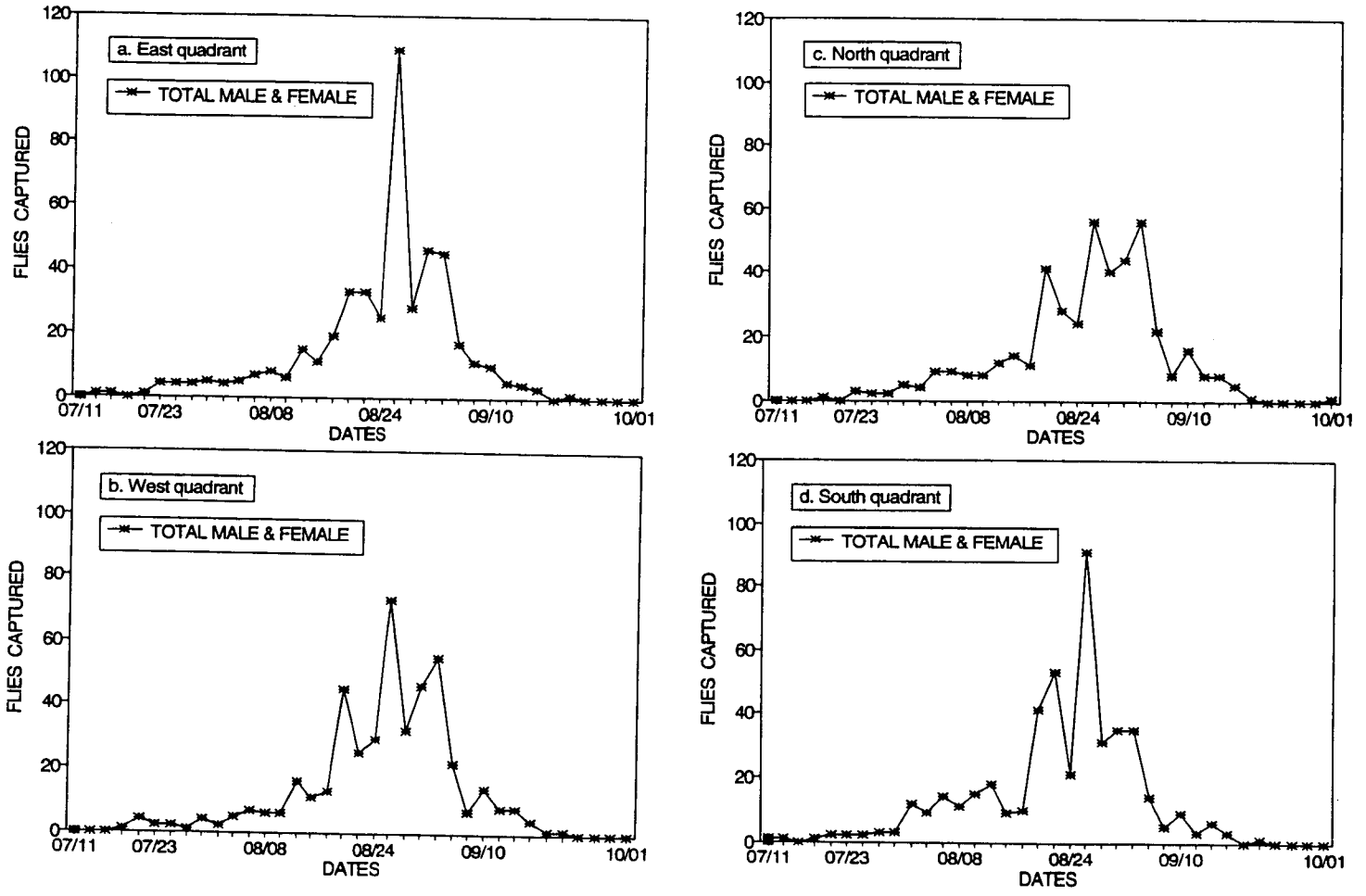

Figure IV-2. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female combined) in different quadrants under walnut trees in the Willamette Valley, OR 1990 [abandoned walnut trees].

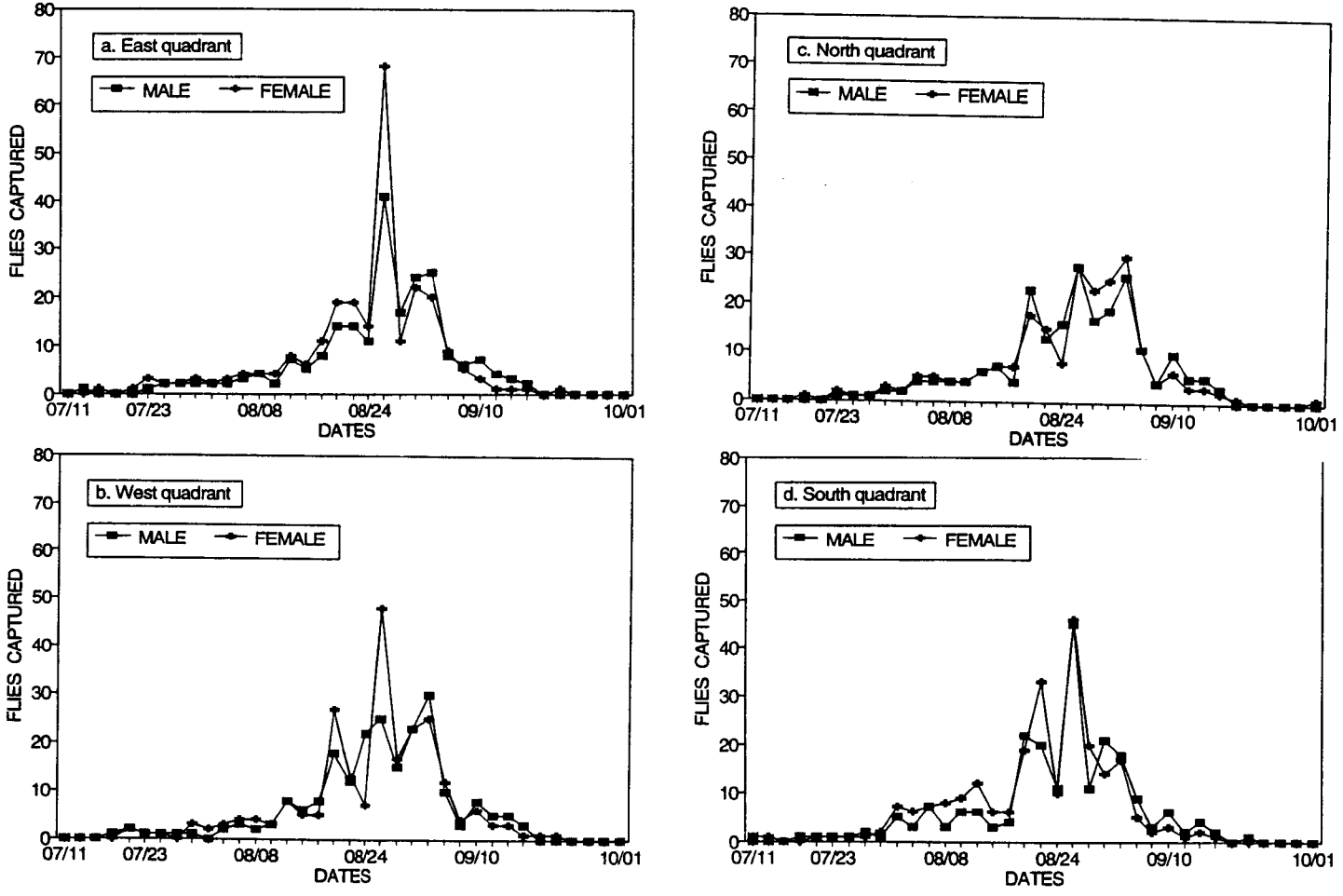

Figure IV-3. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female separate) in different quadrants under walnut trees in the Willamette Valley, OR 1990 [abandoned walnut trees].

and on October 9 in the west and south quadrants (Table IV-2, Figure IV-4&5).

In 1992, the first flies were trapped on July 1 in the west quadrant, on July 3 in the east and south and on July 8 in the north quadrant. The fly catch gradually increased with a seasonal peak on August 10 in east, north, and south quadrants and on August 12 in west quadrants. The fly catch gradually decreased and terminated on September 9 in east and west quadrants, and on September 11 in north and south quadrants (Table IV-2, Figure IV-6&7).

The flies were trapped in all four quadrants beneath the individual trees. No distinct pattern emerged which would suggest flies congregate in any given side of the tree and/ or get trapped in higher number. However, there was some difference in the date of first fly catches. Generally speaking, the earliest activity was seen in the south and the east side, while the north side was last. Fly catch varied from 23 to 26% in various quadrants (Table IV-2). In a closely related fruit fly, *R. pomonella*, Oatman (1964) reported no significant difference in adult activity from different tree quadrants in Wisconsin.

In commercial walnut orchard No. 1 during 1991, the first fly was trapped on August 5, fly catches increased

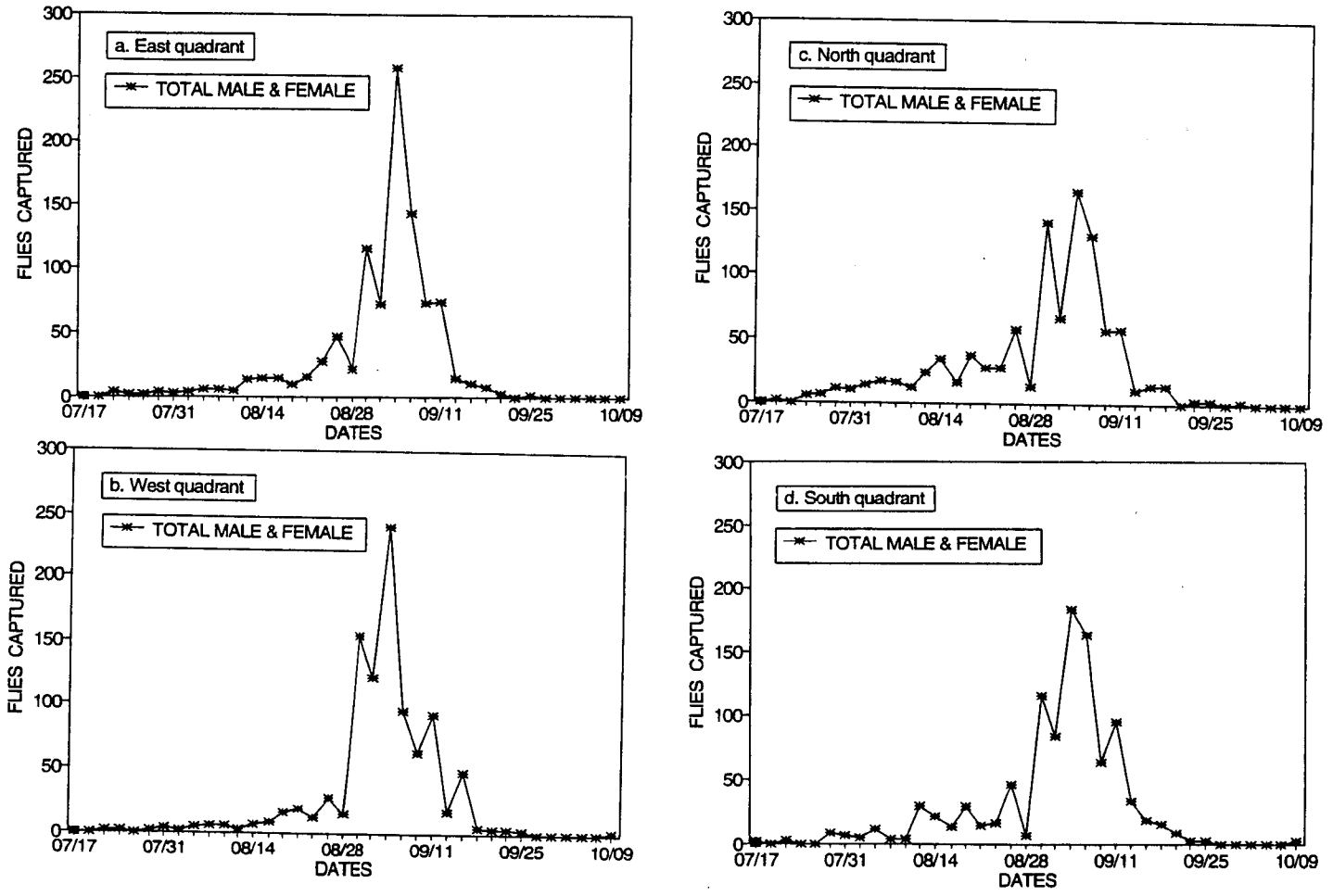

Figure IV-4. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female combined) in different quadrants under walnut trees in the Willamette Valley, OR 1991 [abandoned walnut trees].

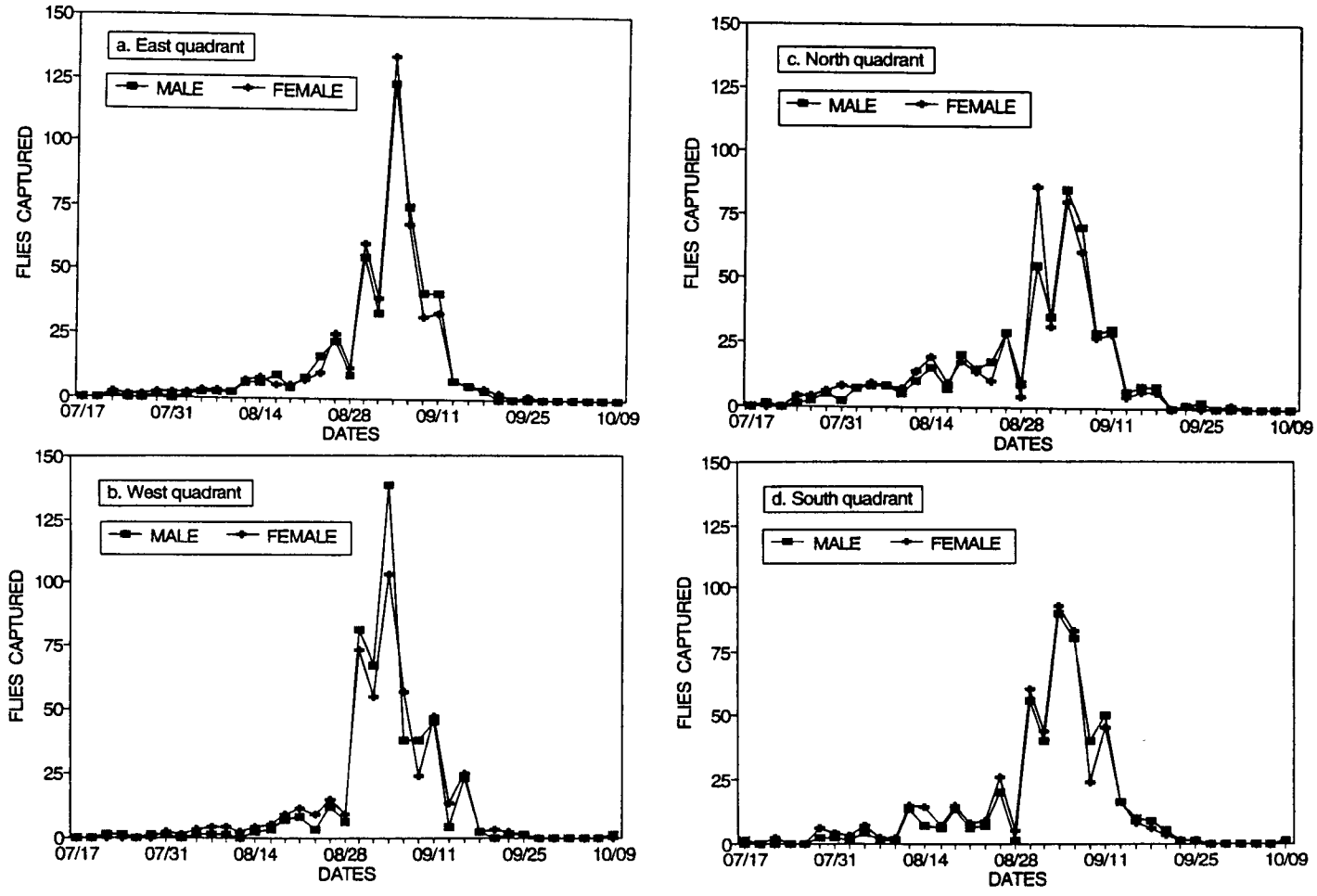

Figure IV-5. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female separate) in different quadrants under walnut trees in the Willamette Valley, OR 1991 [abandoned walnut trees].

