AN ABSTRACT OF THE THESIS OF

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Title: Distribution, Phenology, and Parasitism of the Winter Moth, (Operophtera brumata L.), in Western Oregon.

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Jeffrey C. Miller

An exotic pest of deciduous plants, Operophtera brumata (L.), was discovered in Portland, Oregon in 1978. O. brumata, the winter moth, is native to northern Africa and temperate Eurasia. Its range extends from Scandanavia, Britain, and France to Japan. It is also now well established on the North American continent in Nova Scotia and on Vancouver Island, British Columbia. Surveys for distribution, host range, and levels of parasitism were conducted in the Willamette Valley of Oregon from 1978 to 1980. The seasonal occurrence of all life stages was also monitored. In particular, an investigation to determine the time of larval eclosion was conducted in the field and laboratory. The information obtained from these studies helped to optimize the time of release of two exotic parasitoids, Cyzenis albicans (Fallen) and Agrypon flaveolatum (Gravenhorst), for

biological control of the winter moth.

O. brumata is distributed throughout the northern Willamette Valley and has been detected as far south as Salem. Distribution was determined by the presence of adults in the winter and larvae in the spring on a variety of host plants. Highest numbers of larvae (5+ larvae/ten leaf clusters) were found on Corylus spp. (commercial and native filbert), Prunus cerasifera J.F. Ehrh. (flowering plum), and Malus sylvestris Mill. (crabapple). The widely distributed native oak, Quercus garryana Dougl., was not heavily infested.

The seasonal occurrence of each life stage was monitored in 1979 and 1980. Peak emergence of adult females occurred between 15 November and 5 December in 1979 and 1980. Males were observed in flight early in November of both years. Larvae generally eclose in mid-March and pupate by mid-May. However, there were significant differences in the timing of instar development between years. The occurrence of first instar larvae (50 percent of the accumulated total) differed by 21 days on a calendar time scale. The occurrence of fifty percent of fifth instar larvae differed by 8 days between years. These differences can be attributed to environmental conditions.

Laboratory and field work was conducted each

winter from 1981 to 1984 to determine the timing of larval eclosion. The developmental threshold temperature for larval eclosion was determined to be 4C. Chilling eggs below the developmental threshold temperature affected the subsequent number of thermal units required for eclosion. Chilling accelerated the rate of diapause development and shortened the hatching period. The state of diapause is terminated in mid-January when temperatures above the lower developmental threshold become more frequent.

Surveys for larval parasitism in 1980 and 1981 resulted in the recovery of six species of indigenous parasitoids. However, rates of larval parasitism were low, averaging only 4.5% and 12.2% in both years, respectively.

Two exotic parasitoids, C. albicans and A. flaveolatum, were introduced into areas of known winter moth infestations in 1981 and 1982. C. albicans has been recovered by trapping adults or rearing flies from field collected hosts from four release sites, but no A. flaveolatum have been recovered.

Distribution, Phenology, and Parasitism of the Winter Moth, (*Operophtera brumata* L.), in Western Oregon.

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Contribution of Author

Dr. Richard Penrose, a co-author in the first manuscript, was my supervisor at the Oregon Department of Agriculture until October, 1982. He was in charge of the winter moth research for the State of Oregon from 1978 until his departure in 1982. He directed much of the initial survey and detection work, as well as the releases of the exotic parasitoids.

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INTRODUCTION

The winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), is native across northern Africa and temperate Eurasia. It is a defoliator of a wide range of deciduous trees and has been known to be a serious pest in some regions of Europe (Ferguson, 1978). *O. brumata* was introduced into the eastern seaboard of North America in the early 1930's (Hawboldt and Cuming, 1950). Defoliation of red oak, *Quercus rubra* L., white elm, *Ulmus americana* L., and apple, *Malus* spp., had been attributed to the fall cankerworm, *Alsophila pometaria* (Harr.), and the spring cankerworm, *Paleacrita vernata* (Peck). It was not determined until 1949 that *O. brumata* was responsible for the damage (Hawboldt and Cuming, 1950).

One of the more successful biological control attempts against an insect pest has been the program to suppress populations of the winter moth in Nova Scotia. The Canadian Department of Agriculture began a biological control program for the winter moth in 1954 (Graham, 1958). Initially, six of 63 known parasitoids

from Europe (Wylie, 1960a) were selected for release. Three tachinids, Cyzenis albicans (Fallen), Lypha dubia (Fallen), and Phorocera obscura (Fallen), and three ichneumonids, Agrypon flaveolatum (Gravenhorst), Phobocampe crassiuscule (Gravenhorst), and Pimpla turionellae (L.), were introduced into infested areas. Of these six species, two, C. albicans and A. flaveolatum, became established (Embree, 1966).

Of the two successful parasitoids, C. albicans quickly became dominant and parasitism increased from an average of 10 percent in 1959 to 38 percent in 1962. In some areas, parasitism reached 80 percent (Pschorn-Walcher et al., 1969). A. flaveolatum also increased in numbers, reaching an average of seven percent parasitism in 1961 and 40 percent in 1962, when the pest population declined to a very low level (Pschorn-Walcher et al., 1969).

O. brumata was first detected in western North America on southern Vancouver Island, British Columbia in 1976 and has existed there since at least 1972 (Gillespie et al., 1978). It was initially recognized as being present in Oregon in 1978, although misidentified specimens collected in 1958 indicate it has been established for many years (Ferguson, 1978). C. albicans and A. flaveolatum have recently been

introduced into both western areas for biological control of the winter moth.

Statement of intent

This thesis presents a record of field and laboratory investigations which have been conducted on this introduced pest since its discovery in Oregon. Surveys for distribution, host range, and levels of parasitism were conducted in the Willamette Valley of Oregon from 1978 to 1980. The seasonal occurrence of all life stages was also monitored. An investigation to determine the time of larval eclosion was carried out over four years for the purpose of developing a predictive model. This information was needed to optimize the implementation of a classical biological control program. The introduction of *C. albicans* and *A. flaveolatum* in Oregon in 1981 is documented in this paper as well as the establishment of *C. albicans*.

LITERATURE REVIEW

Systematics and morphology

O. brumata is congeneric with three species native to northwestern North America. The western winter moth, O. occidentalis (Hulst), and Danby's winter moth, O. danbyi (Hulst), are endemic to the Pacific Northwest, while the Bruce spanworm, O. bruceata (Hulst), has a northern distribution throughout the Nearctic region (Miller and Cronhardt, 1982).

The winter moth is difficult to distinguish in appearance from its close relatives. The adult male is a fragile, dusky-brown geometrid with slightly wavy transverse lines and bands on the forewing, and a much less distinctly banded hindwing (Ferguson, 1978). The wing expanse is 27-30mm. The characteristic genitalia of males makes positive identification of the winter moth possible. The short saccus and dilated uncus are distinguishing features. Female O. brumata may be distinguished from most other Operophtera species by their longer vestigial wings. However, Danby's winter moth females also have long wing pads. Danby's winter moth may be distinguished by the reduced tongue which is not easily seen. Other Operophtera species nearly

always have a visible tongue between the labial palpi (Ferguson, 1978).

Larvae of O. brumata pass through five instars, whereas larvae of O. bruceata and O. occidentalis pass through four instars (Eidt and Embree 1968; Miller and Cronhardt 1982). Larvae of O. brumata and O. bruceata may also be distinguished by behavioral differences. The late instar winter moth larva folds a leaf and spins a loose web in which it remains before dropping to the ground. Late instar Bruce spanworm larvae do not exhibit this behavior (Eidt and Embree, 1968). Morphological differences between the two species are very slight. Bruce spanworm hatchlings have a larger head capsule width than those of winter moth.

Pupae of O. brumata can be distinguished from those of O. bruceata by the cremaster. Cremastral spines of Bruce spanworm are longer than the stalk of the cremaster and the angle between them is about 120 degrees. The cremastral spines of winter moth pupae are shorter than the stalk of the cremaster and project at almost a 180 degree angle (Eidt and Embree, 1968).

Other indigenous geometrids which are present in the field at the same time as O. brumata are Erannis tiliaria vancouverensis (Hulst) in the Northwest, Alsophila pometaria (Harr.) (fall cankerworm), and

Erannis tiliaria tiliaria (Harr.) (linden looper) in the Northeast (Ferguson, 1978). These species also have brachypterous females and similar habits, but can be usually be readily distinguished by body size, coloration, and other morphological characteristics.

General life cycle of O. brumata

Winter moth eggs hatch in April and the larvae feed on the foliage of host plants until June. They pass through five instars and then drop to the ground and pupate in the soil. Pupae oversummer and adults emerge in November and December. Brachypterous females crawl up the trunks of trees and attract males by emitting a pheromone. After mating, the female continues to ascend the tree and lays eggs singly or in small groups in lichens on the trunk and branches or in crevices in the bark. Dispersal is accomplished when first instar larvae spin down on silken threads and are carried by air currents to other trees (Embree, 1965).

Biology of C. albicans and A. flaveolatum

C. albicans is a univoltine parasitoid. Adults emerge in the spring at about the same time winter moth larvae hatch. Females contain their full complement of

eggs upon emergence, but these are immature and the adults must feed on sweet sap flux from leaves or nectar for three to five weeks until egg maturation (Varley and Gradwell, 1958). The microtype eggs are laid on the foliage of host plants. They can be ingested by any larval instar of O. brumata, but most eggs are eaten by fifth instar caterpillars which consume greater amounts of leaf biomass (Wylie, 1960a). Larvae of the tachinid hatch in the host midgut, bore a hole in the wall of the alimentary canal, and enter the wall of the salivary gland. The parasitoid completes development there and pupates within the winter moth pupal case. Any intraspecific competition among parasitoid larvae results in the survival of only one individual (Hassell, 1969).

A. flaveolatum is also a univoltine parasitoid. Adults emerge in the spring and oviposit directly in late instar winter moth larvae. However, larval development is delayed. Only after the host pupates does the parasitoid larva mature. The parasitoid larva pupates within the winter moth pupal case. Only one parasitoid will mature in each host (Wylie, 1960a).

Population studies

Life studies of winter moth populations at Wytham

Wood, Berkshire, England were conducted for 17 years (generations) from 1949 to 1966 (Varley et al., 1973). A population model was developed using a key factor analysis. The key factor in a population model is defined as the mortality factor which most accurately reflects population fluctuations from year to year. Varley and Gradwell (1968) determined that the key factor for winter moth population changes was 'winter disappearance.' This term included the mortality of adult moths before completion of egg laying, plus egg mortality and early larval mortality. Early larval mortality was regulated by the degree of synchronization between egg hatch and bud burst. Other factors considered in the model were parasitism and predation. Parasitism never exceeded 30 percent at Wytham Wood (Varley et al., 1973). The mortality caused by the parasitoid C. albicans, other miscellaneous parasitic Diptera and Hymenoptera, and the microsporidian parasite Plistophora operophterae Canning was small and insignificant. However, pupal predation was a greater factor in mortality and it was found to be density-dependent. Frank (1967) concluded that three species of beetles were responsible for half of the pupal predation, whereas Buckner (1969) stated that shrews were the most important mortality factor in the disappearance of winter moth pupae. Despite the

discrepancy, both studies indicate that pupal predation compensates for the changes brought about by 'winter disappearance.'

The role of C. albicans in the population dynamics of the winter moth in England and Nova Scotia is significantly different. In England C. albicans does not play any significant role in the population dynamics of the winter moth, but in Nova Scotia the parasitoid has become a key factor in regulating winter moth populations. C. albicans is an ineffective parasitoid in England because: 1) synchronization with its host is imperfect (Varley and Gradwell, 1958) and 2)puparia are subject to greater mortality than are winter moth pupae because the puparia are in the ground for a longer period and are exposed to predation longer. Adult flies are also subject to predators for more than two months (Varley and Gradwell, 1958). If C. albicans were completely removed from Varley and Gradwell's model of the population in England, there would be an insignificant change in the winter moth population dynamics.

The ineffectiveness of C. albicans as a regulator of winter moth populations in England made its success in Nova Scotia quite surprising. Varley and Gradwell (1968) predicted in their model that the introduction of C. albicans alone would lead to

strong parasite-host oscillations and periodic outbreaks at nine or ten year intervals. This has not occurred. One reason is the lack of density dependent mortality that affects both winter moth and the parasitoid in England. This lack of a regulatory factor allowed the winter moth population to increase to damaging levels in the absence of parasitoids. C. albicans became an effective biological control agent due to its efficiency in decreasing high host populations and its non-random distribution in relation to host location (Hassell, 1980).

Population models based on life tables prior to the introduction of the parasitoids into Nova Scotia showed that the key factor regulating winter moth populations was the degree of synchrony between larval eclosion and bud burst of the host plant (Quercus rubra L.). After the establishment of C. albicans and A. flaveolatum parasitism became the key factor in controlling winter moth outbreaks and maintaining the host at low population densities (Embree, 1971). The combination of A. flaveolatum and C. albicans was fortuitous. The co-existence of two specific and synchronized parasitoids on one host is unusual (Varley and Gradwell, 1969). These two parasitoids are able to co-exist because they operate most successfully at different host densities. A. flaveolatum emerges

later than C. albicans and is more effective at low host densities. It oviposits directly on its host, whereas C. albicans lays its eggs on foliage which must then be consumed by the host larva. C. albicans kills a higher proportion of hosts at high host densities (Embree, 1966). The increased density of host larvae results in an increase in parasitoid egg consumption. Thus, fewer parasitoid eggs are wasted.

