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Title: OVIPOSITION OF THE CODLING MOTH, LASPEYRESIA POMONELLA (L.), ON SEVERAL VARIETIES OF APPLES AND PEARS

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Ovipositional behavior of the codling moth, Laspeyresia pomonella (L.), on several varieties of apples and pears grown in the Pacific Northwest was investigated during the spring/summer of 1979. Field studies showed that early in the season more eggs were laid on the Bosc variety than on several other apple and pear varieties. The number of eggs laid on all varieties, except the early ripening Gravenstein, increased as the season progressed. Additional investigations showed that significantly fewer eggs were laid on cultivars tested after their normal harvest periods. It was suggested that volatiles associated with fruit ripening, such as ethylene, may act as oviposition inhibitors.

The location of eggs on apple and pear cultivars was also investigated. It was found that on apples more eggs were laid on the upper-leaf surface than the lower-leaf surface, while on pears the

"preference" was reversed. This difference was probably due to the moths avoidance of the more pubescent under-side of apple leaves. The percentage of eggs laid on apple and pear fruits did not change significantly throughout the season.

Contrary to previous reports, codling moths were found to "prefer" pear cultivars to apple cultivars when given a choice between the two. This "preference" was seen late in the season but not early in the season, indicating that it was a result of factors associated with the seasonal growth of the plants. Additional data suggested that it was a result of physicial, as well as chemical, factors.

Levels of the known colding moth oviposition stimulant, alpha-farnesene, present in the epicuticular wax of apple and pear fruits, were determined twice during the season for each variety. The total amount per fruit and per unit area of skin was greater for all four pear varieties than the five apple varieties. On all cultivars, the total amount of alpha-farnesene on individual fruits increased with increasing fruit size. However, the amount of the sesquiterpene per cm^2 of fruit skin decreased from early to late season. Varietal differences in the concentrations of alpha-farnesene were positively related to differences in total oviposition per female on apple and pear cultivars.

Oviposition of the codling moth, *Laspeyresia pomonella* (L.), on Several Varieties of Apples and Pears

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I. Introduction

A. Economic Importance and Distribution

The codling moth, *Laspeyresia pomonella* (L.), is the key insect pest of pomaceous fruits throughout the world. It is a constant threat to production and growers must regularly direct seasonal spray programs against it. Despite the use of chemical control programs, damage attributed to this species results in considerable losses annually. The principal damage is inflicted by the larvae as they penetrate into the fruit flesh. These entries are not only unattractive to consumers but also cause problems in sorting and storage. The allowable damage by the codling moth as determined by the various grade standards set for the fresh fruit market, as well as by tolerances set for commercial canning is near zero. Fruits which do not meet minimum standards are classified as culls and cannot be used for fresh shipment or commercial canning. To avoid crop loss, costly sorting of damaged fruits, and exceeding the tolerance for total defects, growers try to keep codling moth damage below 1 percent. Dependence on chemical control to keep this pest below damaging levels has led to problems of environmental contamination, resistance to insecticides, pest resurgence and the development of secondary pests. Growers must combat a variety of previously minor or innocuous species (e.g., the red-banded leafroller, Argyrotaenia velutinana Walker, the pear psylla, Psylla pyricola Foerster, the European red mite, Panonychus ulmi Koch, and the two-spotted spider mite, Tetranychus urticae Koch) which have been released from biological control by the adverse effects of the codling moth sprays on the beneficial species.

From its original home, probably in southern Eurasia, the codling moth has spread throughout the temperate regions of the world, with the exception of Japan and the mainland of Asia east of about the 90th longitude east (Chapman and Lienk, 1971). According to published reports, it arrived on the east coast of North America sometime in the late 18th or early 19th century and probably earlier in South America. In North America, the species gradually spread westward reaching California in about 1874 (Putman, 1963). By the latter half of the 19th century it had also been reported in Australia, New Zealand and South Africa (Huffaker and Messenger, 1976).

B. Hosts

The codling moth attacks a variety of tree crops ranging from nut crops to stone and pome fruit crops. These include apple, pear, quince, apricot, peach, plum, cherry, almond and walnut. All are members of the rose family except for walnut which is in the family Juglandaceae. It is most destructive to apple and pear but has also been reported as a pest of some consequence on apricots in California and South Africa (Madsen and Borden, 1954; Pettey, 1925) and the

Persian walnut, Juglans regia in California and Europe (Quayle, 1926; Putman, 1963). In Columbia the codling moth is commonly found on another non-rosaceous host, Rheedia madruna Planch and Triana (Family Guttiferae) (Garces and Gallego, 1947). It has also been reported on such incidental hosts as chestnut, Castanea spp. (Fagaceae), persimmon, Diospyros spp. (Ebenaceae), hawthorn, Crateaegus spp. (Rosaceae) and ornamental crab-apple, Malus spp. (Rosaceae) (Putman, 1963).