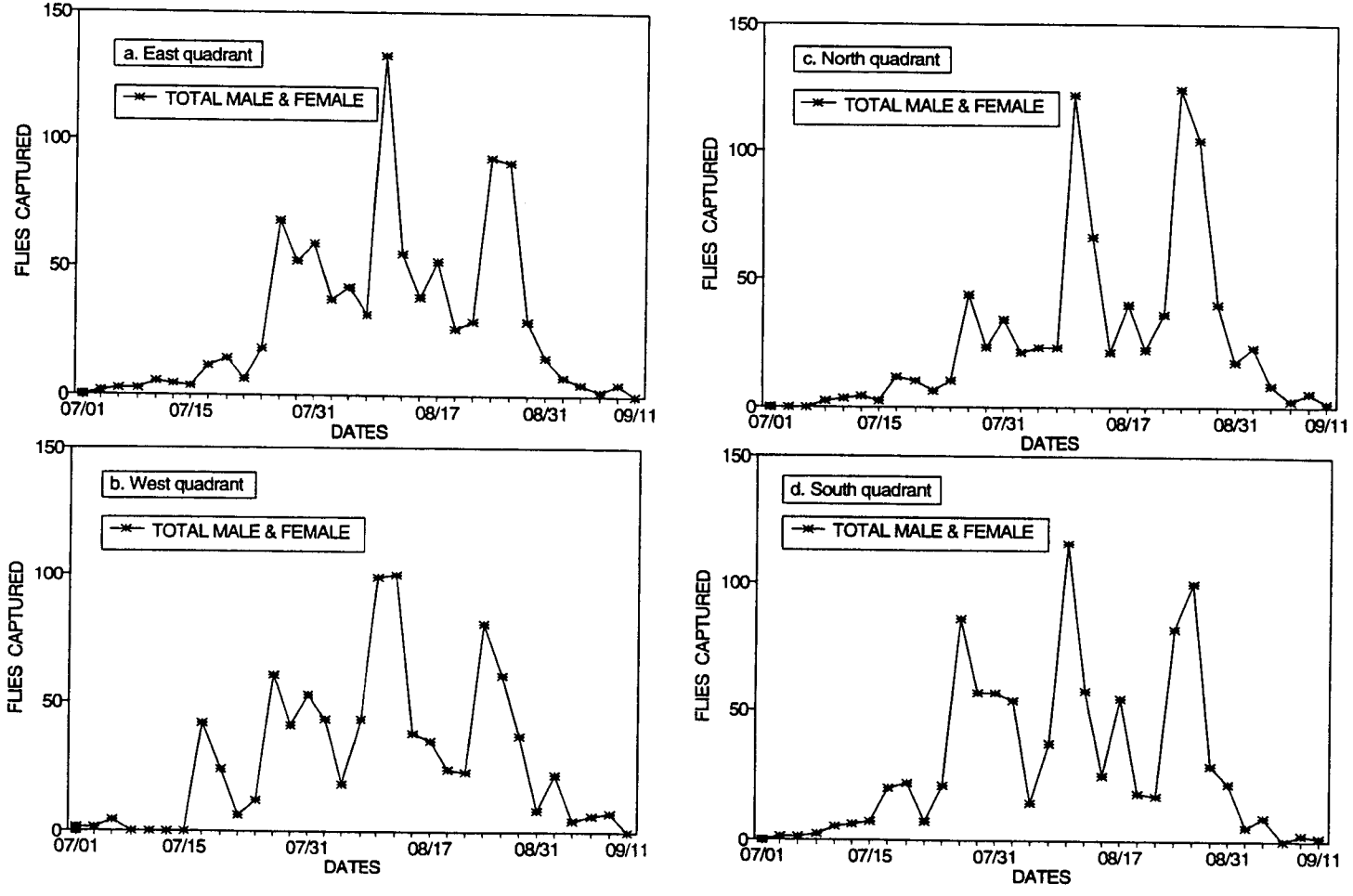

Figure IV-6. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female combined) in different quadrants under walnut trees in the Willamette Valley, OR 1992 [abandoned walnut trees].

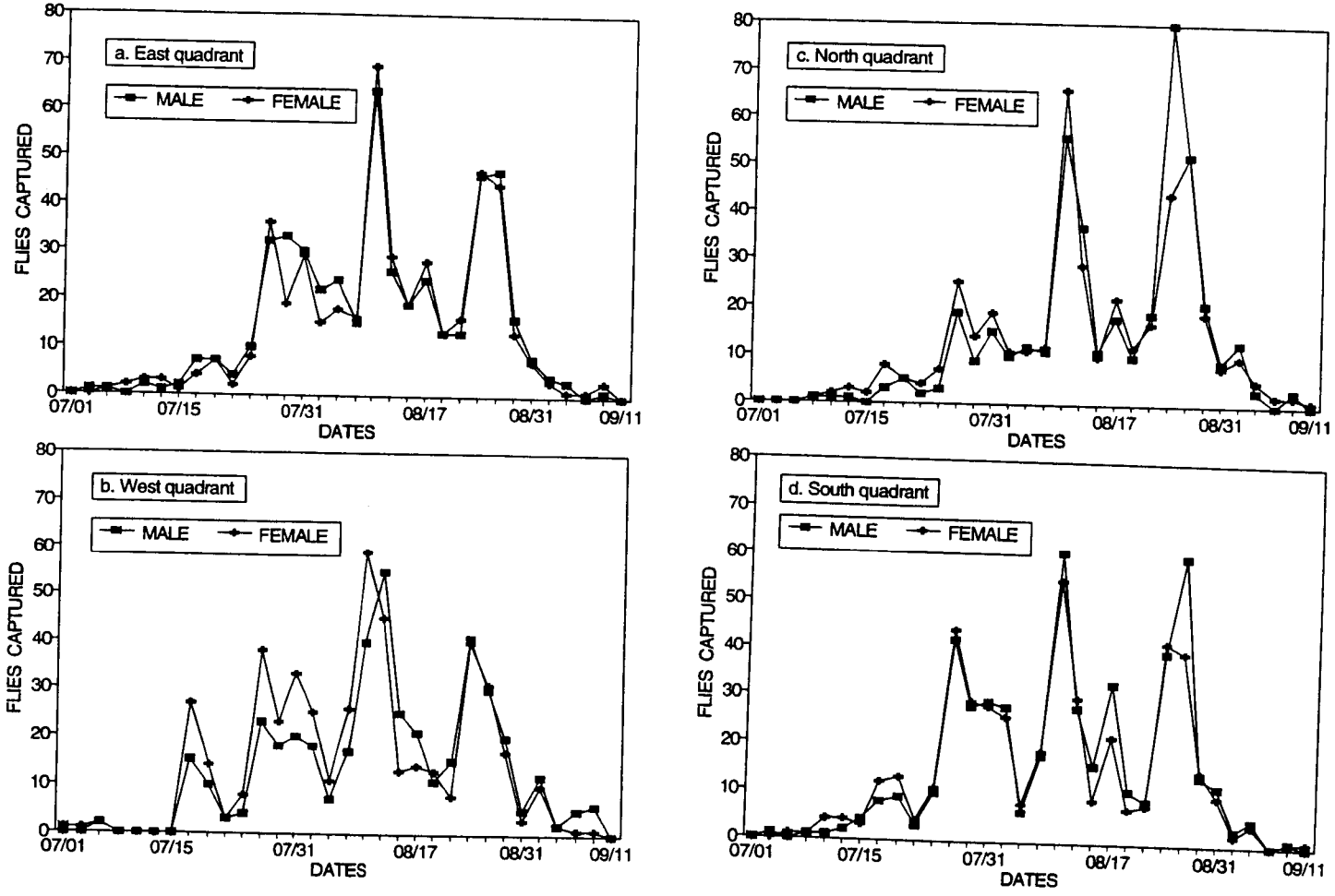

Figure IV-7. Seasonal patterns of flight activity of *Rhagoletis completa* (male and female separate) in different quadrants under walnut trees in the Willamette Valley, OR 1992 [abandoned walnut trees].

Table IV-3. Seasonal patterns of *Rhagoletis completa* catches in Pherocon AM traps in commercial walnut orchards in the Willamette Valley, OR 1991-92.

	DATE OF FLY CATCH						FLIES CAPTURED			
YEAR	FIRST	PEAK	LAST	DATE FIRST MATURE FLY	TFD	DATE LAST IMMATURE FLY	MALES	FEMALES	TOT #	FLIES/ TRAP
Orchard #1										
1991	8/05	9/09	9/23	8/12	49	8/26	108	114	222	111
1992	7/13	8/31	9/14	7/27	63	8/24	343	343	685	342
Orchard #2										
1991	8/05	9/02	9/30	8/19	56	9/02	202	212	414	207
1992	7/13	8/31	9/14	7/27	63	8/17	310	301	611	305

TFD= Total flight duration

with time, a seasonal peak was observed on September 9 and catches terminated on September 23 (Table IV-3, Figure IV-8). Insecticide (Asana) was applied on August 26 to suppress the increasing fly population. The insecticide spray reduced the fly population because a substantially lower fly catch was observed in orchard No. 1 than the orchard No. 2. Total flight activity in orchard No. 1 lasted for 49 days. The sex ratio was close to 1:1, 48.6% male to 51.4% female on a seasonal basis. During 1992, the first fly activity was earlier; the first fly was trapped on July 13, with a seasonal peak on August 31, and no flies were caught after September 14 (Table IV-3, Figure IV-8). The orchard was sprayed on August 26, regardless of three weeks earlier first fly emergence. Perusal of Figure IV-8, reveals that the spray coincided with the peak fly population, and consequently, caused a slight decline in fly catches. Total fly capture in two orchards indicated that sprays of Asana (a synthetic pyrethroid insecticide) had relatively little impact on trap catches (Table IV-3). This may attributed to the efficacy of traps which attracted newly emerged flies before they had a chance to sit on foliage and be exposed to pesticides. No indication of development of resistance in WHF to Asana has been reported. The total flight period during 1992 was 63 days. The sex ratio was close to 1:1, 50.1% male to 49.9% female

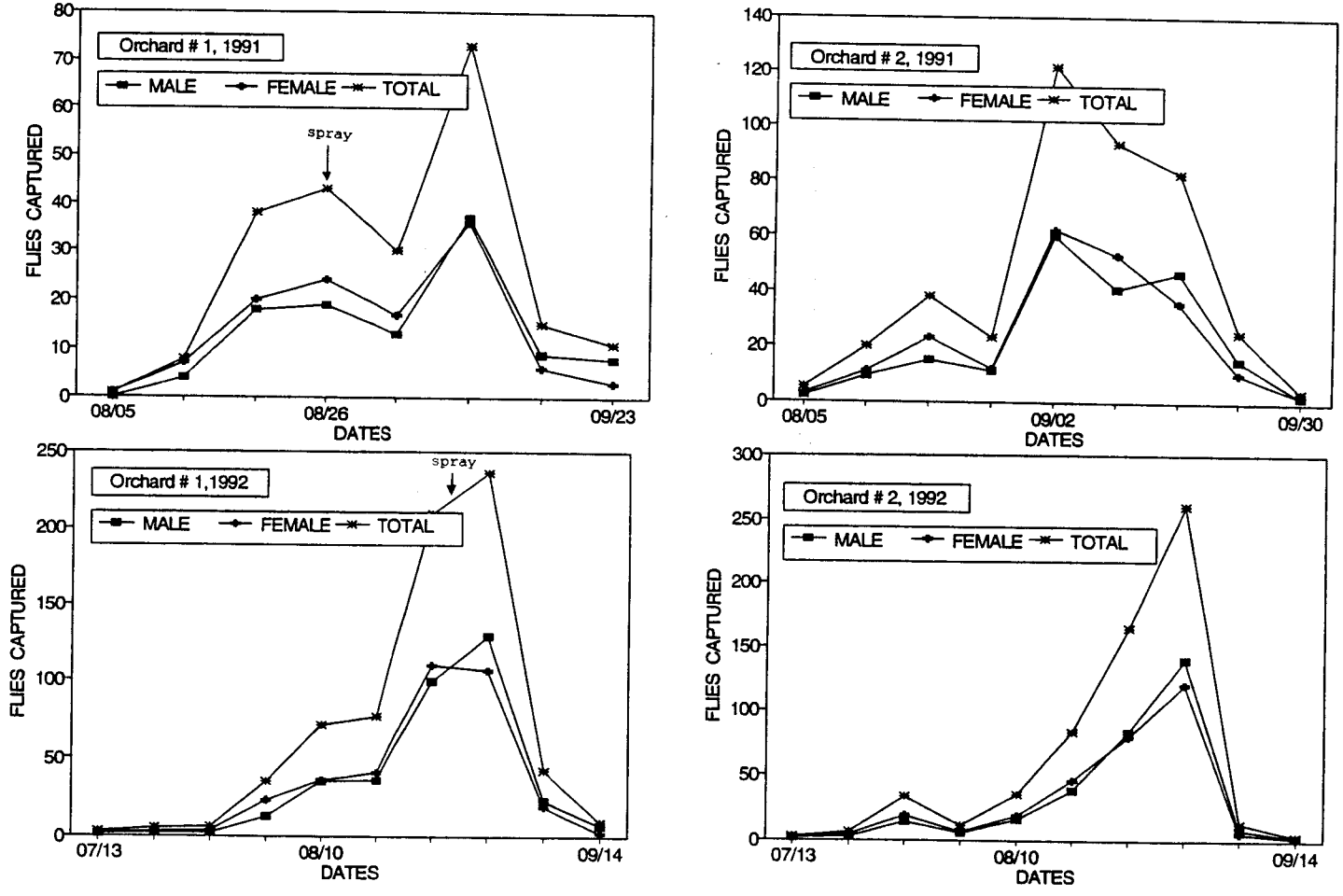

Figure IV-8. Seasonal patterns of flight activity of *Rhagoletis completa* in the Willamette Valley, OR [commercial walnut orchards].

on seasonal basis.