The control of winter moth populations in Nova Scotia was well under way before parasitism by A. flaveolatum reached high levels. The ichneumonid enhanced the decline of host populations, but the tachinid was largely responsible for the initial crash (Hassell, 1980).

A nuclear polyhedrosis virus was first detected in isolated larvae in 1961 and is now generally present throughout the area of winter moth distribution in Nova Scotia. The virus has also contributed to the collapse of at least two winter moth outbreaks (Embree, 1971).

Phenological studies

The winter moth is distributed in western Europe from northern Scandanavia to the south of Italy (Wylie, 1960b). The seasonal and phenological differences

between these regions have resulted in differences in the times of oviposition, hatching, and pupation. The duration of the egg stage is two months in southern Italy, but nearly eight months in northern Europe, whereas the pupal stage lasts over eight months in the former region and less than three months in the latter. It has been suggested that egg diapause is 'obligatory' in the U.S.S.R. (Kozchanikov, 1950), but that no true egg diapause occurs in central Europe (Wylie, 1960b).

Variations in the intensity or duration of diapause may be repeatedly modified in response to diverse environments inhabited by a species (Andrewartha 1952; Tauber and Tauber 1976). The pupal and egg stage of the winter moth exhibit variations in diapause duration along a latitudinal (and altitudinal) gradient (Wylie, 1960b). Eggs collected from Frankfurt, Versailles, and Oldenburg differed in incubation periods when exposed to the same temperature treatments (Wylie, 1960b). These results demonstrated that differences in the egg stage were inherent.

Observations on the hatching of winter moth eggs suggest that a relationship exists between exposure to chilling temperatures and subsequent hatch time. In France, Gaumont (1955) found that eggs which were chilled below freezing before exposure to warmer temperatures required fewer thermal units to hatch and

experienced a decrease in mortality. Briggs (1957) reported similar results from England. Batches of eggs stored at cold temperatures for increasing exposure times and subsequently brought into a 20C laboratory required decreasing time periods for hatching. Embree's investigations in Nova Scotia (1970) led him to conclude that the theoretical developmental threshold temperature for larval eclosion is 39F (3.9C). Mean hatch in the field based on five years of data occurred when 292 degree-days (above 39F) were accumulated from April 1. The winter moth eggs Embree studied were exposed to December field temperatures in Nova Scotia and subsequently held at 1.7C in the laboratory until March. They were maintained below their developmental threshold temperature for three months. These studies indicate that the relationship between temperature and thermal unit requirements for egg hatch is complex.

Adaptations to climatic conditions (i.e. temperature) also influence the interactions between organisms such as the synchrony between a host and parasitoid (Tauber and Tauber, 1981). The adult emergence of the parasitoid C. albicans is affected by temperature and intrinsic factors. Pupae reared from several localities in the same environment yielded adults at times corresponding to natural times of

winter moth larval eclosion in those localities (Wylie, 1960a). This indicates that the tachinid is in synchrony with the development of its host O. brumata within specific geographical areas.

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Distribution, Seasonal Development, and Parasitism of the Winter Moth, *Operophtera brumata* (L.), in Western Oregon

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ABSTRACT

The winter moth, Operophtera brumata, is distributed throughout the northern region of the Willamette Valley, Oregon where it is commonly found on commercial hazelnut (Corylus avellana L.), crabapple (Malus silvestris Mill.), and flowering plum (Prunus cerasifera J.F. Ehrh.). The species is univoltine, adults emerge in early November through December, eggs overwinter, larvae eclose in mid-March and pupae occur from May to November. Larval development varies considerably when compared on a calendar time scale. The occurrence of each instar (50 percent accumulated total) between 1980 and 1981 differed by as much as 21 days for first instar larvae and 8 days for fifth instar larvae.

Six species of native parasitoids were reared from field-collected larvae, but parasitism averaged only 4.5% and 12.2% in 1980 and 1981, respectively. The exotic parasitoids, Cyzenis albicans (Tachinidae) and Agrypon flaveolatum (Ichneumonidae), were released for biological control of the winter moth in 1981 and 1982. C. albicans was recovered from four of seven release sites. No A. flaveolatum have been collected.

INTRODUCTION

The winter moth, Operophtera brumata (L.), is native to and widespread across northern Africa and temperate Eurasia, and has been known to be a major pest in these regions (Ferguson, 1978). As a univoltine defoliator, O. brumata is a pest of fruit, shade, and forest trees.

The winter moth was accidentally introduced into North America prior to 1935, but was not recognized as present until 1949 in Nova Scotia. A successful biological control program initiated by the Canada Department of Agriculture in 1954 has suppressed the pest population in oak woodland areas (Embree, 1971). The success of this biological control program was achieved by the combination of two parasitoid species which are most effective at different host population levels. A tachinid, Cyzenis albicans (Fallen), is more effective at high host densities and an ichneumonid, Agrypon flaveolatum (Gravenhorst), is more successful at low host densities (Embree, 1966).

O. brumata was first detected in western North America on southern Vancouver Island, British Columbia in 1976 (Gillespie et al., 1978). It is not known whether this infestation came from eastern Canada or whether it represents a separate introduction directly

from Eurasia. The successful biological control program in Nova Scotia set a precedence for the release of C. albicans and A. flaveolatum on Vancouver Island in 1978, and the first parasitoid recoveries were made in 1982 (Anonymous, 1982).

The winter moth was first recorded from the United States in Portland, Oregon in the fall of 1978, but evidence indicates it has been locally established for many years. Several male specimens collected in 1958 were misidentified as O. occidentalis (Hulst), a native species (Ferguson, 1978).

The life history of O. brumata is similar to that of three congeneric species native to northwestern North America. The western winter moth, O. occidentalis, and Danby's winter moth, O. danbyi (Hulst), are endemic to the Pacific Northwest, while the Bruce spanworm, O. bruceata (Hulst), has a northern distribution throughout the Nearctic region (Miller and Cronhardt, 1982). All species have brachypterous females and winged males. Adults of each species are active from Nov.-Jan., eggs overwinter, larvae are present in the spring, and pupae oversummer. Differences between O. brumata and O. occidentalis, which are sympatric in some areas of Oregon, are that the exotic species develops through 5 instars (4 in the native species), larvae eclose and pupate 2-3

weeks earlier, and the distribution is over a smaller geographical area (Miller and Cronhardt, 1982).

The discovery of the winter moth in Oregon initiated research to implement a biological control program, with the goal of releasing C. albicans and A. flaveolatum.

C. albicans is a univoltine parasitoid. Adults emerge in the spring in synchrony with winter moth larval eclosion and live for three to five weeks (Wylie, 1960a). They have been observed feeding on sweet sap flux from leaves damaged by caterpillars, and dissections of the crop indicate they also feed on nectar (Varley and Gradwell, 1958). Microtype eggs are laid on the foliage of flowers of host plants. They can be ingested by any larval instar of O. brumata, but most eggs are eaten by fifth instar caterpillars which consume greater amounts of leaf biomass (Wylie, 1960a). Larvae of C. albicans hatch in the host midgut, bore a hole in the wall of the alimentary canal, and enter the wall of the salivary gland. The parasitoid feeds here until the host pupates. Only one parasitoid matures in each host pupa.

A. flaveolatum adults emerge in the spring and oviposit directly in the winter moth larvae. The host pupates, and the parasitoid larva matures in the fall and pupates within the pupal case of O. brumata.

The parasitoid is univoltine and only one matures in each host (Wylie, 1960a).

The present report discusses studies on 1) the distribution, 2) seasonal occurrence, and 3) indigenous parasitoids of the winter moth in western Oregon. We also report on the release of C. albicans and A. flaveolatum with documentation on the establishment of C. albicans.

METHODS AND MATERIALS

Distribution surveys

Intensive geographical surveys were conducted in late fall and winter of 1978. The initial plan, a grid design, involved 906 km sq. within and around the Portland metropolitan area, and included 650 individual sample sites. The criteria for choosing sites included (1) adjacent areas of known infestations (2) major transportation routes, or (3) commercial nurseries or orchards. Potential hosts sampled for O. brumata were Corylus avellana (commercial filbert), C. cornuta (native filbert), Malus spp. (apple), Quercus garryana (oak), Salix spp. (willow), and other deciduous trees.

Various collecting techniques were employed in the

surveys. Adults were collected from sticky bands wrapped around tree trunks, beating sheets, and in-field searches. Larvae were collected from clipped leaf clusters, beating sheets, drop pans, sweep nets, and in-field searches.

Surveys were expanded to include more of the Willamette Valley and western Oregon in 1979 and 1980 and included portions of Clackamas, Marion, Multnomah, Washington, and Yamhill counties.

Seasonal development

Studies on the seasonal development of the winter moth were initiated near Tigard, Washington County from November, 1979 to April, 1980. This site, a commercial filbert orchard, was sprayed with insecticide in the spring of 1980. A new site was located 19 km away in Wilsonville, Clackamas County, where the majority of the developmental studies were conducted from April, 1980 to December, 1981. This site consisted of 6.1 ha abandoned filbert orchard. The trees were surrounded by extensive sucker growth. The ground cover was unmanaged and consisted primarily of grasses with patches of tansy ragwort, fireweed, evergreen blackberries, seedling filbert, and holly trees.

Adult emergence and abundance was monitored by

collecting males and females on sticky bands which encompassed one-half of the basal girth of the tree. Bands were placed alternately around the north, south, east, and west sides of the trunks to avoid any directional bias of female moths in ascending trunks. In 1979, traps were monitored daily on filbert (n=6) at the Tigard site, and twice weekly on apple (n=13), filbert (n=7), flowering plum (n=4), and American elm (n=6) located at various sites in Multnomah County. In 1980, ten traps were monitored three times per week for eight weeks at the Wilsonville site.

Larval eclosion and development to pupation were monitored twice per week in 1980 and three times per week in 1981 at the Wilsonville site. Samples from ten individual trees consisted of a minimum of five leaf clusters from four different branches. One branch was clipped from each quadrant of the tree canopy (N,S,E,W). A total of ten trees comprised a transect along which the samples were taken. The instar distribution of all larvae was established for each sample date. Instar determinations were validated by obtaining a subsample of at least 30 larvae per sample date and measuring head capsule widths. The number of larvae nearing pupation was monitored by placing drop pans partially filled with soapy water near the base of 13 trees at the Wilsonville site from mid-April to late

May. As larvae descended from the canopy, they fell into the pans. Counts were made twice weekly.

Native parasitoids

A survey was conducted to determine if certain native parasitoids, as well as C. albicans and A. flaveolatum, were already present. In the spring of 1979, 1683 late instar winter moth larvae were collected from 23 localities. The larvae were placed with host plant material in containers of a sterilized peat and vermiculite mixture. After all larvae had pupated, the containers were placed in an incubator at 13C to oversummer. There was no photoperiod regimen, and pupae were maintained in total darkness. The pupae were misted weekly with a one percent solution of sodium proprionate, a mold inhibitor. In October, the temperature was lowered to 7C for adult winter moth emergence. Remaining pupae were kept at 7C until March when the temperature was raised to 18C. Parasitoid emergence was monitored daily.

During the spring of 1980, 1366 late instar larvae were collected from 19 sites, and the procedure stated above was repeated.

Release of exotic species

In April, 1981 two small field releases totalling 110 C. albicans and 74 A. flaveolatum were made at the Wilsonville study site. Parasitoids were shipped from the USDA Beneficial Insect Research Laboratory in Delaware. Liberations were made into cages over seedling filberts heavily infested with host larvae. Cages were removed once tachinid eggs were detected on the foliage. In 1982, 11 sites were chosen for release of C. albicans and six sites for liberations of A. flaveolatum. Releases were made in Multnomah, Washington, Yamhill, Clackamas, and Marion counties. A total of 3613 C. albicans and 700 A. flaveolatum adults were released between 31 March and 22 April. The predominant host plant in all locations was filbert, and all liberations were made in open field conditions. Estimates of larval density and instar distribution were obtained on the date of release by sampling 40 twigs with five or six leaf clusters/twig.

The most recent releases were made in Washington County in an unsprayed filbert orchard in April, 1984. A total of 1023 C. albicans adults were liberated at several points within the orchard. A release of 46 A. flaveolatum adults was made in Benton County near a known population of O. occidentalis.

Exotic parasitoid recoveries

In 1982, a total of 1360 late instar winter moth larvae were collected from six parasitoid release sites in the northern Willamette Valley. These sites were chosen to determine if the parasitoids had successfully overwintered. Three of the sites selected were relatively small, isolated areas. Two of the sites were large, unsprayed commercial filbert orchards, and the last was the Wilsonville study area. Collecting began at the point of release and continued along radii from the center. The number of larvae collected from each location ranged from 160 to 610, depending on area and density of the winter moth infestation. In 1983, a similar procedure was carried out. A total of 1600 late instar larvae was collected from six release sites. One of the sites had not been sampled in 1982, and one which had been sampled in 1982 was not in 1983. The larvae were treated in a similar manner as those collected for the natural enemy study.