Several early studies were conducted to determine variations in the resistance or susceptibility of apple varieties to codling moth injury and the factors causing any variations noted. Felt (1910) observed a higher percentage of infestation on McIntosh trees than on Wealthy. Newcomer and Yothers (1924) observed that varieties such as Winesap and Arkansas were attacked less than some of the more fragrant varieties, such as Spitzenburg and Delicious. Cutright (1935) reported the following results in terms of percentage of fruit injured by the codling moth: Ben Davis, 23%; Cortland, 18%; Grimes, 12%; Jonathan, 7%; and King David, 4%. Hall (1929), Cutright and Morrison (1935) and Whitehead (1944) also found Jonathan to be less susceptible. In most of these early studies, resistance was associated with early ripening and harvest prior to emergence of the later codling moth broods. Whitehead (1944) and Cutright and Morrison (1935) indicated that some varieties (e.g., Jonathan, McIntosh, Winesap, Stayman and others) possessed some resistance factors other than date of maturity. Characteristics suggested as being connected with susceptibility to codling moth injury were as follows: (1) above average size (Wolf River, Fallwater), (2) unusual amount of fragrance (Delicious, Spitzenburg), (3) tender skin (Chenango, McIntosh) and (4) sub-acid or sweet varieties (Paradise Sweet, Delicious). Putman (1949) found that an epidermal grease present on Jonathan apples after storage was toxic to newly hatched larvae but he did not determine its pertinence to resistance. More recently, the influence of fruit odor on susceptibility has received considerable attention. Varietal differences in fruit odor, including certain specific constituents which act as larval attractants and/or oviposition stimulants, have been tentatively correlated with host preference (Sutherland, et.al., 1977; Russ, 1976). This area of research, especially as it relates to fecundity and oviposition preference will be reviewed in a later section.

Varietal differences in susceptibility to codling moth injury have also been noted for pears. Westigard, et.al. (1976) found that the varieties Bosc, D'Anjou and Comice were less susceptible to larval entry than Bartlett. This was probably caused by the formation of stone cells in the Winter pear cultivars.

C. Life History

Although there are some differences in biology on different hosts, there is little change in the basic life history. The only major deviation from the basic pattern has to do with the influence of climate on the number of generations. Multiple generations are common in most apple and pear growing regions of the world, including North America, Europe and Asia. The univoltine situation occurs along the northern fringe of apple production in all three of these regions. The last generation in any multivoltine locality includes larvae from preceding generations which also enter diapause and overwinter (Putman, 1963).

The terminology used here for the various stages in the life history is that followed for many years in North America, as described by Putman (1963). A brood includes all individuals in a particular life stage, in any one generation. Each brood is numbered according to the generation to which it belongs. The brood of moths from overwintered larvae is termed the spring brood. These moths produce the first brood of eggs, which together with the first broods of larvae, pupae and adults constitute the first generation. Subsequent broods and generations, when they occur, are numbered accordingly (e.g., second, third, etc.).

Codling moths overwinter as mature diapausing larvae in cocoons under the bark scales on the trunk or main limbs of the host tree, or in other protected places such as litter on the ground, pruning wounds, and bin storage areas. In the spring, overwintering larvae change into light brown pupae. The pupal stage may last anywhere from four to six weeks. Male moths usually emerge continuously for a week prior to the females appearance. Emergence of the moths normally occurs with one or more periods of peak activity, each referred to as a "flight". The females lay their eggs singly on the foliage or fruit. Eggs of the first generation hatch after 10 to 14 days, depending on the temperature, while eggs of the second and subsequent generations usually hatch after 6 or 7 days (Johansen, 1978). Damage by the codling moth occurs during the ensuing larval stage. While larvae may feed on leaves and bore into twigs, principal damage is to the fruit. Larvae usually enter the fruit at the calyx end or through the sides where two fruits or a fruit and a leaf are touching. Usually, they penetrate to the core, consuming any seeds present and other tissues in this general area. Mature, fifth instar larvae, work their way back out and leave the fruit in order to search for a cocooning site. These larvae either enter diapause and overwinter or pupate and emerge as the next adult generation. The presence in fruit of one of more holes plugged with frass is a characteristic sign of codling moth attack. In addition, a syrupy substance may exude from the worm entry or exit holes as the fruit nears maturity. Shallow blemishes on the surface of the fruit, usually caused when a newly hatched larva has penetrated only a short distance and then died (from natural causes or the effects of an insecticide) are referred to as "stings".