In commercial orchard No. 2 during 1991, the first fly was trapped on August 5, catches peaked on September 2, decreased and terminated on September 30 (Table IV-3, Figure IV-8). The total flight period was 56 days, the sex ratio was close to 1:1, 48.8% male to 51.2% female on a seasonal basis. In 1992, the first fly was trapped on July 13, a seasonal peak occurred on August 31, then gradually declined and the catches terminated on September 14 (Table IV-3, Figure IV-8). A total flight period was 63 days, and the sex ratio was 1:1 on a seasonal basis.

A difference of 15 days in 1992, and 19 days in 1991 was observed in trapping first fly in commercial walnut orchards (Junction City) as compared to unsprayed backyard trees (Corvallis). Jones et al. (1989) reported that the apple maggot populations emerged 5 weeks apart in different regions in Utah. AliNiazee and Fisher (1985) reported that the first walnut husk flies of the season are usually trapped in early August in the Willamette Valley. The emergence varies among orchards within a given area and in various locations within a single orchard. In *R. pomonella*, this has been illustrated by the large variations in first emergence recorded among adjacent cages in the same orchard (Glass 1960, Dean and Chapman 1973). Physical factors such as the depth at which the

pupae overwinter, slope, soil type, soil cover, planting density, and genetic factors are probably responsible for this spread of emergence. Variation in adult emergence also may be an evolutionary adaptation for survival because food and mate availability may not be present throughout the life span of these insects.

The time of capture of the WHF in ground emergence cages during 1991 and 1992 (see Chapter III) coincided with the time of their capture in aerial traps. In 1991, the first emergence occurred on the same day as first capture in the aerial traps and in 1992, first emergence was 2 days earlier. In 1991, the number of flies that emerged in ground emergence cages (16 cages) represented about 4% of the total number of flies captured in aerial traps (8 traps), while in 1992 these numbers were about 1.6%. Last emergence was on September 11 in 1991, when 94% of the flies had been captured in aerial traps, and in 1992, the last emergence in ground cages was on August 17 (see Chapter III) when about 66% of the flies had been trapped in aerial traps.

A close relationship existed between first fly emergence in ground emergence cages and first fly catch in the Pherocon AM traps. This close agreement supports the conclusion of Trottier et al. (1975) and Laing and Heraty (1984) that trap catch is a good predictor of apple maggot

emergence. Frick (1952) and Frick et al. (1954) have shown that trap catch also is a good predictor of *R. indifference* emergence and oviposition activity. Based on my results, I believe that Pherocon AM aerial traps are sufficiently reliable to detect fly emergence and can play a useful role in managing this pest. Similar results were reported by workers for other fruit fly species (Maxwell and Parsons 1969, AliNiazee 1979). Recently, Yokoyama et al. (1992) found Pherocon AM traps baited with ammonium carbonate were more effective than ground emergence cages to determine first husk fly emergence.

Catches in AM traps continued for at least 1 month past the end of fly emergence in ground emergence cages suggesting that WHF adults live for at least 1 month under field conditions. An analysis of the rainfall pattern during summer months and the aerial trap data failed to establish any relationship between trap catches and either the amount or pattern of rainfall (IV-9). It appears that unlike the apple maggot, where rainfall may cause flushes of fly emergence (Dean and Chapman 1973, Jones et al. 1989), no such phenomenon occurs in WHF. The evolutionary adaptation may have something to do with this because the WHF seems to be a subtropical species and is perhaps better adapted to drier climate.

The first sexually mature female was trapped on July

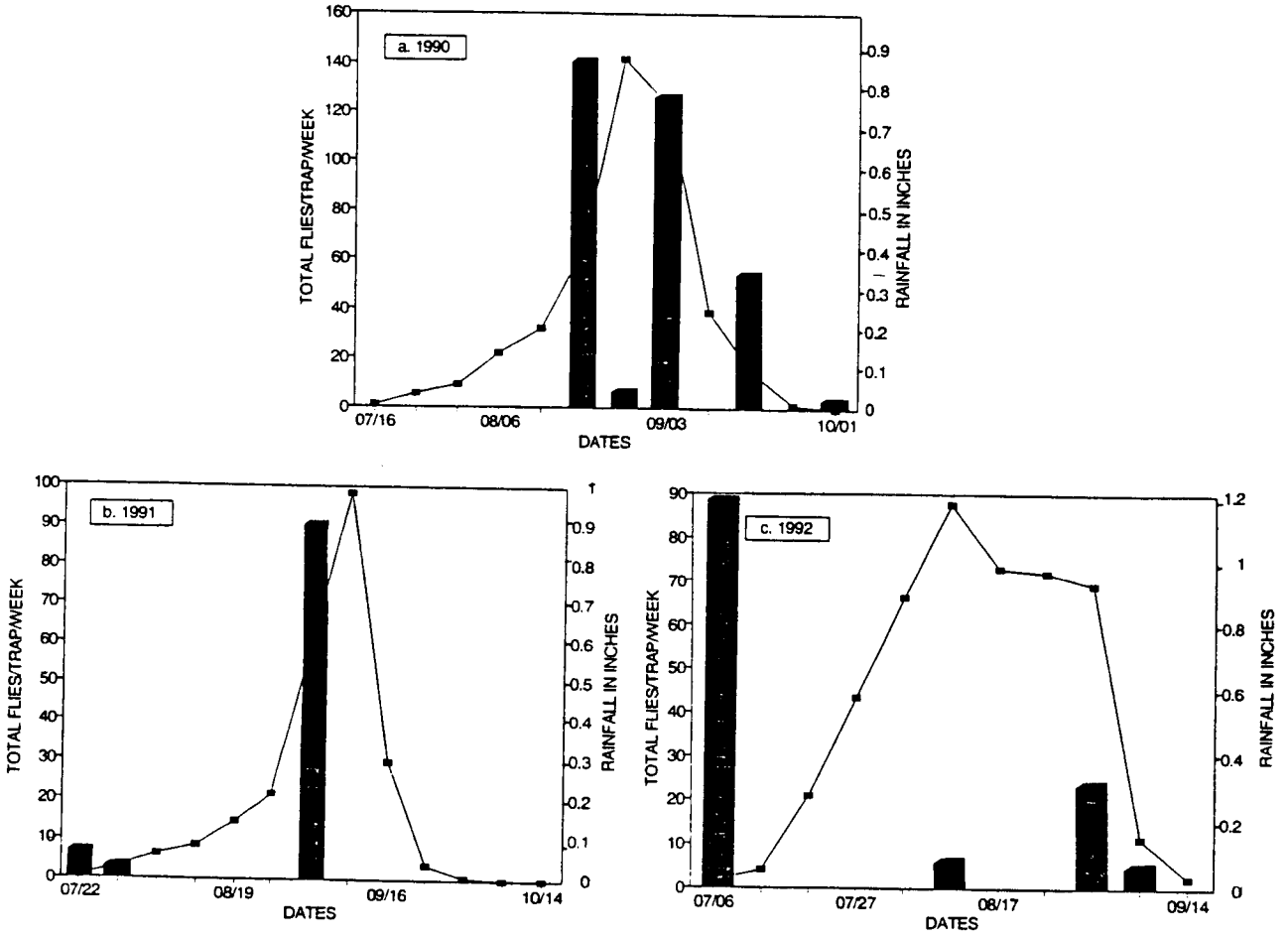

Figure IV-9. The influence of rainfall on flight activity of *R. completa* in the Willamette Valley, OR 1990-92.

Table IV-4. Seasonal fluctuation of *Rhagoletis completa* sexually immature and mature females captured in Pherocon AM traps in abandoned walnut trees in the Willamette Valley, OR 1990-92.

YEAR	NO. OF TRAPS	% IMMATURE FEMALES	% MATURE FEMALES	LAST IMMATURE FEMALES	TOTAL FEMALES	FLIES/ TRAP
1990	4	10.9	89.1	9/10	849	212
1991	8	8.2	91.8	9/16	1972	246
1992	8	20.0	80.0	8/17	1791	224

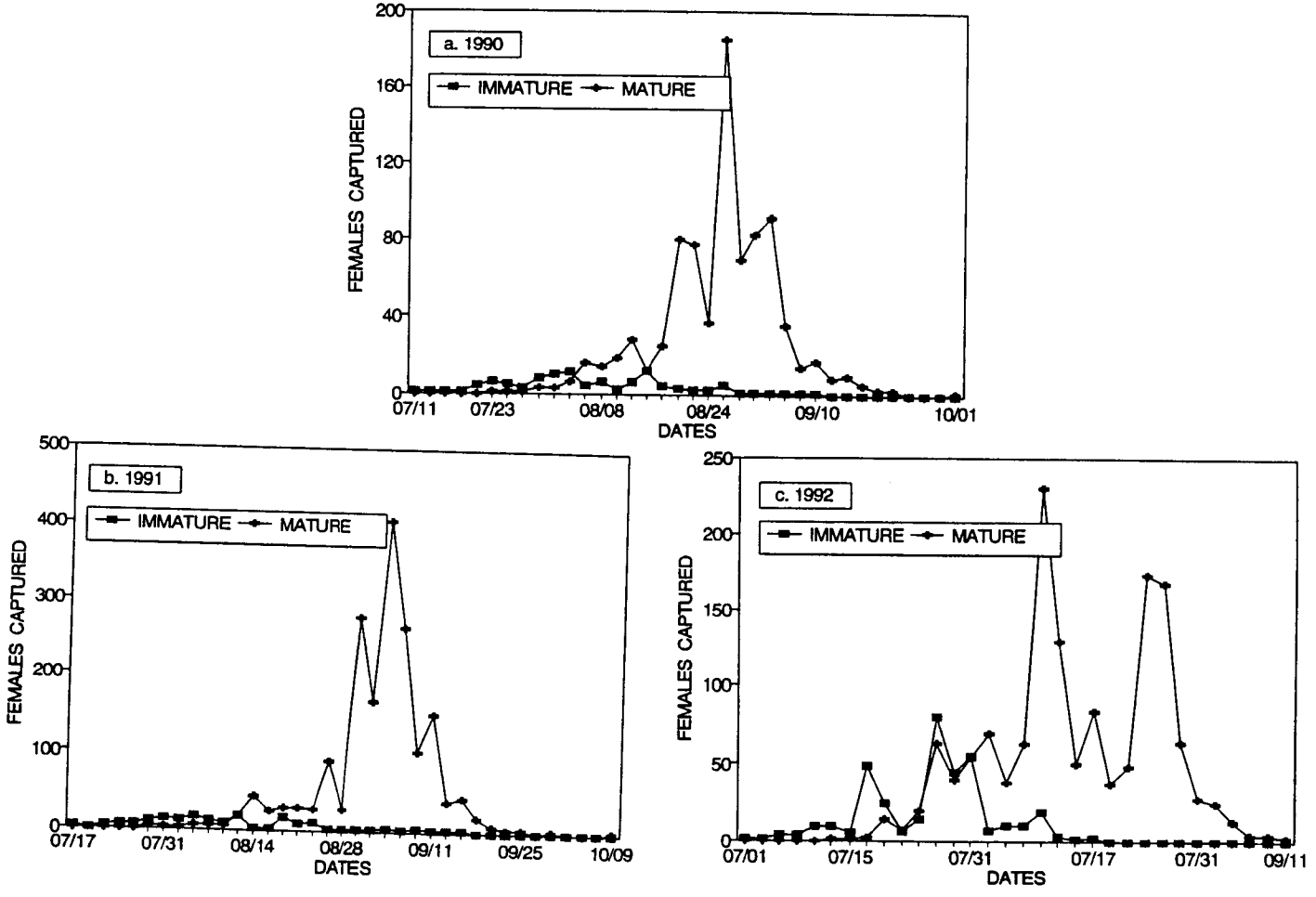

Figure IV-10. Seasonal fluctuation of immature and mature females of *Rhagoletis completa* in the Willamette Valley, OR [abandoned walnut orchards].

23 in 1990, on July 29 in 1991, and July 13 in 1992. The peak activity of sexually mature females was noticed on August 27 in 1990, on September 5 in 1991, and on August 10 in 1992. The last sexually immature female was trapped on September 10 in 1990, September 16 in 1991, and August 17 in 1992 in Corvallis, Oregon (Table IV-4, Figure IV-10). My data suggest that aerial traps were effective in trapping both mature and immature flies. As season progressed, the propensity of mature females increased. The appearance of mature flies in the field has an important bearing on control of this insect. Once it is known that the females have attained sexual maturity under field conditions, the oviposition event can be monitored better and more accurate prediction can be made by using this information. In aerial traps, the lag time between the capture of last sexually immature flies and capture of the last flies of the season was 21 days in 1990, 23 days in 1991, and 25 days in 1992. The absence of immature females in aerial traps toward the end of the season may indicate the absence of a partial second generation, and it also may reflect the fact that ground emergence cage information (Chapter III) is a good estimator of the time required for emergence under field conditions.

Out of a total of 849 females trapped, only 10.8% were sexually immature in 1990, out of a total of 1972,

Table IV-5. Seasonal fluctuation of *Rhagoletis completa* sexually immature and mature females captured in Pherocon AM traps in commercial walnut orchards in the Willamette Valley, OR 1991-92.

YEAR	% IMMATURE FEMALES	% MATURE FEMALES	LAST IMMATURE FEMALES	TOTAL FEMALES	FEMALES/ TRAP
Orchard # 1.					
1991	19.3	80.7	8/26	114	57
1992	10.2	90.7	8/24	342	171
Orchard # 2.					
1991	16.5	83.5	9/02	212	106
1992	9.0	91.0	8/17	301	150

only 8.2% were sexually immature in 1991, and out of 1791, about 20% were sexually immature in 1992 (Table IV-4). This suggests that a relatively small proportion (13-14%) of trapped females were sexually immature.

In commercial walnut orchard No. 1, the first sexually mature female fly was trapped on August 12 in 1991, and July 27 in 1992. In orchard No. 2, the first sexually mature female fly was trapped on August 19 in 1991, and July 27 in 1992 in Junction City, Oregon. The last immature female fly was trapped in orchard No. 1 on August 26 in 1991, on August 24 in 1992, and in orchard No. 2, on September 2 in 1991, on August 17 in 1992 (Figure IV-11). This indicates relatively little difference in the sexual maturity pattern between the abandoned trees and commercial orchards indicating the temperature is the key factor in the maturation process.