A second method of recovery in 1983 was the placement of sticky traps at the release sites. Seven sites were selected for trapping. Traps were hung at north, south, east, and west sides of the canopy of the tree where the parasitoids were released. These traps (for apple maggot, Rhagoletis pomonella Walsh,

detection) were used for their effectiveness in attracting many species of tachinid flies (Buriff and Davis, 1974). Another set of four white sticky board traps were placed approximately one foot from ground level around the base of the tree. Traps were checked weekly from 7 March through 10 May.

RESULTS

Distribution and host plants

The known distribution of O. brumata in Oregon is presently restricted to the northern region of the Willamette Valley and encompasses 1180 km sq. around metropolitan Portland (Fig. I.1). The northern boundary includes Vancouver, Washington, but the infestation in southern Vancouver Island, B.C. suggests that the distribution may be continuous from that region. The eastern boundary extends to Gresham, and the western boundary extends to Hillsboro. The southern boundary is not well delineated. However, the collection of two females in November, 1981 indicates that the winter moth occurs as far south as Salem, Oregon.

Female adults or larvae were collected on species of Acer macrophyllum Pursh (big leaf maple), Aesculus

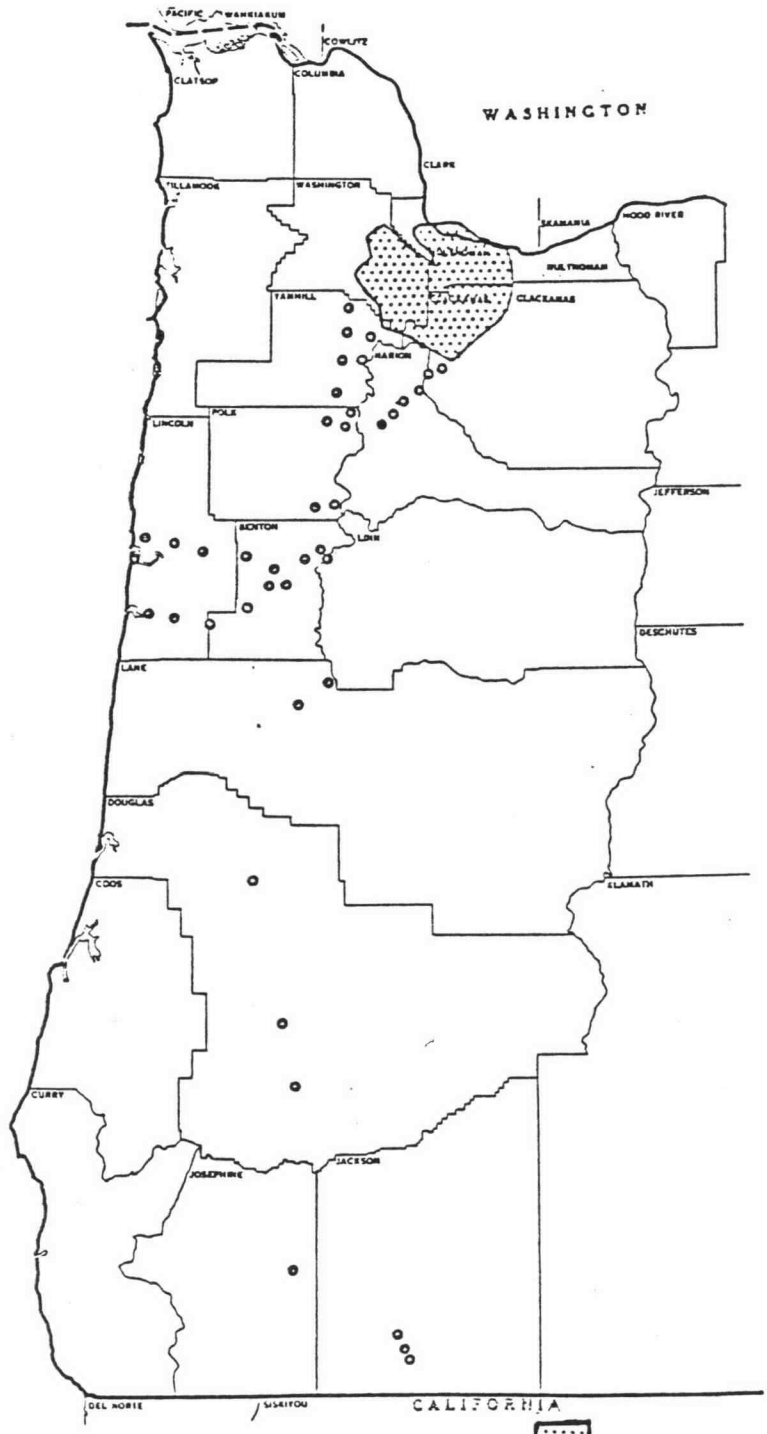

Figure I.1. Known distribution of O. brumata in western Oregon. Results from O. brumata surveys south of Salem provided by J.C. Miller, unpublished data.

hippocastanum L. (horsechestnut), Betula pendula Roth (European white birch), Carpinus caroliniana T. Walt. (American hornbeam), Corylus avellana L. (commercial filbert), C. cornuta Marsh. (native filbert), Cornus stolonifera Michx. (dogwood), Crataegus douglasii Lindl. (black hawthorn), Juglans regia L. (English walnut), Malus pumila Mill. (apple), Malus sylvestris Mill. (crabapple), Prunus cerasifera J.F. Ehrh. Cv. 'Atropurpurea' (flowering plum), Pyrus communis L. (pear), Quercus garryana Dougl. (oak), Rhododendron spp., Rosa spp., Rubus discolor Weihe and Nees (Himalayan blackberry), Salix spp. (willow), Sorbus aucuparia L. (European mountain ash), and Ulmus americana L. (American elm). High numbers of larvae (5+ larvae/ten leaf clusters) were consistently found on filbert and rosaceous ornamentals, particularly flowering plums and crabapples.

Seasonal development

Adult emergence occurred between early November and late December (Fig. I.2). Active females were trapped over a period of 51 and 57 days in 1979 and 1980, respectively. Peak female emergence occurred between 28 November and 5 December with 75% of all

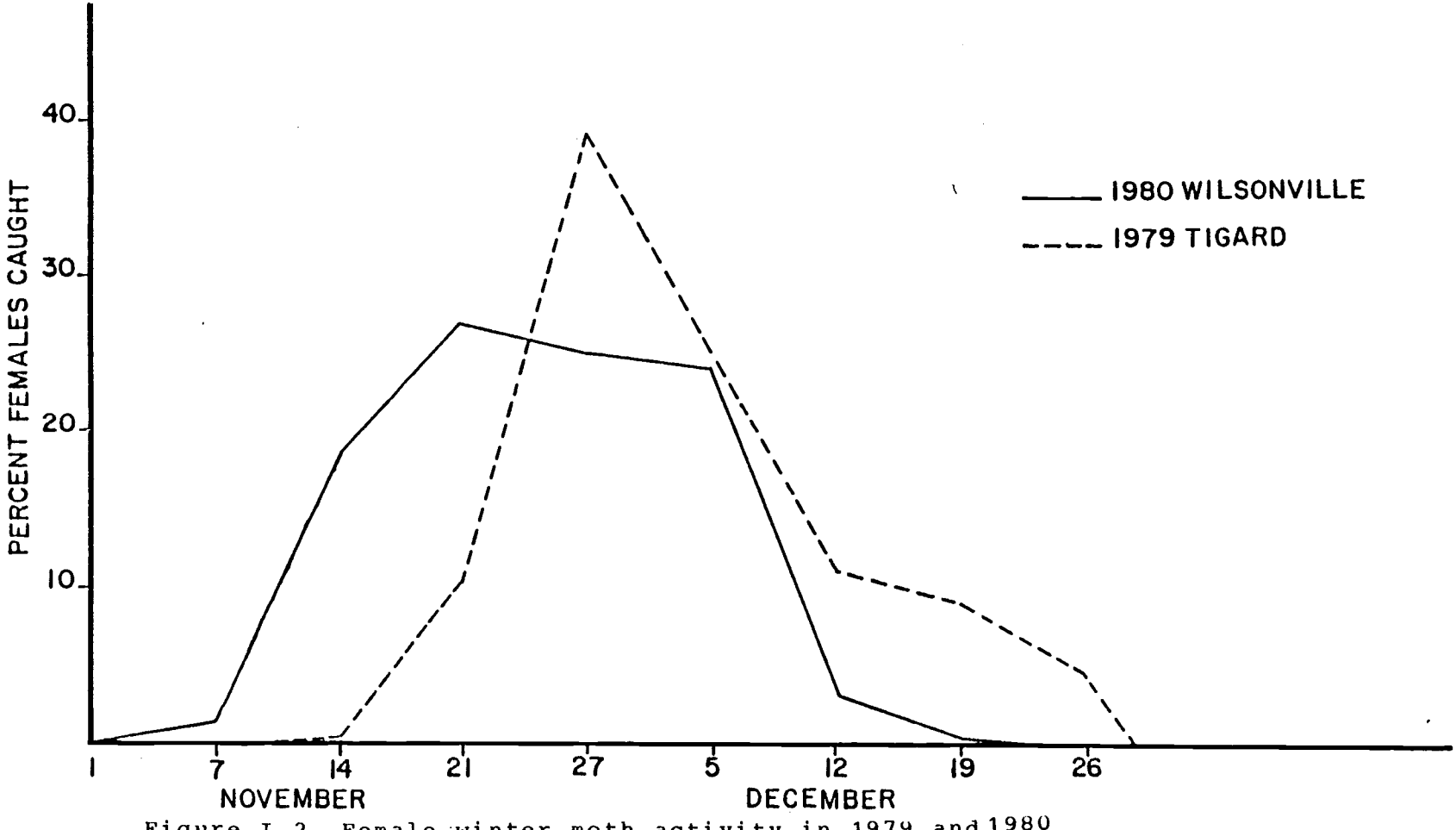

Figure I.2. Female winter moth activity in 1979 and 1980 at Tigard and Wilsonville, Oregon, respectively.

females trapped between 15 November and 5 December. Males were observed in flight as early as 5 November in 1979 and 2 November in 1980. For each year, detection of male activity preceded that of female.

Males generally began flying 1/2 to 1 hour after sunset when temperatures were 4.5C or higher, and flight activity was most common on warm evenings. The brachypterous females were first observed ascending host plants about 1 hour after sunset. Mating pairs were most often observed on the basal portion of tree trunks and low branches of the canopy. Although males did not fly when ambient temperatures were around 2-3C, they were observed ascending tree trunks, and mating with females when temperatures were below 0C. These findings were similar to those of Alma (1970), who stated that the threshold temperature for flight was between 5.0 and 5.5C.

Larvae eclosed in early to mid-March in 1980 and 1981. Development was variable between the two years (Fig. I.3). Fifty percent of the accumulated total of first instar larvae had hatched by April 4 in 1980. This percentage of first instar larvae was present by March 14 in 1981. Similarly, fifty percent of the accumulated total of fifth instar larvae was present by May 2 in 1980, but the same percentage of development occurred by April 24 in 1981 (Table I.1.). In 1980,

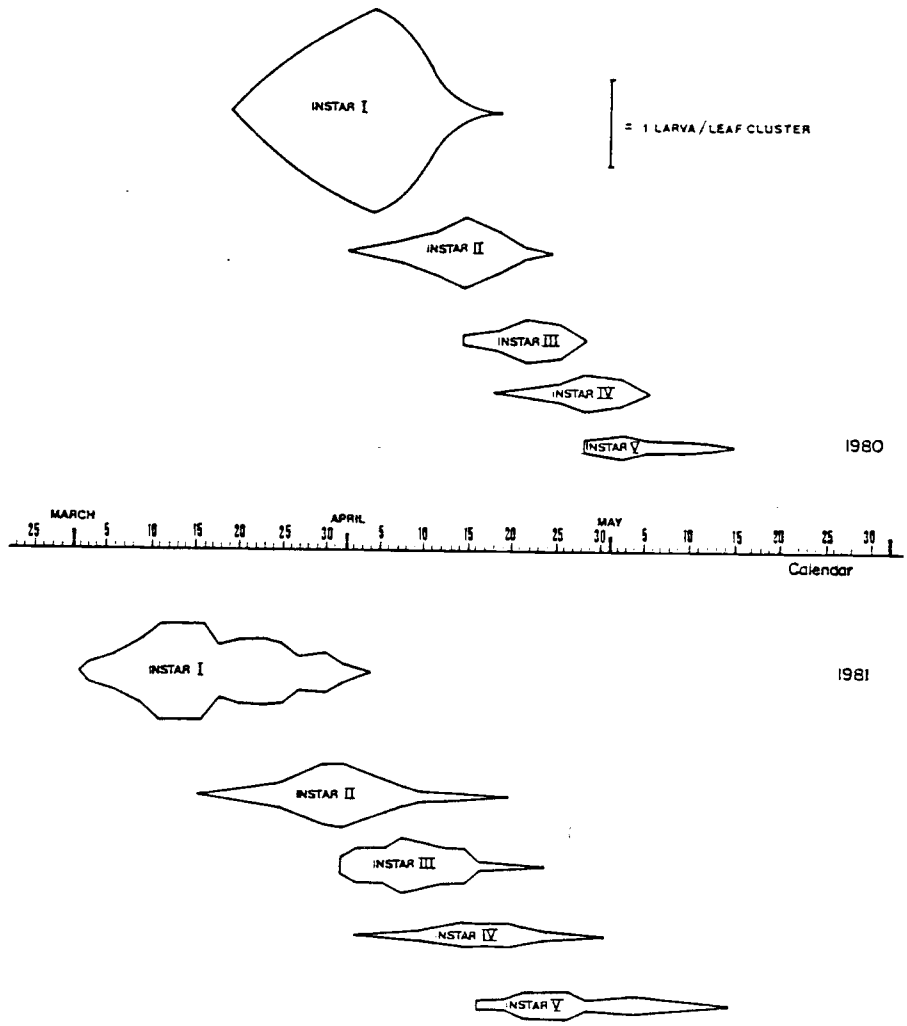

Figure I.3. Comparison of larval development at Wilsonville, Oregon 1980-1981.