D. Control and Management

Control of the codling moth has proceeded from the early use of cultural, biological, and chemical techniques to the domination by broad spectrum insecticides during the past 25 years. From the early 1900s to the mid 1940s, growers relied upon inorganic chemicals (mainly arsenical insecticides) to achieve codling moth control. The use of arsenicals led to problems of relatively poor control, excess residues on fruit and the build up of toxic residues of these compounds in the soil. From the mid 1940s to the present, synthetic organic pesticides (mainly chlorinated hydrocarbons and organophosphorous compounds) have been the tools for codling moth suppression. As noted earlier, dependence on chemical control using these compounds has led to problems of environmental contamination, resistance to insecticides, pest resurgence and the elevation of minor or innocuous species to major pest status. These problems have led to an increased interest in integrated pest management (IPM). IPM involves the use of an array of suitable control techniques (i.e., biological control agents, host plant resistance, cultural controls, pesticides and behavioral controls) in the least disruptive manner. Under a successful IPM program pest densities are kept at sub-economic levels. Several factors have slowed down the implementation of integrated pest management programs in apple and pear orchards. The establishment of economic damage levels is often very difficult. Proper sampling for pests and their natural enemies requires time, expertise and can be economically prohibitive. The complexity of IPM, including horticultural and economic considerations, also determines the feasibility of its implementation.

The different control tactics available for use in an integrated program for codling moth suppression have been extensively studied. In the absence of chemical treatments a variety of biological agents contribute to a general reduction in codling moth numbers. A number of parasites have been reared from overwintering larvae of codling moth and some natural enemies have been imported and established. In Europe, egg parasitism by Trichogramma spp. and larval parasitism by a number of species of ichneumonids, braconids, chalcids and tachinids has resulted in a general reduction of codling moth populations (Huffaker and Messenger, 1976). In Nova Scotia, a sequence of natural mortality agents, attacking all stages except the adult, have been reported (MacLellan, 1958, 1959, 1960, 1962, 1963, 1971; MacPhee and MacLellan, 1971; Jaques and MacLellan, 1965). The eggs are attacked by Trichogramma sp., the egg-larval parasite Ascogaster quadridentata, and several mirid predators. The major larval predators are the mite Anystis agilis Banks and, again, several mirids. Egg-larval predators include several species of thrips, mites, mirids, anthocorids, coccinellids, pentatomids, nabids, clerids, and chrysopids. Natural enemies of mature codling moth larvae in overwintering cocoons include two species of woodpecker, an ostamatid beetle, Tenebroides corticalis Melsh, and at least six species of fungi. A number of natural enemies have also been reported in Australia (Geier, 1961), New Zealand (Wood, 1965) and South Africa (Nel, 1942). In Southern Oregon, egg mortality averaging 26 percent has been attributed primarily to the activity of predators and parasites (Westigard, et.al., 1979).

Despite their abundance and general ability to reduce codling moth populations, natural enemies have been unable to maintain the species under a commercially acceptable degree of control in most areas. Most attempts at biological control of the codling moth have been regarded as failures (LeRoux, 1971; Turnball and Chant, 1961; Huffaker and Messenger, 1976). This lack of success has been accounted for by the direct nature of the injury and the occurrence of multiple generations. However, serious and intensive attempts to discover (especially in Southern Eurasia, apparently the native home of the codling moth) and import natural enemies have been lacking (Huffaker and Messenger, 1976).

Several fungi, including Beauveria bassiana, B. labulifera and Metarrhizium anisopliae have been shown to be toxic to codling moth larvae (Arkhipova, 1965). In field studies these fungi have not looked promising as population regulation agents.

In laboratory tests the codling moth has been effectively killed by Baccillus thuringiensis (Jaques, 1961). However, in field tests control has been inadequate, although 50 percent reduction of fruit injury has been obtained (Oatman, 1965). Jaques and other investigators concluded that it would be best suited for use in combination with other control tactics.

Another possible control agent is a naturally occurring granulosis virus. In preliminary tests the virus was sprayed on apple trees in the field and a majority of larvae died soon after feeding upon the sprayed fruit (Falcon, et.al., 1968; Tanada, 1964). Further studies showed that applications of granulosis virus reduced deep entry damage to apple fruit at harvest considerably but sting or shallow entry injury was still common (Jaques, et.al., 1979; Wearing, 1979). Further study is needed to determine its suitability as part of a program utilizing a combination of control tactics.

More recently, autocidal and phermonal methods of control have received considerable attention. Although the sterile-method of control is technically feasible, the costs have been estimated to be about twice the cost of current spray programs. Again this method may be most feasible if used in conjunction with other methods, such as better sanitation practices, Bacillus thuringiensis and/or codling moth granulosis virus (Hoyt and Burts, 1974). In studies on the use of sex phermone for control of the codling moth through mating disruption, while a high degree of season-long control was achieved on pears in Southern Oregon, significant levels of infestation still occurred. In Washington, (E,E)-8-10-dodecadien-1-ol acetate has been tested for its antiphermone properties and possible use as a mating disruption agent (Hathaway, et.al., 1979). Mass trapping through the use of the sex phermone has also been tested as a possible control tactic (MacLellan, 1976; Madsen, et.al., 1976). As is the case with the previous three control strategies, much work will be needed before its effectiveness in a commercial situation can be determined.