In orchard No. 1, the percentages of sexually immature females among the total flies trapped ranged from 19.3% in 1991 to about 10% in 1992. In general, the number of sexually immature females was about 14% (range 10-19%) (Table IV-5) In orchard No. 1, out of 114 females, only 19.3% were sexually immature in 1991, out of 342 females, only 10.2% were sexually immature in 1992. In orchard No. 2, out of 212 females, only 16.5% were sexually immature in 1991, and out of 301 females, only 9% were sexually

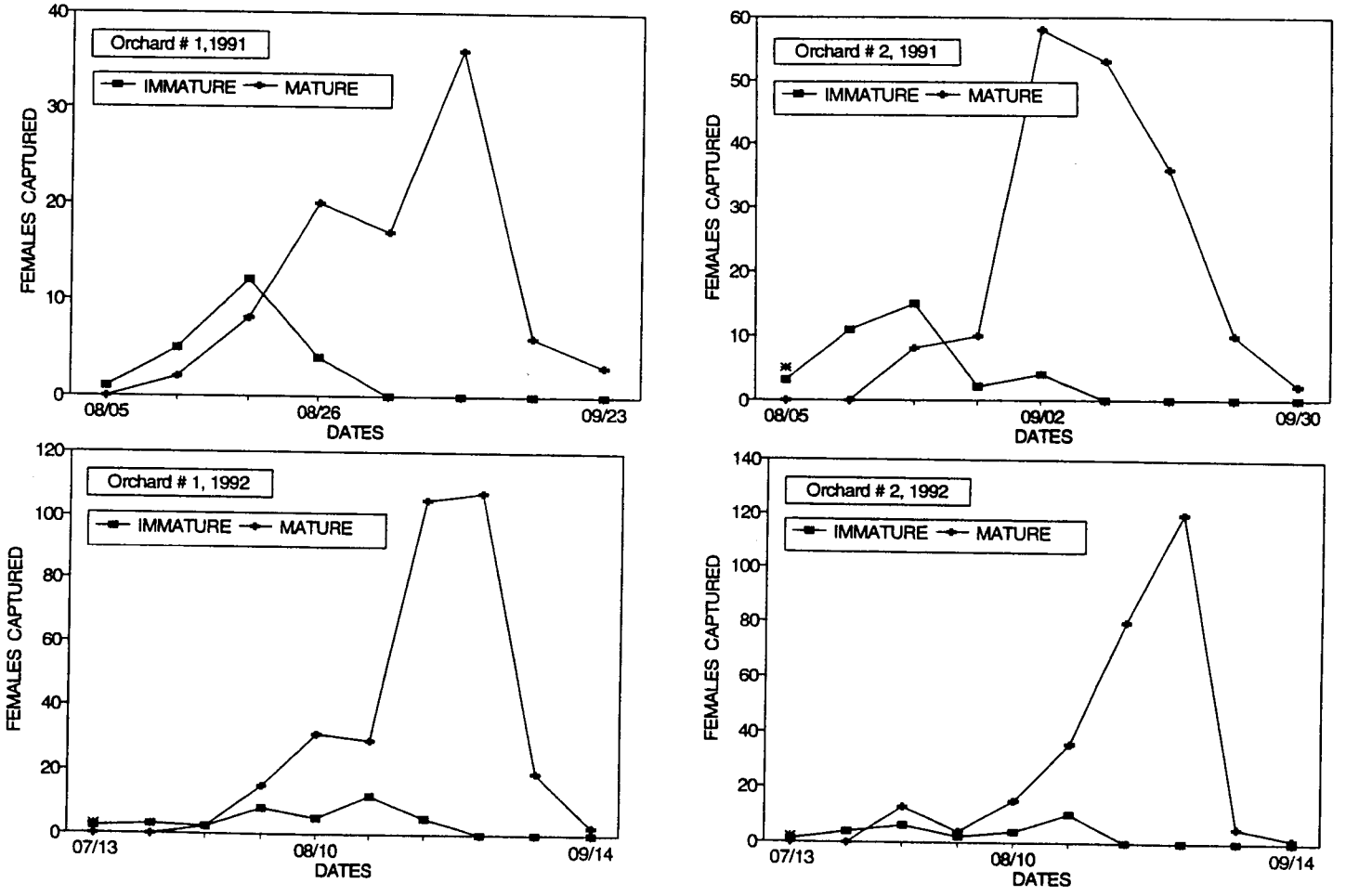

Figure IV-11. Seasonal fluctuation of immature and mature females of *Rhagoletis completa* in the Willamette Valley, OR [commercial walnut orchards].

immature in 1992 with an average of 13% (range 9-17%) (Table IV-5).

In commercial orchards, the dates of first fly catches and first mature female fly catch in aerial traps is not precise, since data were recorded once a week. The lag time between first fly catch and first sexually mature female catch in traps was 7 days in 1991 and 14 day in 1992 in orchard No. 1, while the corresponding lag time was 14 days in 1991 and 1992 in orchard No. 2. Similar lag time also was noticed in abandoned trees. Again, a careful review of these data suggest the absence of a partial second generation has been suspected by some workers. Data in Table IV-3 show that the lag between capture of the last immature female and the last capture of the season in aerial traps was 28 and 21 days in 1991 and 1992, respectively, for orchard No. 1, while the corresponding lag times for orchard No. 2 were 28 days for both 1991 and 1992 seasons. This suggests nearly a month of field longevity time for this insect under Willamette Valley conditions. The oviposition data given in Chapter III also supports this assumption.

In summary, the aerial traps (Pherocon AM) are a good indicator of WHF emergence both in abandoned walnut trees and in commercial orchards. The fly catches in traps started in abandoned trees from July 1 through July 17,

with an average time to first emergence of July 9, and in commercial orchards, the fly emergence varied from July 13 through August 5, with an average time of first emergence on July 23. The adult flight was not influenced by rainfall and was largely determined by the prevailing temperatures. Adult female dissection showed twelve days of lag time between the first emergence and appearance of eggs in the ovaries. Similarly, the mature flies were caught for nearly one month after the immature flies were last detected in the field. There appeared to be no indication for a partial second generation in this insect in western Oregon.

REFERENCES

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette Valley of Oregon. Environ. Entomol. 5:397-402.

AliNiazee, M. T. 1978. The western cherry fruit fly, *Rhagoletis indifferens* (Diptera: Tephritidae). 3. Developing a management program by utilizing attractant traps as monitoring devices. Can. Entomol. 110: 1133-1139.

AliNiazee, M. T. 1979. A computerized phenology model for predicting biological events of *Rhagoletis indifferens* (Diptera: Tephritidae). Can. Entomol. 111: 1101-1109.

AliNiazee, M. T. and G. Fisher. 1985. The walnut husk fly in Oregon *Rhagoletis completa*, pests of walnuts. Fact sheet, OSU Extension Service, Corvallis, Oregon.

AliNiazee, M. T. and R. L. Westcott. 1987. Flight period and seasonal development of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), in Oregon. Ann. Entomol. Soc. Am. 80(6): 823-827.

Anonymous. 1982. Integrated Pest Management for Walnuts. Univ. of Calif. Div. Agric. Sci. Publ. 3270, Berkeley, CA. 96 pp.

Boyce, A. M. 1934. Bionomics of the walnut husk fly, *Rhagoletis completa* Cresson. Hilgardia. 8: 363-579.

Dean, R. W. and P. J. Chapman. 1973. Bionomics of the apple maggot in eastern New York. Search Agric. (Geneva, N. Y.) 3: 1-62.

Frick, K. E. 1952. Determining emergence of the cherry fruit fly with ammonium carbonate bait traps. J. Econ. Entomol. 45: 262-263.

Frick, K. E., H. G. Simkover, and H. S. Telford. 1954. Bionomics of the cherry fruit flies in eastern Washington. Tech. Bull. Wash. Agric. Expt. Stn. No. 13.

Gibson, K. E. and W. H. Kearby. 1978. Seasonal life history of the walnut husk fly [*Rhagoletis completa*] and husk maggot [*Rhagoletis suavis*] in Missouri. Environ. Entomol. 7(1): 81-87.

Glass, E. H. 1960. Apple maggot fly emergence in western New York. N.Y. St. Agric. Expt. Stn. Bull. 789. 29 pp.

Jones, V. P., D. G. Alston, J. F. Brunner, D. W. Davis, and M. D. Shelton. 1991. Phenology of the western cherry fruit fly (Diptera: Tephritidae) in Utah and Washington. Ann. Entomol. Soc. Am. 84: 488-492.

Jones, V. P., D. W. Davis, S. L. Smith, and D. B. Allred. 1989. Phenology of the apple maggot associated with cherry and hawthorn in Utah. J. Econ. Entomol. 82: 788-792.

Laing, J. E., and J. M. Heraty. 1984. The use of degree days to predict emergence of apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae) in Ontario. Can. Entomol. 116: 1123-1129.

Maxwell, C. W. and. C. Parsons. 1969. Relationships between hour-degree F soil temperature summations and apple maggot adult emergence. J. Econ. Entomol. 62: 1310-1313.

Moffitt, H. R. 1958. Rapid determination of sex in *Rhagoletis completa* Cresson. J. Econ. Entomol. Washington D.C.: Entomol. Soc. of America. 51: 551.

Oatman, E. R. 1964. Apple maggot emergence and seasonal activity in Wisconsin. J. Econ. Entomol. 57: 676-679.

Prokopy, R. J. 1975. Selective new trap for *Rhagoletis cingulata* and *R. pomonella* flies. Environ. Entomol. 4: 420-424.

Riedl, H. and S. A. Hoying. 1980. Seasonal patterns of emergence, flight activity, and oviposition of the walnut husk fly in northern California. Environ. Entomol. 9:567-571.

Trottier, R., J. Rivard and W. T. A. Neilson. 1975. Baits traps for monitoring apple maggot activity and their use for timing control sprays. Can. Entomol. 68: 211-13.

Yokoyama, V. Y., G. T. Miller, P. L. Hartsell. 1992. Pest-free period and methyl bromide fumigation for control of walnut husk fly (Diptera: Tephritidae) in stone fruits exported to New Zealand. J. Econ. Entomol. 85: 150-156.

CHAPTER V

A PHENOLOGY MODEL FOR PREDICTING BIOLOGICAL EVENTS OF *RHAGOLETIS COMPLETA* CRESSON (DIPTERA: TEPHRITIDAE)

ABSTRACT

Data from a 3-year (1990-92) field study of the walnut husk fly, *Rhagoletis completa* Cresson, in the Willamette Valley, Oregon indicated that various biological events such as adult emergence, female sexual maturity, oviposition, larval development and pupation commence with the accumulation of a certain number of heat units. Soil surface temperature appeared to be a slightly better predictor of various biological events than air and underground temperatures. Based on a thermal summation scheme using surface temperature data and a lower developmental temperature threshold of 5°C and no upper threshold, the first flies in aerial traps (Pherocon AM traps) were detected at an average of 1160 TU, first mature females at 1358 TU, first oviposition at 1512 TU, 10% fly emergence at 1661 TU, 50% fly emergence at 1912 TU, and 90% fly emergence at 2065 TU. March 1 was the most effective date for initiating the thermal unit summation model. More accurate prediction of various biological events were made by using a heat summation approach than calendar date.

INTRODUCTION

The principle of using temperature and time to describe development of many organisms was recognized as long ago as the middle of the 18th century (Wilson and Barnett 1983). Temperature greatly affects developmental rates of insects, which in turn influences their seasonal occurrence and population dynamics (Andrewartha & Birch 1954, Ratte 1984). The role of the physical environment including temperature, photoperiod, rainfall, and humidity in insect growth and development has been illustrated by many workers (Lathrop and Dirks 1944 & 1945, Boller 1964, Eckenorde and Chapman 1972, AliNiazee 1976 & 1979, Brown and AliNiazee 1977). Temperature-dependent models predicting pest occurrence have become the basis of many agricultural pest management programs (Bateman 1972, AliNiazee 1976, Obrycki and Tauber 1978, AliNiazee 1983 & 1986b, Higley et al. 1986).

Day-degree models are widely used in entomology with many applications. These include: the timing of insecticide applications (AliNiazee 1976), crop damage forecasting (Apple 1952), predicting pest development at different localities (Baker and Miller 1978), studies of climatic limits to species distributions (Messenger 1959), and population dynamics studies (Morris and Fulton 1970).

Day-degree models have been developed for various *Rhagoletis* species, including the apple maggot, *Rhagoletis pomonella* (Walsh) (Maxwell and Parsons 1969, Reid and Laing 1976, Reissig et al. 1979, Laing and Heraty 1984, Jones et al. 1989), the western cherry fruit fly, *R. indifferens* (AliNiazee 1976, 1979 and Jones et al. 1991), the black cherry fruit fly, *R. fausta* (Osten Sacken), the eastern cherry fruit fly, *R. cingulata* (Loew) (Jubb and Cox 1974), the European cherry fruit fly, *R. cerasi* L. (Baker and Miller 1978) and the blueberry maggot, *R. mendax* (Tomlinson 1951). These models have been found to be a useful tool for predicting the temperature-dependent development of these Tephritid flies.

The relationship between developmental rate and temperature is approximately linear at intermediate temperatures. Therefore, the day-degree models provide adequate predictions if the temperatures do not fluctuate substantially out of the intermediate temperatures (Stinner et al. 1974). On the other hand, even if the temperatures fluctuate outside of the intermediate range, the errors in developmental rate predictions may be negligible. This is due to the underestimation of development at low temperatures which is compensated by the overestimation of development at high temperatures.

Population monitoring has been the most important

component of *Rhagoletis* management (Stanley et al. 1975, Trottier et al. 1975, Neilson 1976, Reissig and Tette 1979, AliNiazee 1986a, Jones et al. 1989 & 1991). Monitoring generally involves trapping adult flies. Phenology studies have helped predict emergence in *R. pomonella* (Trottier 1975, Reid and Laing 1976, Laing and Heraty 1984, Welch et al. 1978, Reissig et al. 1979), *R. indifferens* (AliNiazee 1976 & 1979, Jones et al. 1991), and *R. mendax* (Tomlinson 1951).

The efficacy of chemical control of insects is greatly influenced by the timing of spray application. If timing is proper then control is optimized. Seasonal growth and development of insects in a geographical region can vary as much as two to three weeks from year to year, depending on climatic conditions, particularly temperature (Wilson and Barnett 1983). The development of a temperature-based phenology model, therefore, could play a useful role in the development of an IPM program for the walnut husk fly (WHF), *Rhagoletis completa* Cresson.

Relatively little data are available dealing with the phenology of WHF. Ground emergence cages have been used for other *Rhagoletis* (AliNiazee 1974), but they are time consuming and inconvenient. Sometimes, these data can be misleading (AliNiazee 1976) as fly emergence varies from locality to locality (Jones et al. 1989). Therefore, in

the current study, I used both ground emergence cages and aerial traps to monitor WHF emergence to construct phenology models based on each of these monitoring methods.

The thermal unit (TU) requirements for various biological events such as adult emergence, preoviposition period, egg hatch, and mature larval exit from husk, and TU requirements for various population emergence levels such as 10%, 50%, etc. under field conditions were determined and are given in this paper.

MATERIALS AND METHODS

The emergence of WHF was monitored by ground emergence cages and Pherocon AM traps as described in Chapter III & IV. Temperature data were obtained from a weather station (OSU, Hyslop Farm) approximately 6 km from the Corvallis study site and at the same elevation. Temperature data collected, included air (42 inch), surface, 2 inch, and 4 inch below ground level. I calculated the thermal units using all temperature data and chose to use surface temperatures in the model. Since the majority of the WHF pupae overwinter in the top 2.5 cm of soil and litter (Gibson and Kearby 1978, Chapter II), the temperature recorded at surface level and 2 inches below soil surface appears to be most appropriate in predicting emergence of the fly.

Thermal units (TU) were calculated by using the method described by Baskerville and Emin (1969) employing sine curve approximation from maximum and minimum temperature beginning March 1, with a lower threshold of 5°C. March 1 was chosen as it gave the least amount of variation and has been used for other temperate climate fruit flies (AliNiazee 1976). No upper threshold was used since the daily maximum temperature rarely exceeded the upper developmental threshold of 34°C for WHF during the

summer months in Willamette Valley. In reality, the high temperature is seldom high enough to cause any lethal or sublethal effect. The lower developmental threshold of 5°C also has been used in earlier models by AliNiazee (1976, 1979) for *R. indifferens* and for *R. cerasi* (Boller 1966). A more recent study by Van Kirk and AliNiazee (1981) indicated that 8.3°C is a more accurate lower developmental threshold for *R. indifferens*, however, 5°C was quite adequate for use in phenology models.