Table I.1. Comparison of winter moth larval development at Wilsonville, Oregon 1980-1981. Calendar time difference in instar development between years.

50% occurrence of accumulated total Instar	Calendar 1980	1981	Difference (days)
I	April 4	March 14	21
II	April 13	March 31	13
III	April 20	April 8	12
IV	April 27	April 17	10
V	May 2	April 24	8

the peak rate of fifth instar larval drop from the foliage occurred on May 9. Generally, larvae pupated in both years by mid-May.

Larval densities at the Wilsonville site varied considerably between 1980 and 1981. In 1980, the peak density on filbert was 2.5 larvae/leaf cluster. In 1981, the peak density on filbert was 0.6 larva/leaf cluster.

Native parasitoids

Six species of natural enemies were reared from field collected winter moth larvae. These include the ichneumonids, *Agrypon* sp. (probably *provancheri*, H.K. Townes pers. comm.) and *Triclistes* spp. A,B; the braconids *Apanteles* spp. A,B; and a tachinid, *Cyzenis pululla* (Townsend). Overall parasitism was low, 4.5% (host n=1683) in 1979 and 12.2% (host n=1366) in 1980 with a single species of *Triclistes* (sp. A) representing 90%+ of all parasitoids recovered. A nematode (immature Mermithidae) was also recovered from field collected *O. brumata*, accounting for approximately 1% parasitism (host n=1366).

Exotic parasitoid recoveries

Two C. albicans were recovered from host collections made in 1982 from one of the six study sites (Table I.2). The site is located in Multnomah County in southeast Portland. Six filbert trees harbored 0.45 larva/leaf cluster at the time of the parasitoid liberation. The majority (66%) of the winter moth population was in second instar. A total of 127 female and 133 male C. albicans adults were released in April, 1982. The small area (0.05 ha) resulted in a concentration of host and parasitoids, which may have aided searching efficiency for damaged foliage. The number of hosts collected for parasitoid detection totalled 200, providing an estimate of 1% parasitism.

Eight C. albicans were reared from field collected O. brumata larvae in 1983 from a site located in Washington County, five miles east of Hillsboro (Table I.2). This is a relatively isolated area due to construction and development occurring in the vicinity, but other winter moth host plants are prevalent within .8 km. The site (approximately 0.10 ha) consisted of one flowering plum, three filbert, and three apple trees, all infested with larvae. Host density was 0.13 larva/leaf cluster and 59% of the population was in second instar. The number of parasitoid adults released consisted of 152 females and

Table I.2. Release and recovery of *Cyzenis albicans* in Oregon 1981-1983

Site	Date	Release Females	Release Males	No. hosts Collected	*C. albicans* Reared	*C. albicans* Trapped
Tigard	1982	186	106	160	-	-
	1983			400	-	1
Tualatin (orchard)	1982	116	129	100	-	-
	1983			300	-	-
E. Hillsboro	1982	152	110	190	-	-
	1983			200	8	2
SE Portland	1982	127	133	200	2	-
	1983			200	-	-
Tualatin	1982	175	177	150	-	-
	1983			200	-	1
Wilsonville	1981	50	60	-	-	-
	1982	530	501	610	-	-
	1983			-	-	-
Carver	1982	125	101	-	-	-
	1983			300	-	-

110 males. The number of host larvae collected for evaluation of establishment was 200. Thus, parasitism was estimated to be 4%. Two adult C. albicans were also trapped at this site (Table I.2). The total parasitoid recoveries (n=10) from this location give reason for optimism that C. albicans may increase in numbers in the future.

Trapping results in 1983 indicated that C. albicans has successfully established in at least two other locations (Table I.2). One adult was collected on an apple maggot trap near Tualatin, Clackamas County on 5 April, 1983. The site (0.2 ha) consists of 35 unsprayed filbert trees. Larval density was estimated at 0.28 larva/leaf cluster at the time of parasitoid release and 65% of the host population was in second instar. A total of 175 female and 177 male C. albicans were released. No parasitoids were recovered from larval collections (n=200).

A second C. albicans adult was recovered from an apple maggot trap on 26 April, 1983 south of Tigard, Washington County. This location was the original study site, a commercial filbert orchard. The portion of the orchard where parasitoids were introduced was not sprayed with insecticide. A total of 186 female and 106 male parasitoids were released. The winter moth larval density was .24 larva/leaf cluster and the

predominant stage was second instar. None of the 400 late instar larvae collected in 1983 yielded parasitoids.

No exotic parasitoid recoveries were made from any other release sites, including the study area at Wilsonville. The first releases of C. albicans were made at this site in 1981. A total of 50 females and 60 males were liberated. Larval density at the time of the releases ranged from 0.3-0.4 larva/leaf cluster and the predominant stage was fourth instar. In 1982, 610 winter moth larvae were collected and maintained through the following year. No parasitoids were retrieved. A series of parasitoid releases were made in 1982 from 31 March to 9 April. During this period a total of 1031 C. albicans adults were released. The sex ratio was generally 1:1. Larval density ranged from 0.25-0.31 larva/leaf cluster. By 1983 the host population had declined to such a low level that a collection of larvae was not possible. The reasons for this population crash are unknown, as field conditions (i.e. host plants, weather) did not alter greatly between years.

No parasitoids were recovered from a small filbert orchard located in Carver, Clackamas County. The site was a fenced in yard which consisted of 10 unsprayed filbert trees. In 1982 226 C. albicans (125 female

and 101 male) were released. Larval density was .31 larva/leaf cluster and the predominant stage was second instar. A collection of 300 larvae in 1983 failed to yield any parasitoids.

The last site from which no parasitoid recoveries were made is also located in Clackamas County near Tualatin. This site is an 8 ha. commercial filbert orchard, part of which was unsprayed. In 1982 a total of 245 C. albicans (116 female and 129 male) adults were released. Winter moth larval density was 0.71 larva/leaf cluster and 60% of the larvae present were in second instar. No parasitoids were recovered from collections of 100 larvae in 1982 and 300 larvae in 1983.

DISCUSSION

The general biology of O. brumata in Oregon does not differ from its biology in England and Nova Scotia (Embree 1965; Varley et al. 1973). The primary developmental differences between O. brumata in Oregon relative to Nova Scotia were that larvae eclosed earlier in the spring (March vs. late April) and pupated earlier in the year (May vs. late June).

The rate of spread of O. brumata in Oregon has

been slow. Although the winter moth has been present in Portland for at least 26 years, it has not been found more than 65km from the city. In Nova Scotia, the winter moth was first discovered in 1949 (Hawboldt and Cuming, 1950). It extended its range from southeastern Nova Scotia to the neighboring provinces of New Brunswick and Prince Edward Island in about 15 years. By 1950 the winter moth was so well established that it was thought to have been present for at least 30 years (Cuming, 1961). Most notable was the severity of defoliation of certain host plants such as Quercus rubra L. (red oak) and Malus spp. (apple). However, the winter moth is adaptable in host plant selection and temperature tolerances (Masaki 1980; Kozchanikov 1950, Wylie 1960b; MacPhee 1967) and it is feasible that O. brumata will continue to expand its distribution range.

The synchrony between eclosion and bud burst of red oak was demonstrated to be a key factor in survival of larvae (Embree, 1965). In British Columbia, Quercus garryana Dougl. (Oregon white oak) has been severely defoliated (Anonymous, no date), but bud burst of this species does not occur until late spring in Oregon when winter moth larvae are in third instar. This information suggests that the distribution of the winter moth in Oregon may be influenced by the presence

of early flushing host plants. Corylus spp. (filbert) are suitable hosts in this respect, and may be an important factor in the distribution of O. brumata in Oregon.

Few species of native parasitoids were observed and overall parasitism was low. Also, parasitoid recoveries from native O. occidentalis were not congeneric with those of O. brumata. Rates of parasitism of O. occidentalis were only 2% (Miller and Cronhardt, 1982).

The relatively low levels in the recovery of C. albicans in 1982 and 1983 can be placed into perspective by reviewing the early results from Nova Scotia and British Columbia. From 1954 to 1961, 25,000 C. albicans and 2000 A. flaveolatum were liberated at 10 sites in Nova Scotia (Embree, 1966). Thirty-one C. albicans adults were released in 1954 and 1008 were released in 1955. Attempts to recover the parasitoid in May, 1955 were unsuccessful. Rearing of 2100 O. brumata larvae collected after the release of C. albicans in June yielded 32 puparia (1% parasitism) in the fall (Graham, 1958). In 1956, rearing of 1700 winter moth larvae yielded 24 puparia (1% parasitism) which survived from the previous year. Total parasitism by C. albicans and A. flaveolatum in 1957 was only 2.8 per cent, two years after the

first introductions (Graham, 1958). In British Columbia, the first recoveries of C. albicans were made four years after the initial releases (Anonymous, 1982).

The numbers of winter moth larvae collected from each release site in Oregon were much less than those in Nova Scotia. However, one site (5 mi. E. Hillsboro, Washington County) sampled indicated 4% parasitism by C. albicans in 1983, only one year after the release. In 1982, parasitism by C. albicans at another site was 1.3 %. Trapping methods indicated establishment of the parasitoid at two other sites, but rates of parasitism could not be determined.

It should be noted that A. flaveolatum was also released at four of the sites sampled (Wilsonville, Tualatin (commerical orchard), east of Hillsboro, and south of Tigard), but was not recovered through any methods of detection. Early recoveries in Nova Scotia indicated that this parasitoid would be the principal natural enemy in controlling winter moth populations (Graham, 1958). However, later assessments indicated that A. flaveolatum did not reach the levels of parasitism attained by C. albicans (Embree, 1966). The flat functional response pattern exhibited by A. flaveolatum results in a decrease in parasitism as host density increases. This limited response may make

early detection more difficult, as releases were made initially in areas of high host density.

No further exotic parasitoid introductions are planned. Presently, the success of both parasitoids in Oregon is dependent on the field liberations made to date. Assessment of the role of C. albicans and A. flaveolatum in the population dynamics of the winter moth in Oregon remains for future investigations.

Footnotes

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Temperature Effects on Larval Eclosion of the Winter Moth, *Operophtera brumata* (L.), in Western Oregon

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ABSTRACT

Estimates of the developmental threshold temperature and thermal unit requirements for larval eclosion in the winter moth, Operophtera brumata L., were obtained from experiments involving eggs exposed to various temperature conditions. The developmental threshold was determined to be 4C. Laboratory experiments demonstrated that eggs which were chilled below the developmental threshold required fewer thermal units for larval eclosion than did eggs not given a chill treatment. The number of thermal units required for eclosion of similar aged eggs consistently decreased with increased chilling time. Eggs placed directly into a 14C incubator within 24 hours of oviposition required 470 (±47) degree-days to mid-hatch. Eggs chilled for 2 weeks at 1C and subsequently placed at 14C required 382 (±33) degree-days to mid-hatch. Eggs chilled for 12 weeks at 1C and subsequently placed at 14C required 156 (±12) degree-days to mid-hatch. This pattern of decreasing thermal requirements was consistent for eggs chilled for periods of 2, 4, 6, 8, 10, and 12 weeks and subsequently placed in one of six selected temperatures (6, 10, 14, 18, 22, and 4-15 (fluctuating) C).

Eggs collected from the field the second week in

December and placed at 14C required 470 degree-days in the laboratory to mid-hatch, whereas those collected at the end of February and placed at 14C required 120 degree-days in the laboratory to mid-hatch. However, the total number of thermal units accumulated in the field and laboratory reached a constant number (approximately 380) after mid-January. This pattern is consistent with emergence from a state of diapause.

Degree-days accumulated from January 15 to mid-hatch in the field are compared from four years of data. Degree-days accumulated in 1981 and 1982 (214 and 189, respectively) were less than those accumulated in 1983 and 1984 (311 and 304, respectively). The differences may be partly attributed to longer freezing temperature conditions the first two years.

INTRODUCTION

The winter moth, Operophtera brumata (L.), is a univoltine defoliator of a wide range of deciduous plants. Adults emerge in the late fall or early winter, the eggs overwinter, larvae hatch and develop in the spring, and pupae oversummer in the ground. Although the general life cycle of the winter moth is similar throughout its geographical range, the timing of phenological events varies. These life cycle differences may be attributed to climatic influence as well as to intrinsic differences between populations (Wylie 1960b, Masaki 1980). Adaptations of insects to season lengths have been reported in a number of cases (AliNiazee 1976, Andrewartha 1952, Carton and Claret 1981, Masaki 1967, Roff 1980, Tauber and Tauber 1981). Phenological variations (i.e. duration of diapause) may occur systematically along a gradient such as latitude or altitude and insect species with a wide geographic range can exhibit genetic adaptations to local climatic conditions. This phenomenon appears to be occurring in winter moth populations as it continues to expand its range.