WHF emergence was determined by using ground emergence cages as described in Chapter III. The aerial trapping data were obtained by using Pherocon AM traps as described in Chapter IV. The data on oviposition, post oviposition, egg hatch, larval development, and pupal formation were derived from field observations over a 3-year study period as described in Chapter III. The phenology model as described here was constructed using means from three years for different biological activities and calculating the TU requirements for each of these events. The validation of this model was conducted during the 1993 using a 5% validation envelope as suggested by AliNiazee (1979) for *R. indifferens*.

RESULTS AND DISCUSSION

The seasonal emergence of flies of the genus *Rhagoletis* is influenced by many factors such as temperature, photoperiod, and rainfall (AliNiazee 1976). Many studies have indicated that temperature is the most important factor influencing seasonal emergence of temperate climate fruit flies including the genus *Rhagoletis* (Bateman 1972, Boller and Prokopy 1976, AliNiazee 1988). The temperature fluctuates considerably both in space and time, and a consideration of temperature fluctuation is important in determining adult activity.

The thermal units (TU) required for the first fly emergence in the ground emergence cages and subsequent emergence levels is shown in Table V-1. The first fly emerged at the accumulation of 941 TU (using air temperature), 1062 TU (using surface temperature), 1458 TU (using 2 inch below ground temperature), and 1314 TU (using 4 inch below ground temperature) in 1991, while in 1992 the first fly emerged at the accumulation of 1117 TU (using air temperature), 1211 TU (using surface temperature), 1660 TU (using 2 inch below soil temperature), and 1485 TU (using 4 inch below ground temperature). The accumulation of different TUs at different soil depths was expected and have been

Table V-1. Thermal unit (TU) requirements for the ground emergence of *Rhagoletis completa* in the Willamette Valley OR 1991-92.

	FLY EMERGENCE IN GROUND EMERGENCE CAGES					
	FIRST		PEAK		LAST	
DATE	DATE	TU	DATE	TU	DATE	TU
			AIR TEMPERATURE (42 INCH)			
1991	7/17	941	8/05	1232	9/11	1762
1992	6/29	1117	7/20	1427	8/17	1865
			SURFACE TEMPERATURE			
1991	7/17	1062	8/05	1378	9/11	1944
1992	6/29	1211	7/20	1543	8/17	2004
			2 INCH BELOW GROUND TEMPERATURE			
1991	7/17	1458	8/05	1886	9/11	2631
1992	6/29	1660	7/20	2089	8/17	2707
			4 INCH BELOW GROUND TEMPERATURE			
1991	7/17	1314	8/05	1716	9/11	2423
1992	6/29	1485	7/20	1883	8/17	2458

Thermal unit (TU) were accumulated from March 1 each year
[Lower developmental threshold 5°C and no upper dev. threshold]

demonstrated in other fruit fly studies (Stark and AliNiazee 1982). Since most of the pupae overwinter in the soil at a depth of 1 inch or less (Chapter III), it appears that TU derived from temperature in this zone would be more appropriate. However, air temperature data are more common and accessible over a wide geographic area, therefore I chose to use air temperature at surface level in the model. The coefficients of variance (CV) for the different temperatures were not markedly different from each other.

Fly emergence in the ground emergence cages reached a seasonal peak at the accumulation of 1232 air TU, 1378 surface TU, 1886 2 inch below ground TU, and 1716 4 inch below ground TU during 1991 (Table V-1). In 1992, the corresponding TUs values were 1427, 1543, 2089 and 1883 for air, surface, 2 inch and 4 inch below ground temperature, respectively. The figures in Table V-1 show that similar differences were found in TU requirements for last emergence. Year to year fluctuation in the TU requirement for the first fly emergence was 176 (air temperature), 149 (surface temperature), 202 (2 inch below ground temperature), and 171 (4 inch below ground temperature). For the peak emergence, the respective numbers were 195 (air temperature), 165 (surface temperature), 203 (2 inch below ground temperature), and

Table V-2. Thermal unit (TU) requirements for the emergence of *Rhagoletis completa* in the Willamette Valley, OR 1990-92.

	FLY CATCH IN AERIAL TRAPS					
	FIRST		PEAK		LAST	
YEAR	DATE	TU	DATE	TU	DATE	TU
			AIR TEMPERATURE (42 INCH)			
1990	7/11	1066	8/27	1807	10/1	2262
1991	7/17	941	9/4	1669	10/9	2124
1992	7/01	1142	8/10	1731	9/11	2209
			SURFACE TEMPERATURE			
1990	7/11	1182	8/27	1977	10/1	2463
1991	7/17	1062	9/04	1848	10/9	2326
1992	7/01	1237	8/10	1866	9/11	2376
			2 INCH BELOW GROUND TEMPERATURE			
1990	7/11	1583	8/27	2636	10/1	3240
1991	7/17	1458	9/04	2500	10/9	3108
1992	7/01	1693	8/10	2540	9/11	3191
			4 INCH BELOW GROUND TEMPERATURE			
1990	7/11	1438	8/27	2416	10/1	2980
1991	7/17	1314	9/04	2300	10/9	2880
1992	7/01	1518	8/10	2304	9/11	2914

157 (4 inch below ground temperature). As mentioned before, my data indicate that surface temperature is as good parameter for prediction WHF activity as any other temperature evaluated.

Based on fly catches in aerial traps, the number of thermal units required up to the date of first fly catch and subsequent fly catches are presented in Table V-2. In 1990, the first flies were caught at the accumulation of 1066 TU (air temperature), 1182 TU (surface temperature), 1583 TU (2 inch below ground temperature) and 1438 TU (4 inch below ground temperature). Data show that marked differences exist in TU accumulations at various levels at which temperatures were taken. The same trend also was noticed for the other two years during which the studies were conducted, 1991 and 1992. The year to year fluctuation in TU requirement for the first fly catch in aerial traps was substantially lower using surface temperatures TU (175) than either air (201) or underground temperatures (235 for 2 inch and 204 for 4 inch).

In 1990, the peak fly catches in aerial traps were seen at the accumulation of 1807 TU (air temperature) 1977 TU (surface temperature), 2636 TU (2 inch below ground temperature) and 2416 TU (4 inch below ground temperature). Similar results were found for the 1991 and 1992 seasons (Table V-2). The year to year fluctuation in

Table V-3. Thermal unit (TU) requirements for emergence of various population levels of *Rhagoletis completa* in the Willamette Valley, OR 1991-92.

	FLY EMERGENCE IN GROUND CAGES									
	FIRST		10%		50%		90%		LAST	
YEAR	DATE	TU	DATE	TU	DATE	TU	DATE	TU	DATE	TU
				AIR TEMPERATURE (42 INCH)						
1991	7/17	941	7/26	1071	8/05	1232	8/09	1297	9/11	1762
1992	6/29	1117	7/08	1235	7/20	1427	7/27	1527	8/17	1865
				SURFACE TEMPERATURE						
1991	7/17	1062	7/26	1207	8/05	1378	8/09	1448	9/11	1944
1992	6/29	1211	7/08	1338	7/20	1543	7/27	1648	8/17	2004
				2 INCH BELOW GROUND TEMPERATURE						
1991	7/17	1458	7/26	1651	8/05	1886	8/09	1977	9/11	2631
1992	6/29	1660	7/08	1820	7/20	2089	7/27	2234	8/17	2707
				4 INCH BELOW GROUND TEMPERATURE						
1991	7/17	1314	7/26	1494	8/05	1716	8/09	1800	9/11	2423
1992	6/29	1485	7/08	1636	7/20	1883	7/27	2018	8/17	2458

TU requirements for the seasonal fly catch in aerial traps is comparatively less at the soil surface (129 TU) than the air temperature (138 TU), and 2 inches below the soil (136 TU).

The thermal unit requirements for various population levels using ground emergence cages are presented in Table V-3. In 1991, 10% of the flies emerged in the emergence cages at the accumulation of 1071 TU air temperature, 1207 TU surface temperature, 1651 TU 2 inch, and 1494 TU 4 inch below ground temperature. In 1992, the corresponding TUs for 10% emergence were 1235, 1338, 1820, and 1636 for air, surface, 2 inch and 4 inch below ground temperature. The year to year fluctuation in TU accumulation was less for surface soil temperatures than air, 2 inch and 4 inch below ground temperatures. These fluctuations were 148, 131, 165, and 200 TU for first, 10%, 50%, and 90% ground fly emergence, respectively. The corresponding TU were 202, 169, 203, and 257 for two inch below ground temperature, and 176, 164, 195, and 230 TU four inch below ground temperatures. Similar difference were noticed in TU accumulation for 50%, 90%, etc. fly emergence at various temperatures.

Based on aerial trap catch, TU requirements for different population levels are given in Table V-4. In 1990, 10% flies were caught at the accumulation of 1573 TU

Table V-4. Thermal unit (TU) requirements for various population levels of *Rhagoletis completa* in the Willamette Valley, OR 1990-92.

	FLY CAPTURED IN AERIAL TRAPS									
	FIRST		10%		50%		90%		LAST	
YEAR	DATE	TU	DATE	TU	DATE	TU	DATE	TU	DATE	TU
	AIR TEMPERATURE (42 INCH)									
1990	7/11	1066	8/10	1573	8/27	1807	9/05	1929	10/1	2262
1991	7/17	941	8/19	1450	9/04	1669	9/11	1762	10/9	2124
1992	7/01	1142	7/27	1527	8/12	1777	8/26	1994	9/11	2209
	SURFACE TEMPERATURE									
1990	7/11	1182	8/10	1722	8/27	1977	9/05	2107	10/1	2463
1991	7/17	1062	8/19	1615	9/04	1848	9/11	1944	10/9	2326
1992	7/01	1237	7/27	1648	8/12	1912	8/26	2142	9/11	2376
	2 INCH BELOW GROUND TEMPERATURE									
1990	7/11	1583	8/10	2303	8/27	2636	9/05	2800	10/1	3240
1991	7/17	1458	8/19	2203	9/04	2500	9/11	2631	10/9	3108
1992	7/01	1693	7/27	2234	8/12	2590	8/26	2895	9/11	3191
	4 INCH BELOW GROUND TEMPERATURE									
1990	7/11	1438	8/10	2105	8/27	2416	9/05	2566	10/1	2980
1991	7/17	1314	8/19	2018	9/04	2300	9/11	2423	10/9	2880
1992	7/01	1518	7/27	2018	8/12	2348	8/26	2636	9/11	2914

(air temperature), 1722 TU (surface temperature), 2303 TU (2 inch below ground temperature), and 2105 TU (4 inch below ground temperature). In 1991, the corresponding TU for 10% fly catch were 1540, 1615, 2203, and 2018 for air, surface, 2 and 4 inch below ground temperatures, while in 1992, the corresponding TU were 1527, 1648, 2234, and 2018 for air, surface, two and four inch below ground temperatures respectively. The year to year fluctuation in TU accumulation were 123, 106, 99, and 87 for air, surface, two and four inch below ground temperature.

Based on fly activity in ground emergence cages, a comparison between the reliability of the calendar dates vs. TUs as a predictors of fly emergence at various population levels is given in Table V-5. Variation between calendar dates and TUs indicated that the thermal summation scheme was a better predictor of WHF emergence than using calendar dates. Comparatively large differences were observed in calendar dates between years. The TU requirement for emergence of a particular population level remained fairly constant with little deviation from year to year. Considering the deviation between calendar dates and thermal units, surface and below ground temperatures are slightly more reliable than air temperature. Furthermore, TUs were more reliable to predict 10% and 50% population emergence as compared to first emergence (Table

Table V-5. Comparison of methods (Calendar vs. TU) of estimating emergence of *R. completa* at various population emergence levels in the Willamette Valley, OR 1991-92.

	FLY EMERGENCE IN GROUND CAGES														
	FIRST			10%			50%			90%			LAST		
		DFMID			DFMID			DFMID			DFMID			DFMID	
YEAR	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU
	AIR TEMPERATURE (42 INCH)														
1991	7/17	9	7	7/26	9	5	8/05	8	7	8/09	6	9	9/11	13	4
1992	6/29	10	7	7/08	9	6	7/20	8	6	7/27	7	7	8/17	12	3
	SURFACE TEMPERATURE														
1991	7/17	9	6	7/26	9	4	8/05	8	5	8/09	6	7	9/11	13	2
1992	6/29	10	5	7/08	9	4	7/20	8	4	7/27	7	6	8/17	12	2
	2 INCH BELOW GROUND TEMPERATURE														
1991	7/17	9	6	7/26	9	4	8/05	8	5	8/09	6	6	9/11	13	2
1992	6/29	10	5	7/08	9	5	7/20	8	4	7/27	7	5	8/17	12	2
	4 INCH BELOW GROUND TEMPERATURE														
1991	7/17	9	5	7/26	9	4	8/05	8	4	8/09	6	5	9/11	13	1
1992	6/29	10	5	7/08	9	4	7/20	8	4	7/27	7	5	8/17	12	1

DFMID= Deviation from means in days, CA= Calendar date, TU= Thermal unit

Table V-6. Comparison of methods (Calendar vs. TU) of estimating emergence of *R. completa* at various population emergence levels in the Willamette Valley, OR 1990-92.

	FLY CAPTURED IN AERIAL TRAPS														
	FIRST			10%			50%			90%			LAST		
		DFMID			DFMID			DFMID			DFMID			DFMID	
YEAR	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU
							AIR TEMPERATURE (42 INCH)								
1990	7/11	2	1	8/10	2	3	8/27	3	4	9/05	2	2	10/1	6	10
1991	7/17	8	9	8/19	11	4	9/04	11	4	9/11	8	11	10/9	14	7
1992	7/01	8	8	7/27	12	0	8/12	12	1	8/26	8	6	9/11	14	0
							SURFACE TEMPERATURE								
1990	7/11	2	1	8/10	2	3	8/27	3	4	9/05	2	3	10/1	6	10
1991	7/17	8	8	8/19	11	3	9/04	11	4	9/11	8	9	10/9	14	6
1992	7/01	8	6	7/27	12	1	8/12	12	0	8/26	8	5	9/11	14	1
							2 INCH BELOW GROUND TEMPERATURE								
1990	7/11	2	0	8/10	2	2	8/27	3	3	9/05	2	1	10/1	6	6
1991	7/17	8	7	8/19	11	2	9/04	11	4	9/11	8	8	10/9	14	5
1992	7/01	8	6	7/27	12	1	8/12	12	1	8/26	8	6	9/11	14	1
							4 INCH BELOW GROUND TEMPERATURE								
1990	7/11	2	1	8/10	2	2	8/27	3	3	9/05	2	1	10/1	6	5
1991	7/17	8	7	8/19	11	1	9/04	11	3	9/11	8	7	10/9	14	3
1992	7/01	8	6	7/27	12	1	8/12	12	0	8/26	8	5	9/11	14	0

DFMID= Deviation from means in days, CA= Calendar date, TU= Thermal unit

V-5).

Based on fly catch in aerial traps, a comparison between the reliability of calendar dates vs. TUs as a predictors of fly population at various levels is presented in Table V-6. Considering the variation in the fly catch date, it is clear that using TUs are more reliable than using calendar dates especially for 10%, 50%, and 90% fly catch, while using TUs was only slightly more reliable than calendar dates in predicting first fly emergence. In addition to temperature, other factors probably influence the emergence patterns in *Rhagoletis*. Rainfall, amount of sunlight, soil type and larval host variety have been implicated in *R. pomonella* emergence (Glass 1960, Dean and Chapman 1973, Neilson 1976). Temperature above and below ground has an apparently equal influence on fly catch in aerial traps.