O. brumata is an unusual insect in that it enters a state of diapause in two stages of its life cycle (egg and pupal) (Masaki, 1980). Tauber and

Tauber (1976) have stated that diapause is largely a dynamic state, and as the season progresses, diapause depth or intensity decreases. Indeed, by current definition, diapause may be little more than a temporary delay in the development sequence. Beck (1980) defines diapause as a state of suppressed developmental rate, and states that some developmental changes do occur during diapause. The physiogenesis which goes on during the diapause state has been termed 'diapause development' (Andrewartha, 1952). The intensity of diapause is variable, and the upper limit for diapause development can overlap the lower limit for morphogenesis, which occurs near 0C (Andrewartha, 1952).

The ability to determine when diapause in winter moth eggs ends and to predict when larval eclosion will occur is of particular interest. If a calendar date can be determined as an approximate time at which diapause is terminated, a thermal unit (degree-day) model to predict when larval eclosion will occur in the field may be developed. The timing of chemical applications or the release of biological control agents is crucial to an effective pest management program. The larval stage of the winter moth's life cycle is the one that is most effectively controlled.

Egg color changes from green at the time of

oviposition through yellow and orange during mid-development to gray just prior to hatching (Wylie, 1960b). These color changes reflect some of the development which occurs during the winter and can be useful in determining when larvae are ready to eclose. The egg stage is particularly cold-hardy and has a mean freezing point of -35C in Nova Scotia (MacPhee, 1964). Wylie (1960b) found that freshly laid eggs kept at 1.5C turned gray in approximately eight months, but did not hatch. At -4.5C eggs would turn yellow in five months, but did not develop further. Also, eggs kept at -12C remained green (Wylie, 1960b).

Embree (1970) studied the seasonal pattern of winter moth egg hatch in Nova Scotia. He determined that eggs exposed to cold December temperatures in the field and subsequently held at 1.7C until March had a theoretical developmental threshold temperature of 39F (3.9C). Mean hatch in the field, which was based on five years of data, occurred when 292 degree-days >39F were accumulated from April 1. These results were obtained from eggs which were subjected to at least three months exposure to temperatures below the developmental threshold.

Gaumont (1955) successfully incubated eggs which were exposed to a variety of temperatures above freezing, but found that 'chilled' eggs required fewer

thermal units to hatch and mortality was significantly lower.

The relationship between intensity of chilling, diapause, and heat units for development is complex and makes the prediction of larval eclosion difficult. Diapause ends gradually as cold temperatures recede and temperatures above the developmental threshold become frequent. This pattern has been observed in many species of insects (VanKirk and AliNiazee 1982, Masaki 1956). Therefore, it is necessary to quantify this relationship before a predictive model for larval eclosion can be constructed. This paper presents data on the developmental threshold temperature of winter moth eggs in western Oregon, the effects of chilling time on egg hatch, and thermal unit requirements for hatch at selected constant temperatures.

METHODS AND MATERIALS

Three sets of experiments were conducted to gain information for the development of a model to predict when larval eclosion will occur in the field. A calendar date for egg hatch can be selected once the degree-day requirements are determined.

Experiment 1: Temperature effects on larval eclosion

The relationship between chilling and subsequent heat-unit requirements for larval eclosion was studied. A series of temperature treatments was set up to determine the effects of chilling and heating on larval eclosion. Chill treatments consisted of keeping eggs (n=180) at 2C for 0, 30, or 60 days. Following chilling, eggs (n=30) from each treatment were placed in one of six temperatures (2, 6, 10, 14, 18, or 22C). Photoperiod for all temperatures was set at 16D:8L. Relative humidities ranged from 50 to 80 percent. Because of the diurnal pattern of hatching (Embree, 1970), eggs were monitored once daily in each treatment.

Similar experiments were conducted in 1983-1984. Chill treatments consisted of keeping eggs (n=180) at 1C for 0, 2, 4, 6, 8, 10, or 12 weeks. Eggs (n=30) were then held at 6, 10, 14, 18, or 22C (16D:8L) until hatch, which was monitored daily. A diurnal fluctuating temperature was also included: 16 hours at 4C and 8 hours at 15C. Relative humidities were maintained at approximately 70 percent.

Data from the chilling and post-chilling temperature treatments in 1983 and 1984 were analyzed to determine the theoretical developmental threshold for O. brumata. The threshold was obtained by

regressing the reciprocal of the development time in days against temperature and extending the regression line to the x-intercept (Arnold 1959; Campbell et. al. 1974). A regression analysis was performed for each chill treatment (0, 30, 60 days) in 1983. Mean hatch was used for each temperature within each chill treatment. Another set of regression analyses were performed in 1984 using all hatch data for each temperature within each of seven chill treatments. Coefficients of determination (R^2) were calculated for each regression. The highest R^2 value indicated which regression best estimated the value of the dependent variable, the developmental threshold.

The estimate of the developmental threshold was used to determine thermal requirements for winter moth larval eclosion. A thermal constant (K) was calculated for each chilling and heating temperature treatment from the equation $K=y(x-a)$, where y is the mean developmental time in days, x is the constant temperature, and a is the theoretical threshold for eclosion (Andrewartha and Birch, 1954). A slight variation was made in calculating degree-days for the fluctuating temperature chamber. Since only eight hours out of 24 were above the developmental threshold, degree-days were calculated using the formula $K=1/3y(x-a)$. Standard deviations were calculated for

each treatment.

Experiment 2: Monitoring of egg hatch in the field

The timing of egg hatch was observed over four generations. Mating pairs of winter moths (n=40) were collected to ensure the acquisition of fresh fertile eggs. This procedure was carried out in late November in 1980 to 1983. Each pair of moths was placed in an individual plastic petri dish with a rectangular strip of paper for an oviposition substrate and put back into the field. Females typically began ovipositing within a period of 24-72 hours. In 1981 and 1982, eggs (n=200 and n=50, respectively) were monitored under field conditions to determine when larval eclosion occurred. Egg hatch was monitored at Wilsonville (Clackamas County) in 1981, and in Salem (Marion County) in 1982. Daily high and low temperatures were recorded from December 1, 1980 to March 31, 1981 at the North Willamette Experiment Station 25 km from Wilsonville. The elevation was comparable to the study site. From December 1, 1981 to March 31, 1982, daily high and low temperatures were recorded at the Salem airport, 3.8 km from the overwintering eggs.

Additional research was conducted in 1983 and 1984 to compare microclimate and ambient temperature data.

The eggs (n=619) from five females were maintained in field conditions from December 1, 1982 until larval eclosion in mid-March, 1983. A thermograph was placed next to the eggs to record hourly and daily temperatures and humidity. Egg hatch was monitored daily. This procedure was carried out again from December 1, 1983 to mid-March, 1984 with eggs from six females (n=60). Daily high and low temperatures recorded from the Salem airport (32 km distant) were also obtained.

A more complex model was used to determine the thermal constant, or number of degree-days, required for eclosion in the field. Degree-days accumulated per day were calculated using a sine wave model(Arnold 1960; Baskerville and Emin 1969). This method assumes the rate of development is proportional to temperature above the threshold. Degree-days were summed using several calendar dates (1 Dec., 1 Jan., 8 Jan., 15 Jan., 1 Feb.) as the initial point to compare values among the four years.

Experiment 3: Determination of emergence from diapause

An experiment was designed to determine when winter moth eggs emerge from a state of diapause in the field and begin to accumulate heat-units. The

selection of a calendar date for this event is needed in the development of a phenological model to predict when larval eclosion will occur in the field. Groups of overwintering eggs (n=30) which were laid on strips of paper in petri dishes were brought into the laboratory from the field at 14 day intervals and were placed at 14C. Eclosion was monitored daily. Degree-days accumulated in the field and in the laboratory were calculated to see if a pattern in thermal unit summations was evident.

A combination of methods was used to determine heat unit requirements for the eggs brought in from the field at two week intervals. Degree-days accumulated outside were determined by the single sine wave model. This total was added to the degree-days accumulated in the laboratory, using the formula K=y(x-a). The thermal constants within each group were then tested in an analysis of variance. Tukey's multiple pairwise comparison method was used to determine significant differences among all groups.

Development of model to predict time of larval eclosion

A model to predict time of eclosion was developed from the laboratory data. A regression of the number of days to hatch (a dependent variable) against the

number of weeks chilled and temperature above the threshold (4C) was performed.

RESULTS

Experiment 1: Temperature effects on larval eclosion

The amount of chilling affected the value obtained for the developmental threshold temperature as well as the number of degree-days required for eclosion. Data from the temperature treatments in 1983 indicated the theoretical developmental threshold for O. brumata is 4C when eggs have been chilled for 60 days (Fig. II.1.). The threshold value predicted for no chill treatment was -5C and for 30 days of chilling was 2C. These lower developmental threshold values were not reasonable, as eggs did not eclose at 2C.

Further analyses of data obtained in 1984 also indicated that the developmental threshold rises as the duration of chilling lengthens. The coefficients of determination also improved in accounting for variation within each chill treatment (Table II.1.). The mean developmental threshold for eggs chilled from 10 to 12 weeks is 4C and R^2 approaches 0.72. Although the developmental threshold might be questioned, it should be noted that eggs held at 2C failed to eclose, and that those held at 6C did eclose.

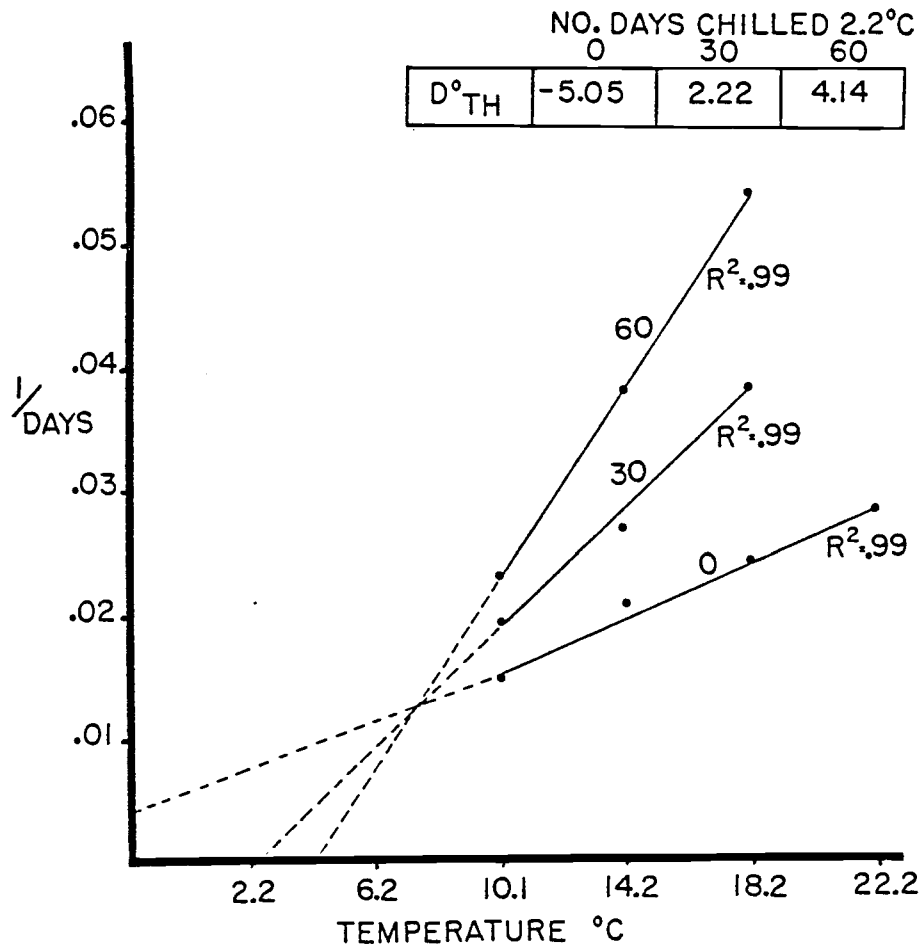

Figure II.1. Developmental threshold temperatures for three chill treatments.

Table II.1. Developmental threshold temperatures for different chilling periods determined by the x-intercept method.

Chilling time (weeks)	Regression equation	Developmental threshold (C.)	R^2
0	y=.000905x + .00423	-4.6	.35
2	y=.001553x - .000164	.1	.57
4	y=.001997x - .002439	1.2	.64
6	y=.002864x - .008427	2.9	.69
8	y=.003325x - .008969	2.7	.69
10	y=.003958x - .01310	3.3	.71
12	y=.00584x - .02776	4.8	.72

The number of days to fifty percent hatch was calculated for each chilling and post-chilling temperature treatment. It is evident that the longer eggs are chilled, the less time (in days) is required for eclosion after exposure to each temperature above the developmental threshold of 4C (Fig. II.2).

Degree-day requirements were also calculated for each chilling and post-chilling temperature treatment. Longer chilling periods reduced the number of degree-days required to fifty percent hatch within each post-chilling temperature (Fig. II.3). Apparently chilling time decreased the effects of the temperatures above the developmental threshold. There were decreasing differences in degree-day requirements to mid-hatch among the post-chilling temperatures as eggs were chilled for longer periods.