The TU requirements for first, peak and last oviposition are given in Table V-7. The year to year fluctuation in TUs, reveals that surface soil temperature is a slightly better predictor of first, peak and last oviposition than calendar dates. The year to year fluctuations in TU from surface temperature accumulation were 134, 167, and 153 for first, peak and last oviposition, respectively. On the contrary, the corresponding TU from air temperature were 173, 207, and

Table V-7. Thermal unit (TU) requirement for oviposition of *R. completa*, Willamette Valley, OR 1990-92 [based on aerial trap catch].

	OVIPOSITION					
	FIRST		PEAK		LAST	
YEAR	DATE	TU	DATE	TU	DATE	TU
			AIR TEMPERATURE (42 INCH)			
1990	7/31	1393	8/24	1763	8/31	1858
1991	8/08	1284	8/31	1607	9/09	1737
1992	7/22	1457	8/14	1814	8/21	1927
			SURFACE TEMPERATURE			
1990	7/31	1530	8/24	1930	8/31	2031
1991	8/08	1434	8/31	1784	9/09	1918
1992	7/22	1573	8/14	1951	8/21	2071
			2 INCH BELOW GROUND TEMPERATURE			
1990	7/31	2057	8/24	2578	8/31	2702
1991	8/08	1954	8/31	2428	9/09	2593
1992	7/22	2133	8/14	2636	8/21	2798
			4 INCH BELOW GROUND TEMPERATURE			
1990	7/31	1877	8/24	2362	8/31	2478
1991	8/08	1779	8/31	2232	9/09	2387
1992	7/22	1924	8/14	2390	8/21	2545

190. A comparison of the reliability of calendar dates vs. TU (which is presented in Table V-8) as a predictor of various oviposition levels, suggests that the TU scheme was a better predictor of the various levels of oviposition, especially the first oviposition, than the calendar dates. First oviposition is a critical event for fly control because the first insecticide application for control is generally initiated at or before this event.

Based on fly catch in aerial traps, TU requirements for various biological events in the life cycle of WHF is given in Table V-9. Since surface temperature gave the least amount of variation, I felt that the surface temperature was a better predictor of first fly emergence, mature females, oviposition and other activities than air temperature and 2 and 4 inch below ground temperature. In 1990, the first mature females were caught at the accumulation of 1272 TU (air temperature), 1400 TU (surface temperature), 1872 TU (2 inch below ground temperature), and 1705 TU (4 inch below ground temperature). The corresponding numbers for 1991 were 1124, 1262, 1723, and 1561, while in 1992 the corresponding TUs were 1305, 1412, 1922, and 1729. The year to year fluctuation in surface temperature was 149, 150, 139, for first emergence, mature female and oviposition, respectively. The corresponding TUs from air

Table V-8. Comparison of methods (calendar vs. TU) of estimating oviposition levels of *R. completa* in the Willamette Valley, OR 1990-92 [based on aerial trap catch].

	OVIPOSITION								
	FIRST			PEAK			LAST		
		DFMID			DFMID			DFMID	
YEAR	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU
				AIR TEMPERATURE (42 INCH)					
1990	7/31	0	0	8/24	1	3	8/31	0	1
1991	8/08	8	5	8/31	8	13	9/09	9	7
1992	7/22	9	6	8/14	9	4	8/21	10	7
				SURFACE TEMPERATURE					
1990	7/31	0	1	8/24	1	4	8/31	0	2
1991	8/08	8	4	8/31	8	11	9/09	9	6
1992	7/22	9	4	8/14	9	3	8/21	10	5
				2 INCH BELOW GROUND TEMPERATURE					
1990	7/31	0	0	8/24	1	2	8/31	0	0
1991	8/08	8	4	8/31	8	10	9/09	9	6
1992	7/22	9	4	8/14	9	4	8/21	10	5
				4 INCH BELOW GROUND TEMPERATURE					
1990	7/31	0	2	8/24	1	2	8/31	0	0
1991	8/08	8	4	8/31	8	7	9/09	9	5
1992	7/22	9	3	8/14	9	3	8/21	10	4

DFMID= Deviation from means in days, CA= Calendar date, TU= Thermal unit

Table V-9. Thermal unit (TU) requirements for various biological events in life cycle of *R. completa* in the Willamette Valley, OR 1990-92 [Based on aerial trap catch].

YEAR	FIRST OCCURRENCE									
	EMERGENCE		MATURE FEMALE		OVIPOSITION		LARVA		LARVAL EXIT	
	DATE	TU	DATE	TU	DATE	TU	DATE	TU	DATE	TU
	AIR TEMPERATURE (42 INCH)									
1990	7/11	1066	7/23	1272	7/31	1393	8/10	1573	9/10	2006
1991	7/17	941	7/29	1124	8/08	1284	8/16	1401	9/13	1786
1992	7/01	1117	7/13	1305	7/22	1457	7/27	1527	8/25	1978
	SURFACE TEMPERATURE									
1990	7/11	1182	7/23	1400	7/31	1530	8/10	1722	9/10	2191
1991	7/17	1062	7/29	1262	8/08	1434	8/16	1562	9/13	1971
1992	7/01	1211	7/13	1412	7/22	1573	7/27	1648	8/25	2226
	2 INCH BELOW GROUND TEMPERATURE									
1990	7/11	1583	7/23	1872	7/31	2057	8/10	2303	9/10	2901
1991	7/17	1458	7/29	1723	8/08	1954	8/16	2133	9/13	2667
1992	7/01	1660	7/13	1922	7/22	2133	7/27	2234	8/25	2873
	4 INCH BELOW GROUND TEMPERATURE									
1990	7/11	1438	7/23	1705	7/31	1877	8/10	2105	9/10	2660
1991	7/17	1314	7/29	1561	8/08	1779	8/16	1951	9/13	2457
1992	7/01	1485	7/13	1729	7/22	1924	7/27	2018	8/25	2616

temperature were 176, 181, and 173.

A comparison of the reliability of calendar date vs. TU as a predictor of various biological events in the life cycle of WHF is given in Table V-10. The comparison indicated that TUs were a better indicators of various biological events, especially for sexual maturity of the female. Using this information is important, especially in mixed variety orchards where the oviposition is difficult to predict using TU accumulation, mainly because early and late varieties become susceptible at different times depending on husk softness.

The air vs. ground temperature data given in this paper is enlightening, although in a practical sense, it is more academic. Very few farmers would be able to use ground emergence cages and under ground temperature data. It seems that early flies emerge from the upper 1 inch of soil and litter and late flies emerge from deeper levels. Data show that surface temperature is a better predictor and may be easier to obtain.

An analysis of the weather pattern suggests that the winter and spring of 1990 were normal, while they were colder in 1991 and warmer in 1992. Using surface temperature, 276 and 860 TUs accumulated by the end of March and June, respectively in 1990. In 1992, TUs accumulated faster because of warmer winter and spring

Table V-10. Comparison of methods (calendar vs. TU) of estimating various biological events in life cycle of *R. completa* [based on aerial trap catch].

	FIRST OCCURRENCE														
	EMERGENCE			MATURE FEMALE			OVIPOSITION			FIRST LARVAE			LARVAL EXIT		
		DFMID			DFMID			DFMID			DFMID			DFMID	
	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU	DATE	CA	TU
AIR TEMPERATURE (42 INCH)															
1990	7/11	2	1	7/23	2	3	7/31	0	0	8/10	4	4	9/10	6	5
1991	7/17	8	8	7/29	8	6	8/08	8	5	8/16	10	7	9/13	9	13
1992	7/01	8	6	7/13	8	5	7/22	9	6	7/27	10	2	8/25	10	3
SURFACE TEMPERATURE															
1990	7/11	2	1	7/23	2	3	7/31	0	1	8/10	4	4	9/10	6	6
1991	7/17	8	7	7/29	8	5	8/08	8	4	8/16	10	5	9/13	9	10
1992	7/01	8	4	7/13	8	3	7/22	9	4	7/27	10	0	8/25	10	1
2 INCH BELOW GROUND TEMPERATURE															
1990	7/11	2	0	7/23	2	1	7/31	0	0	8/10	4	3	9/10	6	4
1991	7/17	8	6	7/29	8	5	8/08	8	4	8/16	10	4	9/13	9	8
1992	7/01	8	5	7/13	8	4	7/22	9	4	7/27	10	0	8/25	10	3
4 INCH BELOW GROUND TEMPERATURE															
1990	7/11	2	1	7/23	2	2	7/31	0	0	8/10	4	3	9/10	6	4
1991	7/17	8	6	7/29	8	5	8/08	8	4	8/16	10	3	9/13	9	7
1992	7/01	8	4	7/13	8	3	7/22	9	3	7/27	10	0	8/25	10	2

DFMID= Deviation from means in days, CA= Calendar date, TU= Thermal unit

i.e., 403 and 1025 TUs by the end of March and June, respectively. In 1991, the TU accumulation lagged behind especially during the spring months (April through the end of June) and a total of 695 TUs accumulated during this period, but only 304 TUs had accumulated by the end of March. Apparently, this explains the early emergence of the first fly in 1992 (June 29). In 1990, the emergence was 13 days later (July 11) than in 1992 and in 1991 the emergence was 19 days later (July 17) than that in 1992. Data suggest that the length of the cold period experienced by pupae also may affect TU requirements for postdiapause development, and this could have a significant effect on the year to year variation on emergence in the field. Neilson (1962) reported that diapause development of apple maggot required a shorter time period for first emergence if the preceding cold period was 40 weeks or more. The effect of the length of cold period on the physiological response of *R. indifferens* has been reported by Brown and AliNiazee (1977) and *R. cerasi* by Baker and Miller (1978). Some earlier investigators (Reid and Laing 1976, Laing and Heraty 1984) have proposed that variations in emergence are related to differences in the length of the cold period that pupae experienced during winter months. Recently, Smith and Jones (1991) investigated the effects

of cold period duration on *R. pomonella* emergence, and reported that pupae exposed to longer cold periods (79-191 days) required fewer heat units for emergence.

Based on this 3-year field study supplemented by the laboratory studies (Chapter 2) a phenology model was constructed (Table V-5, 6 & 10). This model predicts occurrence of various biological events of the life cycle of WHF with a high degree of accuracy and is a much better predictor of various population events in the field than calendar dates. Therefore, a thermal summation scheme in combination with aerial traps could be an improvement over the current practices of depending on calendar dates for application of insecticides. Similar attempts have been successful with other *Rhagoletis* species including *R. indifferens* (AliNiazee 1976 & 1979, Jones et al. 1991), *R. cingulata and R. fausta* (Jubb and Cox 1974), and *R. pomonella* (Maxwell and Parsons 1969, Reid and Laing 1976, Reissig et al. 1979 Laing and Heraty 1984, Jones et al. 1989). As discussed earlier in Chapter III, the difference in time of first fly emergence and first oviposition event in *Rhagoletis* vary from relatively consistent to quite variable. A phenology model of the emergence and /or female sexual maturity will only be a single component in the walnut pest management system. Under these circumstances, the model will be useful in determining

when monitoring of fly emergence should begin, and when the earliest possible time of female sexual maturity occurs, so that nut inspection for detection of oviposition stings can be initiated. This is especially critical in mixed variety orchards.

REFERENCES

AliNiazee, M. T. 1974. The western cherry fruit fly, *Rhagoletis indifferens* (Diptera: Tephritidae) 1. Distribution of the diapausing pupae in the soil. Can. Entomol. 106: 909-12.

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette Valley of Oregon. Environ. Entomol. 5:397-402.

AliNiazee, M. T. 1979. A computerized phenology model for predicting biological events of *Rhagoletis indifferens* (Diptera: Tephritidae). Can. Entomol. 111: 1101-1109.

AliNiazee, M. T. 1983. A degree day model for predicting the filbertworm emergence. Proc. Oreg. Wash. & B.C. Nut Grower Soc. 68: 37-39.

AliNiazee, M. T. 1986a. Management of western cherry fruit fly, *Rhagoletis indifferens* in western North America. *In* Fruit Flies of Economic Importance, (R. Cavalloro, Editor), A. A. Balkema Press, Boston. pp. 197-206.

AliNiazee, M. T. 1986b. Seasonal history, adult flight activity, and damage of the obliquebanded leafroller, *Christoneura rosaceana* in filbert orchards. Can. Entomol. 118: 353-61.

AliNiazee, M. T. 1988. Diapause modalities in some *Rhagoletis* species. *In* M. T. AliNiazee [Editor], Ecology and Management of Economically Important Fruit Flies. Agric. Exp. Sta. Oreg. State Univ. Special Report 830.

Andrewartha, H. G. and L. H. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Apple, J. W. 1952. Corn borer development on canning corn in relation to temperature accumulation. J. Econ. Entomol. 45: 877-879.

Baker, C. R. B. and G. W. Miller. 1978. The effect of temperature on the post-diapause development of four geographical populations of the European cherry fruit fly (*Rhagoletis cerasi*). Entomol. Exp. Appl. 23:1-13.

Baskerville, G. C., and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514-516.

Bateman, M. A. 1972. The ecology of fruit flies. Ann. Rev. Entomol. 17: 493-518.

Boller, E. F. 1964. Auftreten der Kirschenfliege (*Rhagoletis cerasi* L.) Und. Pragnose mittels Bodentemperature. Schweiz. Z. Obst. Weinbou. 73: 53-58.

Boller. E. F. 1966. Drei Jahre Erfahrung in der Zeitpunktsprognose fur die Kirschenfliegenbekampfung mittle Bodentemperatumessung. Schweiz. Z. Obst. Weinbou. 75: 63-67.

Boller, E. F., and R. J. Prokopy. 1976. Bionomics and management of *Rhagoletis*. Ann. Rev. Entomol. 21:223-246.

Brown, R. D. and M. T. AliNiazee. 1977. Synchronization of adult emergence of the western cherry fruit fly in the laboratory. Ann. Entomol. Soc. Am. 70: 678-680.

Eckenrode, C. J., and R. K. Chapman. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Ann. Entomol. Soc. Am. 65: 151-156.

Gibson, K. E. and W. H. Kearby. 1978. Seasonal life history of the walnut husk fly [*Rhagoletis completa*] and husk maggot [*Rhagoletis suavis*] in Missouri. Environ. Entomol. 7: 81-87.

Higley, L. G., L. P. Pedigo and K. R. Ostlie. 1986. DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ Entomol. 15: 999-1016.

Jones, V. P., D. G. Alston, J. F. Brunner, D. W. Davis, and M. D. Shelton. 1991. Phenology of the western cherry fruit fly (Diptera: Tephritidae) in Utah and Washington. Ann. Entomol. Soc. Am. 84: 488-492.

Jones, V. P., D. W. Davis, S. L. Smith, and D. B. Allred. 1989. Phenology of the apple maggot associated with cherry and hawthorn in Utah. J. Econ. Entomol. 82: 788-792.

Jubb, G. L. Jr., and J. A. Cox. 1974. Seasonal emergence of two cherry fruit fly species in Eric County, Pennsylvania: a 25- year summary. J. Econ. Entomol. 67: 613-615.

Laing, J. E., and J. M. Heraty. 1984. The use of degree days to predict emergence of apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae) in Ontario. Can. Entomol. 116: 1123- 1129.

Lathrop, F. H. and C. O. Dirks. 1944. Timing the seasonal cycles in insects. J. Econ. Entomol. 37: 199-204.