An analysis of variance was performed to test for any interaction between chilling and post-chilling temperatures. The ANOVA indicated a significant interaction between these two factors ($P<.001$). Problems with the experimental design (i.e. lack of true replication) suggest that this result is not statisically rigorous, but the pattern is evident. Therefore, further ANOVAS could not be performed.

A comparison of groups of eggs exposed to field temperatures and eggs chilled at 1C (during the same

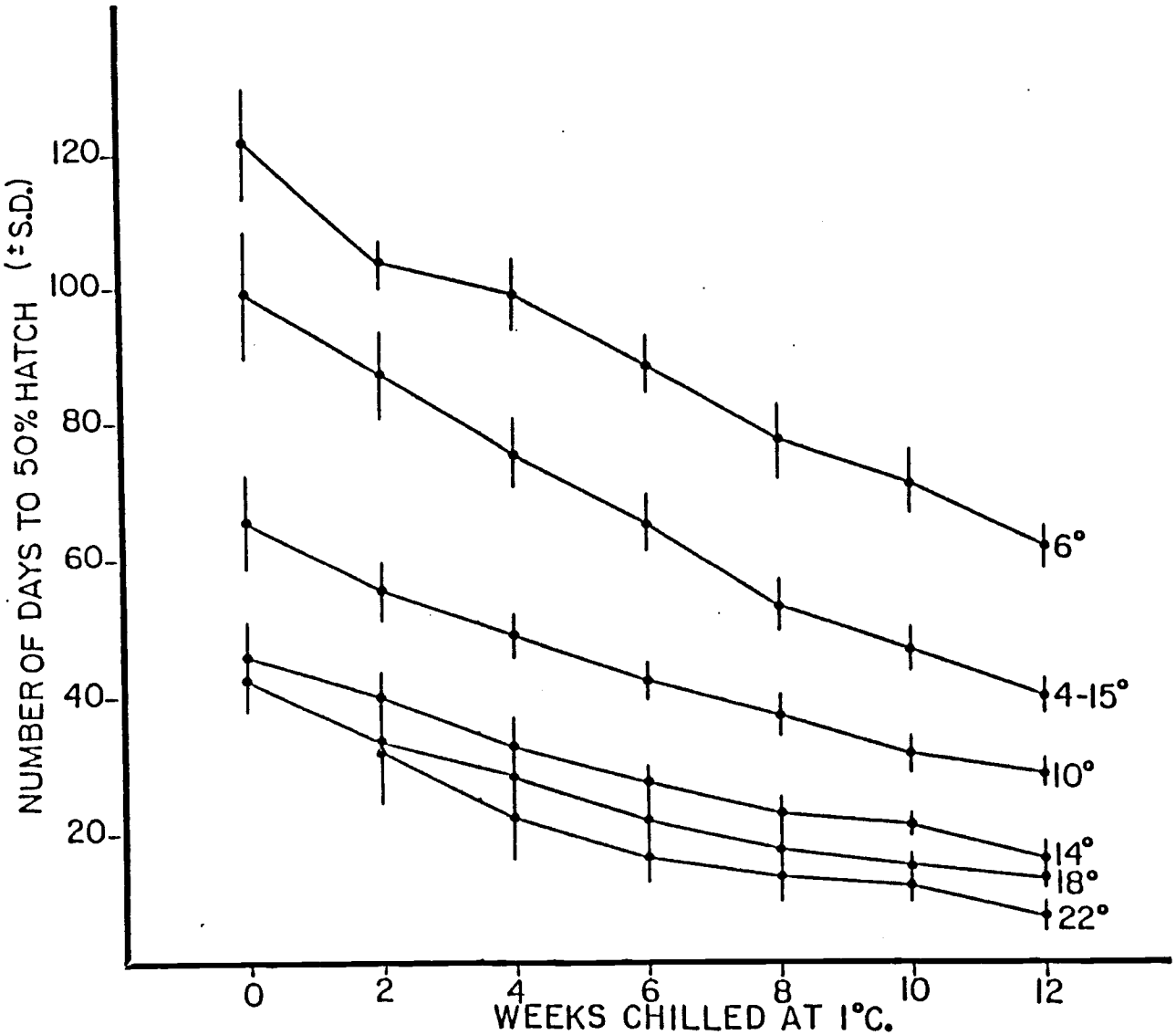

Figure II.2. Number of days to 50% hatch for six temperature treatments.

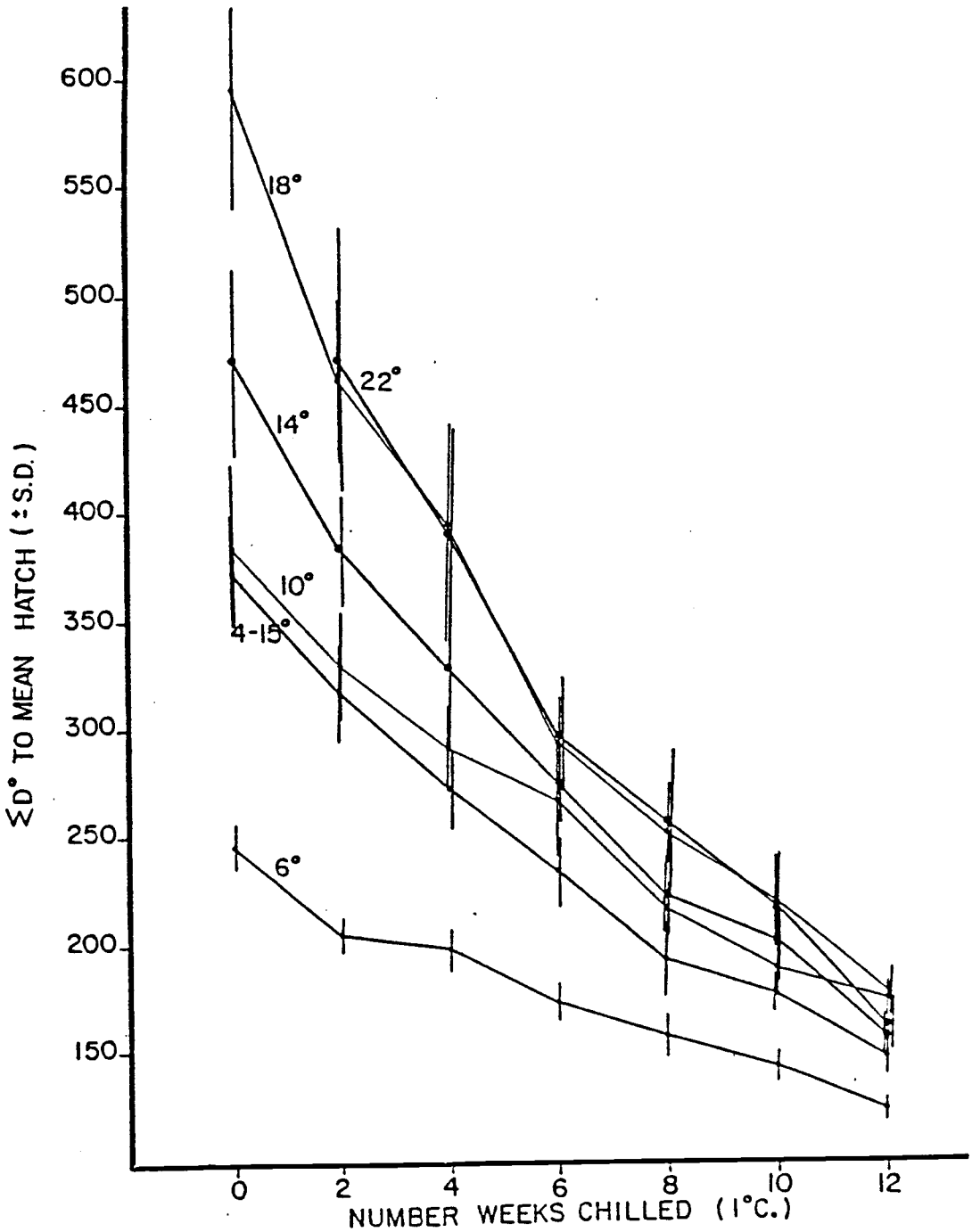

Figure II.3. Total degree-days required to mean hatch for six temperature treatments.

period) which were subsequently placed at 14C shows that the exposure to the constant lower chill temperature resulted in a decrease in thermal units required for eclosion (Fig. II.4). This suggests that exposure to a constant chilling temperature is more effective in increasing the rate of diapause development than the fluctuating temperatures in the field.

Eggs placed in the fluctuating temperature treatment required a mean hatching time between those placed at 6C and those at 10C. This result is consistent with the number of heat units accumulated. Assuming a 4C threshold, two degree-days per day were accumulated at 6C, and six degree-days per day were accumulated at 10C. The formula for calculating degree-days in the fluctuating temperature chamber indicates 3.67 degree-days were added each day.

Experiment 2: Monitoring of egg hatch in the field

The monitoring of egg hatch in the field for four seasons provided interesting results. Fifty percent of the accumulated total winter moth larval eclosion in the field occurred by 14 March in 1981, by 15 March in 1982, by 9 March in 1983, and by 17 March in 1984.

Thermal units were calculated from four years of

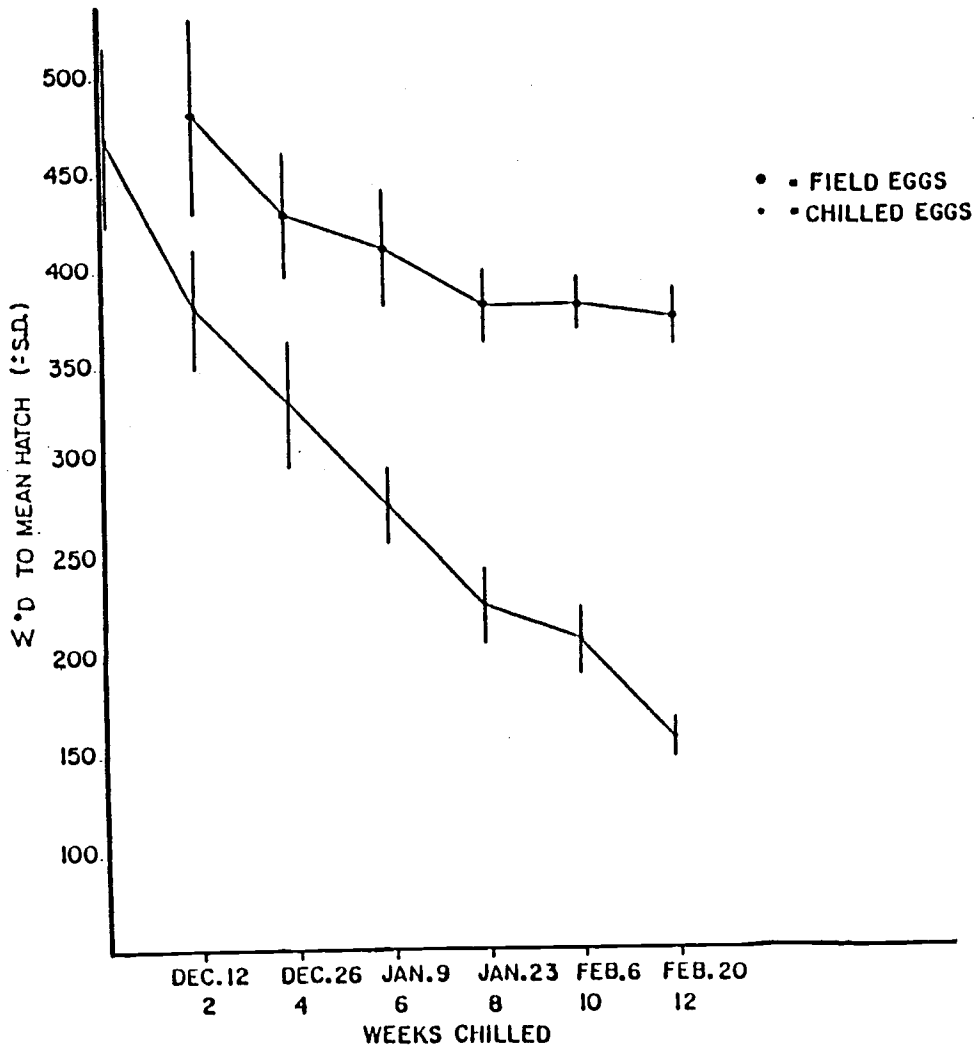

Figure II.4. Comparison of degree-days required to mean hatch between field and chilled eggs placed at 14C.

weather data using 1 December, 1 January, 8 January, 15 January, and 1 February. There was wide variation among the years on a calendar basis (Table II.2). If any of these calendar dates was appropriate for degree-day initiation, each year of data would produce a similar value for thermal unit accumulation. It may be argued that the use of official weather station data in the first two years affected these results. However, a comparison of weather data from Salem in 1984 with thermograph data in the field in Buena Vista (32 km distant) indicated a difference of about 1C for the mean daily temperature over a two week period. Discrepancies between thermograph data and official meterological temperatures would not be great enough to affect the observed differences in degree-day summations.

Experiment 3: Determination of emergence from diapause

A pattern of degree-day requirements to 50 percent hatch was observed for those eggs which were brought in from the field at two week intervals (Fig. II.5.). The number of thermal units accumulated in the field plus those accumulated in the laboratory continually declined until mid-January. After mid-January, thermal unit accumulation to 50 percent hatch reached a fairly

Table II.2. Variations in degree-day accumulation for 50% larval eclosion and freezing temperatures among years.