Lathrop, F. H. and C. O. Dirks. 1945. Timing the seasonal cycles of insects: the emergence of *Rhagoletis pomonella*. J. Econ. Entomol. 38: 330-334.

Maxwell, C. W. and. C. Parsons. 1969. Relationships between hour-degree F soil temperature summations and apple maggot adult emergence. J. Econ. Entomol. 62: 1310-1313.

Messenger, P. S. 1959. Bioclimatic studies with insects. Ann. Rev. Entomol. 4: 183-206.

Morris, R. F. and W. C. Fulton. 1970. Models for the development and survival of *Hyphantria cunea* in relation to temperature and humidity. Entomol. Soc. Can. Mem. 70: 1-60.

Neilson, W. T. A. 1962. Effects of temperature on development of overwintering pupae of the apple maggot, *Rhagoletis pomonella* (Walsh). Can. Entomol. 94: 924-929.

Neilson, W. T. A. 1976. The apple maggot (Diptera: Tephritidae) in Nova Scotia. Can. Entomol. 108: 885-92.

Obrycki, J. J. and M. J.Tauber. 1978. Thermal requirements for development of Coleomegilla maculata (Coleoptera: Coccinellidae) and its parasites *Perilitus coccenillae* (Hymenoptera: Braconidae). Can. Entomol. 110: 407-412.

Ratte, H. T. 1984. Temperature and insect development, pp. 33-66. *In* K. H. Hoffman [ed.], Environmental physiology and biochemistry. Springer Verlag, Berlin.

Reid, J. A. K., and J. E. Laing. 1976. Developmental threshold and degree days to adult emergence for overwintering pupae of the apple maggot, *Rhagoletis pomonella* (Walsh) collected in Ontario. Proc. Entomol. Soc. Ont. 107: 19-22.

Reissig, W. H., J. Barnard, R. W. Weires, E. H. Glass, and R. W. Dean. 1979. Prediction of apple maggot fly emergence from thermal unit accumulation. Environ. Entomol. 8: 51-54.

Reissig, W. H. and J. H. Tette. 1979. Apple maggot (Diptera: Tephritidae) monitoring in an apple pest management program. Can. Entomol. 111: 621-25.

Smith, S. L., and V. P. Jones. 1991. Alteration of apple maggot (Diptera: Tephritidae) emergence by cold period duration and rain. Environ. Entomol. 20: 44-47.

Stanley, B. H., W. H. Reissig, W. L. Roelofs, M. R. Schwarz and C. A. Shoemaker. 1987. Timing treatments for apple maggot (Diptera: Tephritidae) control using sticky sphere traps baited with synthetic apple volatiles. J. Econ. Entomol. 80: 1057-1063.

Stark, S. B. and M. T. AliNiazee. 1982. Model of postdiapause development in the western cherry fruit fly. Environ. Entomol. 11: 471-474.

Stinner, R. E., A. P. Gutierrez and G. D. Butler, Jr. 1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106: 519-524.

Tomlinson, W. E. 1951. Influence of temperature on emergence of the blueberry maggot. J. Econ. Entomol. 28: 198-203.

Trottier, R. J. 1975. A warning system for pests in apple orchards. Can. Agric. 20: 31-32.

Trottier, R., J. Rivard and W. T. A. Neilson. 1975. Baits traps for monitoring apple maggot activity and their use for timing control sprays. Can. Entomol. 68: 211-13.

Van Kirk, J. R., and M. T. AliNiazee. 1981. Determining low- temperature threshold for pupal development of the western cherry fruit fly for use in phenology models. Environ. Entomol. 10: 968-971.

Welch, S. M., B. A. Croft, J. F. Brunner, and M. F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7: 487-494.

Wilson, L. T. and W. W. Barnett. 1983. Degree-days: an aid in crop and pest management. Calif. Agric. 37: 4- 7.

VI. SUMMARY AND CONCLUSIONS

The effect of temperature on growth and development, and seasonal phenology of the walnut husk fly (WHF), *Rhagoletis completa* Cresson (Diptera: Tephritidae) were studied for three years during 1990-92 in the Willamette Valley of western Oregon. Data suggest that temperature had a major effect on the developmental rate of this insect. Preoviposition, egg and larval developmental rates increased with increasing temperature and were fastest at 28°C, but decreased above 28°C. The pupal postdiapause development also increased with increasing temperature and was fastest at 24°C, but started to decrease above this temperature. No flies emerged at 32°C. The oviposition activity of mature females increased with increasing temperature and the highest number of eggs were deposited at 24°C. In addition, different life stages of this insect have different developmental thresholds. Developmental thresholds of 6.6, 5.4, 2.9, and 5°C were determined for adult preoviposition, egg, larval, and pupal stages, respectively. The upper thresholds for adult preoviposition, egg, and larval stages were 34°C, but 30°C for the pupal stage.

The fly emergence, in ground emergence cages, showed a large variation in emergence from year to year. The fly

emergence period averaged 53 days. The relationship between first fly emergence and oviposition was consistent during study period. The average preoviposition period was about 3 weeks under Willamette Valley conditions. The oviposition duration in the field was approximately 1 month. On average about 98% of the eggs hatched and approximately 80% of the larvae survived. The fruit infestation reached over 95% in abandoned walnut trees during the months of August and September. The mature larvae emerged from husk during the month of August, September and October and overwintered within a puparia, 1 to 3 inch below the soil surface and stayed in this stage for about 8 months.

Adult flight dynamics of the WHF were studied in abandoned walnut trees, and commercial walnut orchards from 1990 to 1992 using Pherocon AM aerial traps. In abandoned walnut trees, the first flies were detected on July 1 through 17, but the average time of first detection was July 9. The fly catches peaked on August 10 through September 11, and last flies were detected September 11 through October 9. In commercial orchards, flies were first detected on July 13 through August 5, and flies were detected September 14 through 30. Peak flies were detected on August 31 through September 9. Data showed that fly capture varied from year to year. There appeared to be

relatively minor difference in the flight patterns in abandoned trees and commercial orchards, which was primarily modulated by the prevailing temperature. Rainfall had no impact on the flight pattern. Females were most abundant during the early part of the season, and males were more abundant in the later part of the season. The sex ratio was close to 1:1 on a seasonal basis. There appeared to be a close relationship between the first emergence in ground emergence cages and aerial traps. Female dissections suggested only one generation of this insect per year in the Willamette Valley of Oregon.

A phenology model was developed for WHF based on three years of data. The model predicts the first occurrence of adult emergence and subsequent emergence levels (i.e., 10%, 50%, etc.), female sexual maturity, oviposition, larval maturity, and pupal formation with a high degree of accuracy. Surface temperature was a better predictor of various biological events than the above and below ground temperature. Also, the phenology model based on thermal summation scheme was more consistent than the calendar dates in predicting first fly emergence.

In conclusion, the developmental biology of walnut husk fly, under well defined environmental conditions, is reported here for the first time. The developmental rates of preoviposition, egg and larval stage were fastest at

28°C, but oviposition, pupation and pupal developmental rate decreased at this temperature. Thus, 24°C appears to be the optimum temperature for laboratory rearing of this insect. The walnut husk fly population from the Willamette Valley of Oregon has different lower and upper developmental thresholds for various life stages. Both the temperature that pupae experience and the availability of nuts suitable for oviposition influences the seasonal phenology of this insect. The coincidence of fly appearance in ground emergence cages and aerial traps suggests that aerial traps are a good indicators of fly emergence. A host preference and varietal susceptibility study is reported in the appendix.

BIBLIOGRAPHY

AliNiazee, M. T. 1974. The western cherry fruit fly, *Rhagoletis indifferens* (Diptera: Tephritidae) 1. Distribution of the diapausing pupae in the soil. Can. Entomol. 106: 909-12.

AliNiazee, M. T. 1976. Thermal unit requirements for determining adult emergence of the western cherry fruit fly (Diptera: Tephritidae) in the Willamette Valley of Oregon. Environ. Entomol. 5:397-402.

AliNiazee, M. T. 1978. The western cherry fruit fly, *Rhagoletis indifferens* (Diptera: Tephritidae). 3. Developing a management program by utilizing attractant traps as monitoring devices. Can. Entomol. 110: 1133-1139.

AliNiazee, M. T. 1979. A computerized phenology model for predicting biological events of *Rhagoletis indifferens* (Diptera: Tephritidae). Can. Entomol. 111: 1101-1109.

AliNiazee, M. T. 1983. A degree day model for predicting the filbertworm emergence. Proc. Oreg. Wash. & B.C. Nut Grower Soc. 68: 37-39.

AliNiazee, M. T. 1986a. Management of western cherry fruit fly, *Rhagoletis indifferens* in western North America. *In* Fruit Flies of Economic Importance, (R. Cavalloro, Editor), A. A. Balkema Press, Boston. pp. 197-206.

AliNiazee, M. T. 1986b. Seasonal history, adult flight activity, and damage of the obliquebanded leafroller, *Christoneura rosaceana* in filbert orchards. Can. Entomol. 118: 353-61.

AliNiazee, M. T. 1988. Diapause modalities in some *Rhagoletis* species. *In* M. T. AliNiazee [Editor], Ecology and Management of Economically Important Fruit Flies. Agric. Exp. Sta. Oreg. State Univ. Special Report 830.

AliNiazee, M. T. and G. Fisher. 1985. The walnut husk fly in Oregon *Rhagoletis completa*, pests of walnuts. Fact sheet #168, OSU Extension Service, Corvallis, Oregon.

AliNiazee, M. T. and R. L. Westcott. 1987. Flight period and seasonal development of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), in Oregon. Ann. Entomol. Soc. Am. 80(6): 823-828.

Andrewartha, H. G. and L. H. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Anonymous. 1982. Integrated Pest Management for Walnuts. Univ. of Calif. Div. Agric. Sci. Publ. 3270, Berkeley, CA. 96 pp.

Anonymous. 1983. Growing Walnuts in the Pacific Northwest. A Pacific Northwest Ext. Publ. 235.

Anonymous, 1993. Walnut Pests. PNW Insect Control Handbook. Ext. Services of OSU, WSU, and UI. pp.

Apple, J. W. 1952. Corn borer development on canning corn in relation to temperature accumulation. J. Econ. Entomol. 45: 877-879.

Arnold, C. Y. 1959. The determination and significance of base temperature in a linear heat unit system. Proc. Am. Soc. Hort. Sci. 74: 430-445.

Averill, A. L. and R. J. Prokopy. 1989. Distribution patterns on *Rhagoletis pomonella* (Diptera: Tephritidae) eggs in hawthorn. Ann. Entomol. Soc. Am. 82: 38-44.

Back, E. A. and C. E. Pemberton. 1917. The melon fly in Hawaii. U. S. Dept. Agric. Bull. 491:1-64.

Baker, C. R. B. and G. W. Miller. 1978. The effect of temperature on the post-diapause development of four geographical populations of the European cherry fruit fly (*Rhagoletis cerasi*). Entomol. Exp. Appl. 23:1-13.

Barnes, M. M., C. S. Davis, G. S. Sibbett, W. W. Barnett. 1978. Integrated Pest Management in walnut orchards [*Rhagoletis completa*, *Chromaphis juglandicola*, *Juglans*, biological control] Calif. Agric. 32(2):14-15.

Barnes, M. M., and J. C. Ortega. 1958. Glycine-sodium hydroxide solution as an attractant for walnut husk fly. J. Econ. Entomol. 51: 532-534.

Barnes, M. M., and J. C. Ortega. 1959. Experiments with protein hydrolysate bait sprays for control of the walnut husk fly. J. Econ. Entomol. 52: 279-285.

Barnes, M. M., and H. T. Osborne. 1958. Attractants for the walnut husk fly. J. Econ. Entomol. 51: 686-689.

Baskerville, G. C., and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514-516.

Bateman, M. A. 1972. The ecology of fruit flies. Ann. Rev. Entomol. 17: 493-518.

Berlocher, S. H. 1976. The genetics of speciation in *Rhagoletis* (Diptera: Tephritidae). Ph.D. Thesis, Univ. of Texas, Austin. 203 pp.

Berlocher, S. H. 1984a. Genetic changes coinciding with the colonization of California by the walnut husk fly, *Rhagoletis completa*. Evolution. 38: 906-918.

Boller, E. F. 1964. Auftreten der Kirschenfliege (*Rhagoletis cerasi* L.) Und. Pragnose mittels Bodentemperature. Schweiz. Z. Obst. Weinbou. 73: 53-58.

Boller. E. F. 1966. Drei Jahre Erfahrung in der Zeitpunktsprognose fur die Kirschenfliegenbekampfung mittle Bodentemperatumessung. Schweiz. Z. Obst. Weinbou. 75: 63-67.

Boller, E. F., and R. J. Prokopy. 1976. Bionomics and management of *Rhagoletis*. Ann. Rev. Entomol. 21:223-246.

Boyce, A. M. 1931. The diapause phenomenon, in insect, with special reference to *Rhagoletis completa* Cresson (Diptera: Trypetidae). J. Econ. Entomol. 34: 318.

Boyce, A. M. 1934. Bionomics of the walnut husk fly, *Rhagoletis completa* Cresson. Hilgardia. 8: 363-579.

Boyce, A. M., and B. R. Bartlett. 1941a. Lures for the walnut husk fly. J. Econ. Entomol. 34(2): 318.

Brown, R. D. and M. T. AliNiazee. 1977. Synchronization of adult emergence of the western cherry fruit fly in the laboratory. Ann. Entomol. Soc. Am. 70: 678-680.

Bush, G. L. 1966. The taxonomy, cytology and evolution of the genus *Rhagoletis* in North America (Diptera: Tephritidae). Harvard Univ. Mus. Comp. Zool. Bull. 134(11): 231-562.

Chiang, H. C. and V. Sisson. 1968. Temperature relationships of the development of northern corn rootworm eggs. J. Econ. Entomol. 61: 1406-10.

Cirio, U. 1972. Osservazioni sul comportamento di ovidepositione della *Rhagoletis completa* Cresson (Diptera: Trypetidae) in laboratorio. Atti IX Congresso Nazionale Italiano di Entomologia 1972, pp. 99-117.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13:26-38.

Dean, R. W. 1935. Preoviposition period of the apple maggot fly, *Rhagoletis pomonella* (Walsh), in eastern New York. J. Econ. Entomol. 28:504.

Dean, R. W. and P. J. Chapman. 1973. Bionomics of the apple maggot in eastern New York. Search Agric. (Geneva, N. Y.) 3: 1-62.

Delrio, G., B. Conti, and A. Crovetti. 1986. Effect of abiotic factors on *Ceratitis capitata* (Wied) (Diptera: Tephritidae) I. Egg development under constant temperatures. In R. Cavalloro [Editor], Fruit Flies of Economic Importance 84. Balkema, Rotterdam, pp. 131-141.

Eckenrode, C. J., and R. K. Chapman. 1972. Seasonal adult cabbage maggot populations in the field in relation to thermal-unit accumulation. Ann. Entomol. Soc. Am. 65: 151-156.

Fletcher, B. S. and E. T. Kapatos. 1983a. An evaluation of different temperature-dependent rate models for predicting the phenology of the olive fly, *Dacus oleae*. *In* R. Cavalloro (Editor), Fruit Flies of Economics Importance. Balkema, Rotterdam, 321-329 pp.