Year	Date of degree-day initiation (C.)					No. days below OC
	Dec. 1	Jan. 1	Jan. 8	Jan. 15	Feb. 1	
1981	327	247	226	214	167	18
1982	288	196	195	189	143	17
1983	474	364	327	311	239	6
1984	417	361	326	304	256	7

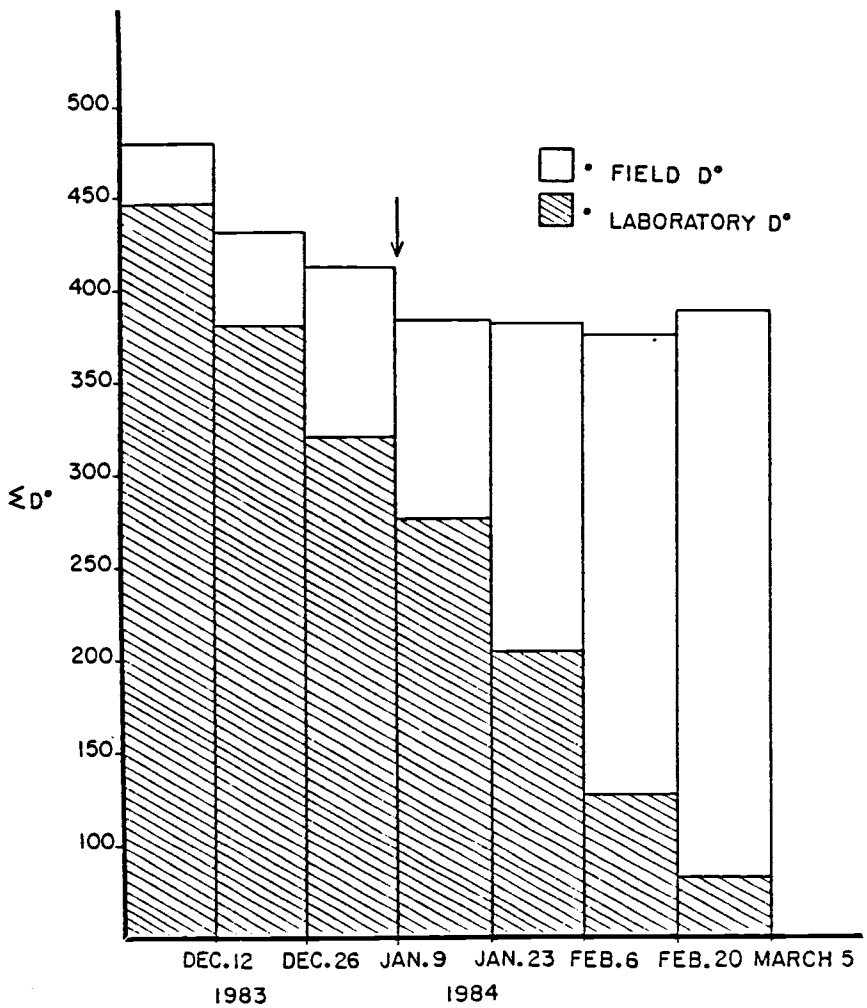

Figure II.5. Laboratory and field degree-days accumulated to mean hatch (Developmental threshold=4.0C). Arrow indicates date that degree-day summations begin to approach a constant value.

constant value. Tukey's multiple range test indicated that batches of eggs brought into the laboratory from 23 January to 5 March were not significantly different (with 95% confidence limits) in thermal unit requirements. This result indicates that thermal units are not accumulating from the time of oviposition (1 December).

The date 15 January was selected for initiation of degree-day summation because of the statistical results explained above. This date will be used later in the development of a model to predict when larval eclosion will occur in the field.

Development of model to predict time of larval eclosion

To account for effects of chilling, a model was developed from the laboratory data. This model could be used to predict time of eclosion at constant temperatures. The equation $\hat{n}=aw + b(\text{sqrt } t) + c$, where $\hat{n}$=mean number of days to hatch, t=temperature-4, and w=number of weeks chilled, was tested. The estimated parameters of the model (a,b, and c) were determined. The square root function was used because the influence of each 4C increment on hatch decreases from the lowest to the highest temperature. The equation $\hat{n}=(-2.8)(w) + (-24.7)(\text{sqrt } t) + 131.4$ estimated days to hatch. The

coefficient of determination (R^2) was 0.88. Table II.3 ranks each chilling and post-chilling temperature treatment in order of best fit to the model. Those treatments with the least amount of difference between the observed mean number of days to hatch and predicted mean number of days to hatch have the lowest ranking.

Table II.4 shows the rank sums of each chilling time and post-chilling temperature treatment. Rank sums for chilling periods indicated that the model was most accurate for those eggs chilled for six weeks. All other chilling periods ranked closely together. The rank sums of the post-chilling temperature treatments indicate that hatch time is most accurately predicted by the model when eggs are maintained at 18C. Predictive accuracy of the model declines at 14, 6, 4-15, and 22C, respectively. The model is least accurate in predicting hatch time when eggs are maintained at 10C.

DISCUSSION

One of the prerequisites for the determination of an appropriate developmental threshold temperature is that the data from which it is calculated involves a temperature range normally encountered by the stage of

Table II.3. Comparison of observed and predicted mean number of days to hatch. Treatments ranked in order. Model: $\hat{n}=(-2.8)(w) + (-24.7)(\text{sqrt temp}) + 131.4$

Rank	CT	C	O-P
1.5	2	18	0
1.5	4	18	0
4.5	6	18	-1
4.5	8	18	+1
4.5	4	4-15	+1
4.5	12	6	-1
7.5	6	6	+2
7.5	6	4-15	-2
9	10	6	+3
11.5	8	6	+4
11.5	10	14	-4
11.5	12	14	-4
11.5	0	18	+4
14.5	2	22	+5
14.5	10	18	+5
16.5	0	14	-6
16.5	6	22	+6
18.5	4	22	+7
18.5	0	10	-7
22	12	10	-8
22	8	14	-8
22	12	18	+8
22	2	4-15	+8
22	8	4-15	-8
26	10	4-15	-9
26	6	14	-9
26	4	14	-9
29.5	2	10	-10
29.5	6	10	-10
29.5	2	14	-10
29.5	8	22	+10
33	12	4-15	-11
33	10	10	-11
33	4	10	-11
35	2	6	+12
37	4	6	+13
37	8	10	-13
37	10	22	+13
39	12	22	+16
40	0	4-15	+17
41	0	6	+26

CT =chilling time in weeks
C =temperature after chilling
O-P=difference between observed and predicted days

Table II.4. Rank sums (RS) by chilling time and temperature treatment.

Chilling time (weeks)	RS	Temperature	RS
0	127.5	6	145.5
2	132.0	10	202.5
4	120.5	14	143.0
6	91.5	18	60.0
8	126.5	22	155.0
10	131.0	4-15	151.0
12	132.0	--	--

development being examined. Since this normal temperature range may vary among geographical locations, the appropriate developmental threshold temperature may vary also. Therefore, it is necessary to re-evaluate the base temperature of 3.9C determined by Embree (1970) in Nova Scotia for winter moth larval eclosion.

The results of the regression analyses of chilling and post-chilling temperatures against the reciprocal of development time were quite interesting. Instead of obtaining one base temperature, the x-intercept method yielded different values which increased as chilling periods increased. Embree's estimation of 3.9C was obtained only for those eggs chilled from 10 to 12 weeks. Indeed, the winters in Nova Scotia easily keep winter moth eggs below their developmental threshold temperature for this period of time. Coefficients of determination (R^2) improved with each increase in chilling time in the laboratory experiments in Oregon which suggested that chilling improved the estimates obtained for a base temperature. Weather data from the Willamette Valley in Oregon indicate that temperatures do not usually fall below freezing for more than a few weeks (Fig. II.6.). This would imply a lower developmental threshold of 2 or 3C from the regression data (Table II.1). However, winter moth eggs do not

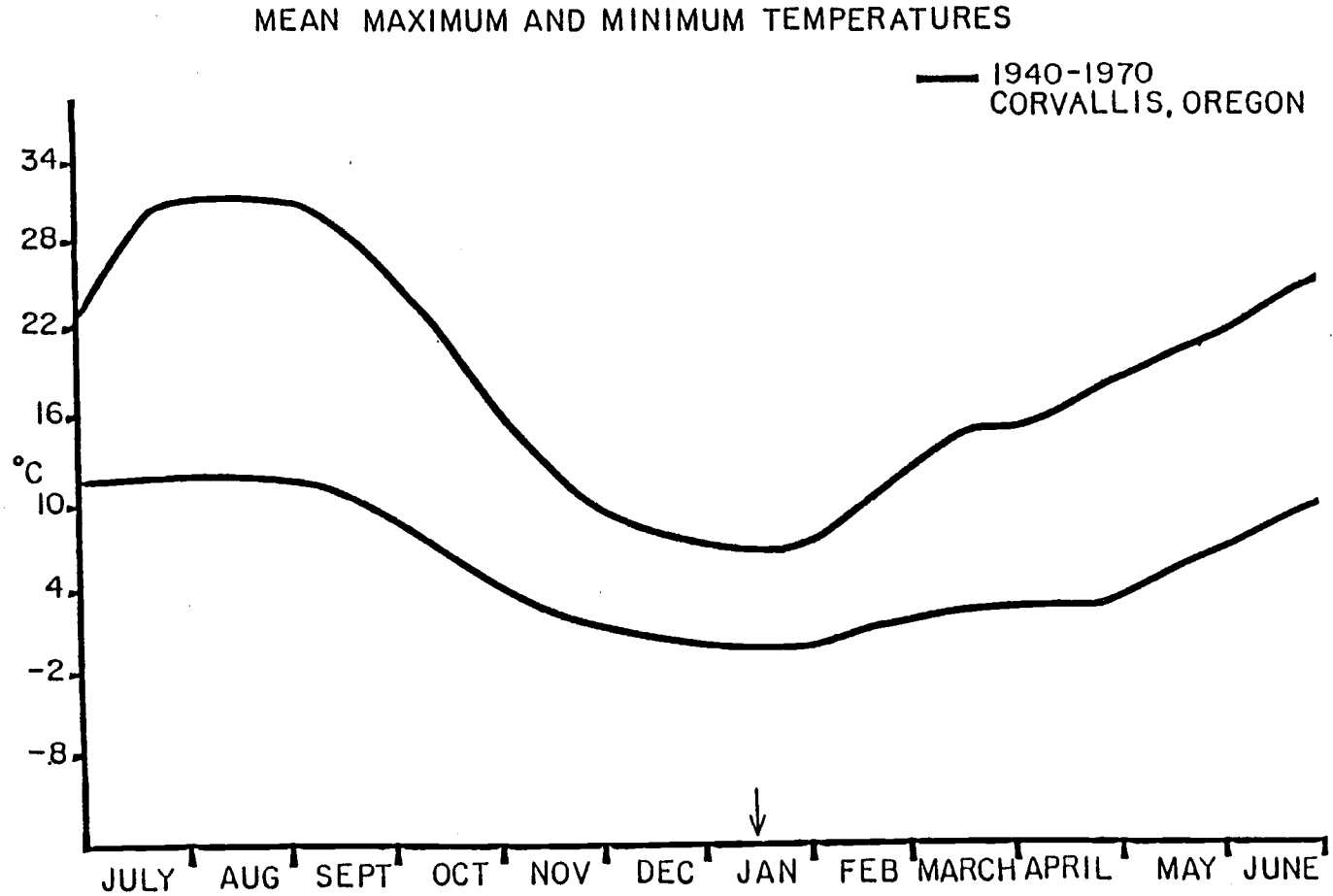

Figure II.6. Weather data accumulated for 30 years from Corvallis, Oregon in the mid-Willamette Valley.

hatch at 2C even when maintained well into the summer months. Furthermore, Wylie (1960b) found that no larval eclosion occurred below 6C in populations from Europe. This information indicates a 4C developmental threshold is valid for the Oregon winter moth population.

There has been some dispute as to the occurrence of diapause in the egg stage of winter moths from different geographical regions (Embree 1970, Wylie 1960b). Kozhanchikov (1950) stated that diapause was 'obligatory' in the U.S.S.R., and Wylie has suggested that no true diapause occurs in central Europe. Briggs (1957) suggested that eggs develop in the field in England continuously from the time of oviposition. Because of seasonal and phenological differences between localities, egg hatch occurs in early May in Estonia, in early April in northern Switzerland, and in early March in southern Italy (Wylie, 1960b). The duration of the egg stage is only two months in southern Italy, but nearly eight months in northern Europe. Masaki (1980) explains these differences in the life cycle as variations in diapause traits. These variations may be partly due to the direct effect of temperature and partly due to the genetic variation in the intensity of diapause.

Temperature effects on diapause induction,

maintenance, and termination are well known. Thermoperiodic induction of diapause has been demonstrated in a number of species (Beck, 1982). Among insects in which the embryonic diapause is determined by the maternal system, the termination of diapause is usually insensitive to photoperiod but is accelerated by exposure to low temperatures (Beck, 1980). Diapause intensity (or duration) in the winter moth appears to be largely determined by responses to temperature, rather than photoperiod.