Forde, H. I. 1981. Persian Walnuts in the Western United States. *In* Nut Tree Culture In North America. Jaynes, R. A., Editor. The Northern Nut Growers Assoc., Inc. pp. 466.

Frick, K. E. 1952. Determining emergence of the cherry fruit fly with ammonium carbonate bait traps. J. Econ. Entomol. 45: 262-263.

Frick, K. E., H. G. Simkover, and H. S. Telford. 1954. Bionomics of the cherry fruit flies in eastern Washington. Tech. Bull. Wash. Agric. Expt. Stn. No. 13.

Gibson, K. E. and W. H. Kearby. 1977. Black walnut nutmeat quality in relation to the presence of husk fly maggots in the husks. 67th Ann. Rept. Northern Nut Growers Assoc. for 1976. pp. 109-13.

Gibson, K. E. and W. H. Kearby. 1978. Seasonal life history of the walnut husk fly [*Rhagoletis completa*] and husk maggot [*Rhagoletis suavis*] in Missouri. Environ. Entomol. 7: 81-87.

Girolami, V., A. Strappazon, R. Crnjar, A. M. Angioy, P. Pietra, J. G. Stoffalano, Jr., and R. J. Prokopy. 1986. Behavior and sensory physiology of *Rhagoletis pomonella* in relation to oviposition stimulants and deterrents in fruit, pp. 183-190. *In* R. Cavalloro [ed.], Fruit flies of economic importance. Balkema, rotterdam, The Netherlands.

Glass, E. H. 1960. Apple maggot fly emergence in western New York. N.Y. St. Agric. Expt. Stn. Bull. 789. 29 pp.

Grimo, E. 1981. Carpathian (Persian) Walnuts. *In* Nut Tree Culture In North America. Jaynes, R. A., Editor. The Northern Nut Growers Assoc., Inc. pp. 466.

Higley, L. G., L. P. Pedigo and K. R. Ostlie. 1986. DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ Entomol. 15: 999-1016.

Hislop, R. G., H. Riedl, and J. L. Joos. 1981. Control of the walnut husk fly with pyrethroids and bait. Calif. Agric. 35(9/10): 23-25.

Illingworth, J. F. 1912. A study of the biology of the apple maggot, *Rhagoletis pomonella*, together with an investigation of methods of control. New York (Cornell) Agric. Expt. Stn. Bull. 324.

Jones, S. C. 1967. The walnut husk fly and its control. Nut- Growers-Soc-Oreg-Wash-Proc., 53:59-62.

Jones, V. P., D. G. Alston, J. F. Brunner, D. W. Davis, and M. D. Shelton. 1991. Phenology of the western cherry fruit fly (Diptera: Tephritidae) in Utah and Washington. Ann. Entomol. Soc. Am. 84(5): 488-492.

Jones, V. P., D. W. Davis, S. L. Smith, and D. B. Allred. 1989. Phenology of the apple maggot associated with cherry and hawthorn in Utah. J. Econ. Entomol. 82: 788-792.

Joos, J. L., C. S. Davis, and F. M. Charles. 1974. Walnut husk fly trapping procedures. Univ. Calif. Ext. Service OSA 176.

Jubb, G. L. Jr., and J. A. Cox. 1974. Seasonal emergence of two cherry fruit fly species in Eric County, Pennsylvania: a 25- year summary. J. Econ. Entomol. 67: 613-615.

Kamal, A. S. 1954. Ecological and nutritional studies on the cherry fruit fly. J. Econ. Entomol. 47: 959-65.

Keck, C. B. 1951. Effect of temperature on development and activity of the melon fly. J. Econ. Entomol. 44: 1001-1003.

Laing, J. E., and J. M. Heraty. 1984. The use of degree days to predict emergence of apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae) in Ontario. Can. Entomol. 116: 1123- 1129.

Lathrop, F. H. and C. O. Dirks. 1944. Timing the seasonal cycles in insects. J. Econ. Entomol. 37: 199-204.

Lathrop, F. H. and C. O. Dirks. 1945. Timing the seasonal cycles of insects: the emergence of *Rhagoletis pomonella*. J. Econ. Entomol. 38: 330-334.

Legner, E. F. and R. D. Goeden. 1987. Larval parasitism of *Rhagoletis completa* (Diptera: Tephritidae) on *Juglans microcarpa* (Juglandaceae) in western Texas and southeastern New Mexico.

Litsinger, J. A. and J. W. Apple. 1973. Thermal requirements for embryonic and larval development of the alfalfa weevil in Wisconsin. J. Econ. Entomol. 66: 309-311.

Liu, H. J., F. L. McEwen, and G. Ritcey. 1982. Forecasting events in the life cycle of the onion maggot, *Hylemya antiqua* (Diptera: Anthomyiidae): Application to control schemes. Environ. Entomol. 11(3): 751-755.

Maxwell, C. W. and. C. Parsons. 1969. Relationships between hour-degree F soil temperature summations and apple maggot adult emergence. J. Econ. Entomol. 62: 1310-1313.

McGranaban, G. and C. Leslie. 1991. Walnuts (*Juglans*). *In* Genetic resources of temperate fruit and nut crops. J. N. Moore and J. R. Ballington Jr. Pub. by the International Soc. for Hort. Sci.

Messenger, P. S. 1959. Bioclimatic studies with insects. Ann. Rev. Entomol. 4: 183-206.

Messina, F. J., D. G. Alston, and V. P. Jones. 1991. Oviposition by the western cherry fruit fly (Diptera: Tephritidae) in relation to host development. J. Kans. Entomol. 64: 197-208.

Messina, F. J., and V. P. Jones. 1990. Relationship between fruit phenology and infestation by the apple maggot (Diptera: Tephritidae) in Utah. Ann. Entomol. Soc. Am. 83: 742-752.

Michelbacher, A. E. and J. C. Ortega. 1958. A technical study of insects and related pests attacking walnuts. Calif. Agric. Exp. Stn. Bull. 764. 86 pp.

Moffitt, H. R. 1958. Rapid determination of sex in *Rhagoletis completa* Cresson. J. Econ. Entomol. Washington D.C.: Entomol. Soc. of America. 51: 551.

Mohammed, A. B. and M. T. AliNiazee 1989. Malathion Bait Sprays for Control of Apple Maggot (Diptera: Tephritidae). J. Econ. Entomol. 82: 1716-1721.

Morris, R. F. and W. C. Fulton. 1970. Models for the development and survival of *Hyphantria cunea* in relation to temperature and humidity. Entomol. Soc. Can. Mem. 70: 1-60.

Neilson, W. T. A. 1962. Effects of temperature on development of overwintering pupae of the apple maggot, *Rhagoletis pomonella* (Walsh). Can. Entomol. 94: 924-929.

Neilson, W. T. A. 1969. Rearing larvae of the apple maggot on an artificial Medium. J. Econ. Entomol. 62: 1028-1031.

Neilson, W. T. A. 1976. The apple maggot (Diptera: Tephritidae) in Nova Scotia. Can. Entomol. 108: 885-92.

Neilson, W. T. A. 1978. Female apple maggot captures and injury to unsprayed apples. J. Econ. Entomol. 71:755-56.

Neilson, W. T. A., A. D. Knowlton, and K. B. McRae. 1981. Preoviposition and oviposition periods of the apple maggot, *Rhagoletis pomonella* [Diptera: Tephritidae]. Can. Entomol. 113: 1061-67.

Neter, J., W. Wasserman, and M. H. Kutner, 1989. Applied linear regression models. Richard D. Irwin, Inc. pp. 667.

Nickel, J. L., and T. T. Y. Wong. 1966. Control of the walnut husk fly, *Rhagoletis completa* Cresson, with systemic insecticides. J. Econ. Entomol. 59: 1079-1082.

Oatman, E. R. 1964. Apple maggot emergence and seasonal activity in Wisconsin. J. Econ. Entomol. 57: 676-679.

Obrycki, J. J. and M. J.Tauber. 1978. Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasites *Perilitus coccenillae* (Hymenoptera: Braconidae). Can. Entomol. 110: 407-412.

Okumura, M., T. Ide, and S. Takagi. 1981. Studies of the effect of temperature on the development of the melon fly, *Dacus cucurbitae* Coq. Res. Bull. Plant Protection Service Japan. 17: 51-56.

Pritchard, G. 1969. The ecology of a natural population of Queensland fruit fly, *Dacus tryoni* II. The distribution of eggs and its relation to behavior. Aust. J. Zool. 17: 293-311.

Prokopy, R. J. 1968. Influence of photoperiod, temperature and food on initiation of diapause in the apple maggot. Can. Entomol. 100: 318-329.

Prokopy, R. J. 1975. Selective new trap for *Rhagoletis cingulata* and *R. pomonella* flies. Environ. Entomol. 4: 420-424.

Prokopy, R. J. and E. F. Boller. 1971. Stimuli eliciting oviposition of European cherry fruit fly, *Rhagoletis cerasi* (Diptera: Tephritidae) into inanimate objects. Entomol. Exp. Appl. 14: 1-14.

Ramos, D., G. McGranahan and L. Hendricks. 1984. Walnuts. Fruit Var. J. 38: 112-120.

Ratte, H. T. 1984. Temperature and insect development, pp. 33-66. *In* K. H. Hoffman [ed.], Environmental physiology and biochemistry. Springer Verlag, Berlin.

Riedl, H., M. M. Barnes, and C. S. Davis. 1979. Walnut pest management: historical perspective and present status pp. 15-80. *In* D. J. Boethel and R. D. Eikenbary, Editors. Pest management programs for deciduous tree fruits and nuts. Plenum Press, New York, 256 pp.

Riedl, H., W. W. Barnett, W. W. Coates, R. Coviello, J. Joos, W. H. Olson. 1989. Walnut husk fly (Diptera: Tephritidae): evaluation of traps for timing of control measures and for damaged predictions. J. Econ. Entomol. 82(4):1191-1196.

Riedl, H. and S. A. Hoying. 1980. Seasonal patterns of emergence, flight activity, and oviposition of the walnut husk fly in northern California. Environ. Entomol. 9:567-571.

Reid, J. A. K., and J. E. Laing. 1976. Developmental threshold and degree days to adult emergence for overwintering pupae of the apple maggot, *Rhagoletis pomonella* (Walsh) collected in Ontario. Proc. Entomol. Soc. Ont. 107: 19-22.

Reissig, W. H., J. Barnard, R. W. Weires, E. H. Glass, and R. W. Dean. 1979. Prediction of apple maggot fly emergence from thermal unit accumulation. Environ. Entomol. 8: 51-54.

Reissig, W. H. and J. H. Tette. 1979. Apple maggot (Diptera: Tephritidae) monitoring in an apple pest management program. Can. Entomol. 111: 621-25.

Retan, A. H. 1980. Walnut husk fly, *Rhagoletis completa*. EM-Washington State Univ. Coop-Ext-Serv. Pullman, Wash., Publ. 3846.

Ries, D. T. 1934. Biological studies of the walnut husk fly [*Rhagoletis suavis* Loew]. Mich. Acad. Sci. Arts and Letters. 20: 717-23.

Ryugo, K. 1988. Nut crops, pp.271-280. *In* Fruit Culture: its art and science. John Wiley & Sons, New York.

Saeki, S., M. Katayama, and M. Okumura. 1980. Effect of temperature upon the development of the oriental fruit fly and its possible distribution in the mainland of Japan. Res. Bull. Plant Protection Service Japan. 16: 73-76.

Shelford, V. E. 1930. Phenology and one of its modern descendants. Q. Rev. Biol. 5: 207-216.

Shelton, M. D. and J. L. Anderson. 1990. Walnut cultivars: Evidence for differential susceptibility to insect pests. Fruit Varieties J. 44(4): 179-182.

Smith, D. C. 1984. Feeding, mating, and oviposition by *Rhagoletis cingulata* (Diptera: Tephritidae) flies in nature. Ann. Entomol. Soc. Am. 77: 702-704.

Smith, D. C. 1988. Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. Nature. 336: 66-67.

Smith, S. L., and V. P. Jones. 1991. Alteration of apple maggot (Diptera: Tephritidae) emergence by cold period duration and rain. Environ. Entomol. 20: 44-47.

Solomon, M. E. 1951. Control of humidity with potassium hydroxide, sulfuric acid, or other solutions. Bull. Entomol. Res. 42: 543-54.

Stanley, B. H., W. H. Reissig, W. L. Roelofs, M. R. Schwarz and C. A. Shoemaker. 1987. Timing treatments for apple maggot (Diptera: Tephritidae) control using sticky sphere traps baited with synthetic apple volatiles. J. Econ. Entomol. 80: 1057-1063.

Stark, S. B. and M. T. AliNiazee. 1982. Model of postdiapause development in the western cherry fruit fly. Environ. Entomol. 11: 471-474.

Stinner, R. E., A. P. Gutierrez and G. D. Butler, Jr. 1874. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106: 519-524.

Stoffolano, J. G., Jr., and L. R. S. Yin. 1987. Structure and function of the ovipositor and associated sensilla of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae). Int. J. Insect Morphol. Embryol. 16: 41-69.

Tassan, R. L., K. S. Hagen, A. Cheng, T. K. Palmer, G. Feliciano, and T. L. Blough. 1983. Mediterranean fruit fly life cycle estimations for the California eradication program. In R. Cavalloro (Editor), Fruit Flies of Economic Importance. Balkema, Rotterdam, pp. 564-570.

Tomlinson, W. E. 1951. Influence of temperature on emergence of the blueberry maggot. J. Econ. Entomol. 28: 198-203.

Trottier, R. J. 1975. A warning system for pests in apple orchards. Can. Agric. 20: 31-32.

Trottier, R., J. Rivard and W. T. A. Neilson. 1975. Baits traps for monitoring apple maggot activity and their use for timing control sprays. Can. Entomol. 68: 211-13.

Trottier, R. and J. L. Townshend. 1979. Influence of soil moisture on apple maggot emergence, *Rhagoletis pomonella* (Diptera: Tephritidae). Can. Entomol. 111: 975-976.

Tsiropoulos, G. J. 1978. Holidic diets and nutritional requirements for survival and reproduction of the walnut husk fly. J. Insect Physiol. 24, 239-242.

Tsiropoulos, G. J. 1981. Effects of antibiotics incorporated into defined adult diets on survival and reproduction of the walnut husk fly, *Rhagoletis completa* Cresson (Diptera: Tephritidae). Z. ang. Entomol. 91:100-106.

Tsiropoulos, G. J. and K. S. Hagen. 1987. Effects of nutritional deficiencies, produced by antimetabolites, on reproduction of *Rhagoletis completa* Cresson (Diptera: Tephritidae). Z. Angew. Entomol. 103: 351-354.

Van Kirk, J. R., and M. T. AliNiazee. 1981. Determining low-temperature threshold for pupal development of the western cherry fruit fly for use in phenology models. Environ. Entomol. 10: 968-971.

Van Kirk, J. R. and M. T. AliNiazee. 1982. Diapause development in the western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae). Z. Angew. Entomol. 93: 440-45.

Welch, S. M., B. A. Croft, J. F. Brunner, and M. F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7: 487-494.

Wilson, L. T. and W. W. Barnett. 1983. Degree-days: an aid in crop and pest management. Calif. Agric. 37(1): 4-7.

Yokoyama, V. Y., G. T. Miller, P. L. Hartsell. 1992. Pest-free period and methyl bromide fumigation for control of walnut husk fly (Diptera: Tephritidae) in stone fruits exported to New Zealand. J. Econ. Entomol. 85: 150-156.