Tauber and Tauber (1976) have hypothesized that the temperature optimum for diapause development rises as diapause development progresses, and when the optimum temperature for diapause development reaches the developmental threshold temperature, diapause ends and morphogenesis resumes. The results of the Oregon experimental data suggest that there is some sort of physiogenesis occurring below 4C. The insect's embryonic development is continuing at temperatures below the base temperature, but the entire developmental sequence (hatching) can not be completed. This has been documented in other species (Lin, et.al., 1954). Increased chilling periods may be raising either the developmental threshold temperature or the threshold for diapause development. Consequently diapause is maintained throughout the chilling period.

This response to chilling is accepted as evidence that winter moth eggs are in a diapause state.

Chilling enhances the rate of physiogenesis, or diapause development, but it is not necessarily a requirement for successful eclosion. However, it does decrease mortality and compresses the hatching period. The effects of chilling on termination of diapause and post-diapause development are documented in a number of species of insects (Church and Salt 1952; Vankirk and Aliniazee 1982; Strong 1962; Johansen and Eves 1973).

With the acceptance of 4C as the developmental threshold for winter moth larval eclosion in Oregon, further analyses of experimental data are possible. Using this base temperature, estimates indicated that increased chilling periods decreased the thermal constants required for hatch within each temperature treatment (Fig. II.3.). Also, the differences in thermal constants among temperature treatments decreased with longer chilling periods (Fig. II.3.). The exposure to the fluctuating temperature regime did not appear to increase or decrease thermal unit requirements (=development rate).

If the assumption that winter moth eggs are in a state of diapause is correct, the termination of diapause and resumption of morphological growth and differentiation will occur at some time. The

determination of the timing of this event is necessary in developing a phenological model.

The date for initiation of degree-day summation is often selected by comparing thermal constants from a number of years. Several calendar dates are tested, and the one showing the least amount of deviation among years (from mean numbers of thermal units required for emergence or hatch) is selected as the initiation date (Aliniazee 1979, Gage, Mukerji and Randell 1976, Reissig, et.al. 1979).

The results of this method for determining an initiation date for thermal unit accumulation in winter moth eggs were not consistent (Table II.2). However, the results from the third experiment indicated that diapause is broken in mid-January.

The egg hatch model developed for the winter moth in Oregon has four assumptions:

1. Winter moth eggs enter a state of diapause which is maintained by chilling below the base temperature.

2. Chilling enhances the rate of diapause development and decreases the thermal units required for eclosion during post-diapause development.

3. The developmental threshold of 4C is valid, based upon observations in the laboratory that eggs do

not hatch below this temperature.

4. Thermal units summed after 15 January are functionally related to time of hatch.

Assumption 2 holds the key to the completion of this model. The effects of chilling on winter moth eggs must be taken into account. Weather data from the four years show that freezing temperatures occurred more frequently in the winters of 1981 and 1982 than in 1983 and 1984 (Table II.2). The variation in thermal unit summation among the years may be explained by these differences in 'chilling' time. Differences in degree-day requirements for emergence of the apple maggot, Rhagoletis pomonella Walsh, have been correlated with the duration of the cold period in winter. This correlation indicates that the length of chilling time preceding morphogenesis affects the number of degree-days required to complete post-diapause development or that the threshold temperature for development is affected (Laing and Heraty, 1984). Results from the winter moth experiments suggest that it is the former situation which is occurring.

Little research has been conducted on accumulation of chill units for insects. It has been reported that the rate of movement of alfalfa weevil adults can be

accurately predicted from the cumulative degree days below their metabolic threshold (Huffaker, 1980). The phenomenon of chill units is well recognized in plants (Richardson et.al. 1974, Ashcroft et.al. 1977, Shaltout and Unrath 1983). Deciduous fruit trees experience a physiological condition each winter known as rest. After trees have been exposed to sufficient cold temperatures, rest is completed and buds respond to warm temperatures by physiological development (Richardson, 1975). A chill unit model has been developed to determine the completion of rest for two peach cultivars (Richardson, et.al., 1974). The model is based on the concept of two required constants-the chill units necessary to complete rest, and the growing degree hours required to reach full bloom (Ashcroft, et.al., 1977).

The application of a chill unit model to estimate winter moth larval eclosion seems appropriate from the results of laboratory and field data analyses. The difficulty in developing such a model is that chilling enhances diapause development, but it is not a requirement. Therefore the model requires two variables, the second (degree-day accumulation) being dependent on the value of the first (chilling unit accumulation). This complication makes the completion of a phenological model difficult without further

research on the effects of chilling. Different chilling temperatures (-1C, -4C) may have a greater chilling 'contribution' than 1C or 2C to diapause development. Richardson (1974) assigned different chill unit contributions (less than 1) to temperatures above or below a standard equivalent (1 hour at 6C=1 C.U.). Wylie (1960b) demonstrated that winter moth eggs in Europe showed some development when maintained at -4.5C, but showed no developmental changes at -12C. Diapause development appears to continue at temperatures well below the developmental threshold and effective chilling temperatures may exist within a minimum 8C range.

The computerized program developed by Richardson (1974) converts hourly temperatures to equivalent chill-unit values. Since hourly temperatures are usually not available, hourly estimates are made from maximum and minimum temperatures taken at 12 hour intervals. Another model for calculating "heating degree days" and "cooling degree days" has been proposed by Allen (1976). This modified sine wave method allows for the calculation of the area below the developmental threshold. The calculation of this area approximates the number of cooling degree days which could be useful in the developing the winter moth phenological model. A good estimate of effective chill

units will be the key to an accurate estimate of the thermal units required for hatch in post-diapause development of the winter moth.

CONCLUSION

Investigations of the winter moth and its parasitoids in Oregon have provided information which will be useful in future management programs. The Oregon winter moth population is an example of a seasonally well-adapted biotype. The seasonal differences between Nova Scotia and Oregon may account for high larval densities occurring on different plant species. In Nova Scotia hatch is synchronized with bud burst of Quercus rubra, whereas in Oregon hatch occurs earlier in the year and is synchronized with earlier flushing Corylus cornuta.

The genetic heterogeneity within winter moth populations has allowed the species to adapt to the many variations in climate encountered over its extensive distribution. Similar adaptations have been observed in other widely distributed species (Masaki 1956; Masaki 1967; AliNiazee 1976; Campbell, et. al. 1974). Seasonal adaptations are most evident by the differences in diapause duration among different geographical areas. The duration of egg diapause in the winter moth decreases along a climatic gradient from north to south, whereas the duration of pupal diapause increases along the same gradient (Wylie, 1960b). This is observed in North America where larval

eclosion occurs in May in Nova Scotia and in March in Oregon.

Three inherent traits may contribute to differences in diapause duration between geographic races of a species: 1) the intensity of diapause 2) the insect's reactions to temperature during diapause development, and 3) responses to photoperiod during diapause (Tauber and Tauber, 1976). Evidence from the literature and studies in Oregon suggests that the former two traits are most applicable to winter moth development. Wylie (1960b) found that the inherent differences in the duration of the egg and pupal stages from various localities increased the effect of temperature differences.

The developmental threshold for eclosion of the winter moth is 4C. Variations in heat requirements for eclosion among the chilling times not only indicate the adaptability of the winter moth, but also demonstrate the difficulty in determining the timing of certain phenological events (i.e. hatch, termination of diapause). Evidence suggests that diapause is broken in mid-January in Oregon. As chilling time influences the rate of diapause development and subsequently the thermal requirements for larval eclosion, it will have to be incorporated into any predictive model. Therefore, before postdiapause heat requirements can be

used to accurately predict eclosion, the responses to temperatures during diapause and the transition period to postdiapause development should be established (Tauber and Tauber, 1976). The data presented have shown that the length of the chilling period affects the timing of eclosion, but more information is required on the effects of exposure to different chilling temperatures. Optimally, a predictive model should include the number of degree-days required for eclosion which are dependent on the number of chill units accumulated during diapause.

Because the intraspecific diversity in the winter moth's seasonal cycles among geographical areas has been demonstrated, it would be beneficial to examine the interactions with its parasitoids. Current biological control practice has been to import natural enemies, when possible, from areas having a similar climate to the release area. In this particular program, Cyzenis albicans and Agrypon flaveolatum were introduced from Nova Scotia into Oregon. The winter climate of Nova Scotia is generally much harsher than Oregon's and subfreezing temperatures can prevail for several months. Temperature has been demonstrated to have differential effects on rates of development and fecundity in a host and its parasite (Burnett 1949; DeBach 1965; Heron 1961; Nealis, et.al. 1984;

Maslennikova 1959). Climate can affect the success of a parasite population in regulating the host population among different geographical areas. The establishment of C. albicans in Oregon has been a positive step in the biological control of winter moth, but the impact of the parasitoid on the host population will not be known for several years. The relationship between the host and parasitoid may initially be unstable.

The synchronization between a host and parasite can be the result of independent adaptations to the environment or the result of a dependence of the parasitoid upon the physiology of the host (Maslennikova, 1959). Puparia of C. albicans from different geographical areas will yield adults at times which correspond to the time of winter moth larval eclosion in each area (Wylie, 1960a). Whichever case applies here, C. albicans initially may have an adjustment period before synchronizing with Oregon's winter moth population.

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APPENDIX

APPENDIX I

Laboratory culture of C. albicans

An experiment to determine the most susceptible larval instar to parasitism by C. albicans was conducted. Second through fifth instar larvae were fed C. albicans eggs. Mature adult female parasitoids were induced to oviposit on damaged filbert leaves. Leaves were damaged naturally by feeding larvae or artificially by punching holes. Foliage was then cut into small sections containing one to three eggs and these were placed with larvae which had no other food source. After consumption, larvae were allowed to continue feeding on host plant material until pupation.

This experiment to determine host stage susceptibility to parasitism indicated that fourth instar larvae were most likely to be parasitized through egg consumption. Of 91 fourth instar larvae fed parasitoid eggs, 30 (33%) became parasitized and 20 C. albicans adults were reared successfully. The least susceptible stage was second instar, probably due to eggs being damaged during consumption. None of the 31 second instar larvae were successfully parasitized. Of 70 third instar larvae induced to swallow parasitoid eggs, 11 (16%) became parasitized and 7 parasitoid

adults were recovered. Seven fifth instar larvae out of 36 (19%) were successfully parasitized, but only two C. albicans adults emerged. The results of this experiment indicated that third through fifth instar O. brumata caterpillars are susceptible to parasitism by C. albicans.

An attempt was also made to mass culture C. albicans in the laboratory to augment introductions in the field and to have a source for biological research. In 1981, leaves with parasitoid eggs were fed to 354 O. brumata larvae. This procedure was repeated in 1982 and 2237 late instar larvae were fed parasitoid eggs. The larvae had been collected from the field early in the season. Pupae oversummered in total darkness at 13C and were misted weekly with a one percent solution of sodium proprionate. The temperature was lowered to 7C from October to March. In March it was raised to 18C for parasitoid emergence.

Of the 354 O. brumata larvae inoculated in 1981 with C. albicans eggs, 39 adult parasitoids were retreived in 1982. The result suggested that mass culturing the parasitoid was feasible, even with only 11% success.

The inoculation of 2237 O. brumata in 1982 proved to be not only labor intensive, but relatively unsuccessful. In the fall of 1982, 66% of the larvae

inoculated emerged as winter moth adults. The following spring, only 47 C. albicans adults were recovered. Random dissections of 1234 pupae yielded 67 C. albicans puparia.

A possible reason for such a low success ratio is that there may have been a fertility problem with the eggs, although some male and female parasitoids were observed mating prior to oviposition. There were also problems with mold and fungus, despite misting with the recommended sodium proprionate solution (Maybee and Wylie, 1961). Also, peat and vermiculite may not be the best medium for maintaining moisture. Survival in the laboratory of C. albicans puparia is highest when contact moisture is present continuously (Maybee and Wylie, 1961).

Another factor in the failure of some of the parasitoids to emerge may have involved temperature. Maybee and Wylie (1961) suggested reducing the storage temperature to -3.3C from January to May to maximize survival. As winter moth larvae eclose in March in Oregon, the length of cold storage had to be decreased. Also, Oregon winter temperatures do not usually remain below freezing for any duration. Consequently, the incubator temperature was maintained at 7C from October to March. These differences may have limited parasitoid rearing success, as the puparia were

collected in Nova Scotia and adults were shipped directly to Oregon. The onset of adult emergence is affected by temperature and also by intrinsic differences among regionl populations (Wylie, 1960b).

Van den Bosch (1968) has stated that diapause in host and parasitoid stocks can severely limit propagation of entomophagous insects. This may have been one of the technical difficulties in rearing C. albicans. A complicated biology, as that of Cyzenis, increases the number of factors to be considered in mass rearing. Females contain their full complement of eggs on emergence, but these are immature and the adults must feed until egg maturation. Hassell (1968) demonstrated that female Cyzenis adults respond to leaf damage in selecting an oviposition site. They do not distinguish between artificially damaged leaves and those damaged by larval feeding, but they do prefer foliage sprayed with a honey solution. Damaged leaves which were sprayed with a honey solution was a successful technique in inducing oviposition.

Mass rearings of winter moth larvae in Nova Scotia have shown that first and second instar larvae are not parasitized by C. albicans. Parasitism of the remaining instars reaches a peak as the host nears pupation (Embree and Sisojevic, 1965). This information suggested that host stage was not a problem

in mass culturing the parasitoids. Many of the larvae inoculated with parasitoid eggs were nearing pupation.