Both the natural controls operating on the codling moth and those in the preceding paragraphs are unable to maintain population density at a level below the current injury threshold of about one percent. Therefore, the most prevelant control tactic is the use of broad spectrum insecticides. These are usually applied on a calendar basis with application dates being determined by adult trap catches or computer predicted emergence. However, in order to minimize the problems associated with the indiscriminate use of these chemicals, some growers have used various monitoring techniques (e.g., blacklight and sex phermone baited traps) to forecast the need for treatment and/or to aid in the timing of insecticide treatments. In addition, the least disruptive (most selective materials) are used (see for example, Westigard, et.al., 1979; Hoyt and Burts, 1974).

Despite the difficulties inherent in the implementation of an integrated pest management program in apple or pear orchards, some successes have been registered; especially in areas where the codling moth is univoltine and has a reduced fecundity or where populations are low (Wood, 1965; Oatman, 1966; MacPhee and MacLellan, 1971). For example, in Nova Scotia where the moth is univoltine, a combination of several natural mortality agents and the use of a selective chemical (ryania) when natural fluctuations of moth populations occur has proved successful. In areas where the moth is multivoltine, more effort must be directed toward the use of several non-chemical tactics in conjunction with the selective, warranted and properly timed use of an insecticide.

E. Influence of Environmental Factors on Flight and Oviposition

Several climatic factors affect the behavior of the codling moth. Flight and oviposition may be influenced by temperature, light intensity, rainfall, humidity and air movements. Egg-laying is partially dependent on a combination of these factors being favorable at a specific time.

Oviposition by first and second generation codling moth females was highly correlated with the average hourly temperature between 5-11 p.m. (Hagley, 1976). Many authors have found that oviposition of caged moths is virtually stopped at temperatures below about 60-62 degrees F. (Isely and Ackerman, 1923; Hall, 1929; Cutright, 1937; Isely, 1938). Parker (1959) reported a somewhat higher threshold of 65 degrees F. while Klinger, et.al. (1958) reported a decidedly lower threshold of 53.6 degrees F. Isely (1938) found that oviposition increased with temperature to an optimum of about 27 degrees C. (= 80 degrees F.). Oviposition was reduced as temperatures increased above this point. Hagley (1976) reported that in the laboratory the optimum range for oviposition was 23-25 degrees C. In some moths, a reduction in egg production was masked by a very high rate of oviposition (Isely, 1938). Egg production was also reduced in moths exposed to high temperatures at larval, pupal and adult stages of development (Isely, 1938; Proverbs and Newton, 1962).

It is generally agreed that maximum codling moth flight occurs during the period of low light intensity associated with sunset.

The flight response appears to be circadian and entrained to the daily photoperiod. Where not limited by other factors, Batiste, et.al. (1973) reported that the daily mating-flight response began about three hours before sunset and extended to about two hours after sunset. Borden (1931) found flight in orchards to be greatest at a light intensity of 25 to 52 foot candles. Eyer (1934) reported a similar range of 30 to 50 foot candles. However, Headlee (1932) stated that flight and oviposition began at about 30 foot candles and increased as the intensity fell to less than one foot candle. Dickson, et.al. (1952) reported that oviposition was stimulated by a decreasing intensity below 50 foot candles but not by an increasing intensity over a similar range. The rate of oviposition was greater under natural light conditions as opposed to artificial lighting. Although most egg-laying takes place within a narrow range of decreasing light intensity, some activity occurs during increasing intensity and above and below the observed limits.

Borden (1931) found that even under favorable temperature and light intensities the faintest air movements over the tree tops effectively cut down flight. More specifically, oviposition by greenhouse confined moths was prevented by a current of four miles per hour (Parker, 1959). In contrast, Russ (1961, in Putman, 1962) reported that flight in the orchard was not hampered by winds below 13 miles per hour. The degree to which flight and egg-laying is suppressed by air movement has not been adequately investigated. Even if flight has been effectively cut down by winds of a given velocity, oviposition could possibly take place within the more protected areas of a single tree.

The inhibitory effect of rainfall on flight has been observed by several early authors. Even as little as one mm. of rain was found to slow or stop flight (Russ, 1961, in Putman, 1962). Russ also found that a combination of high relative humidity and intermittent rain inhibited flight. Hagley (1976) reported that oviposition by first generation females appeared to be reduced by rainfall.

F. Reproductive Capacity

Published estimates of the number of eggs laid per female have been reviewed by Putman (1962) and Geier (1963). Hall (1929) obtained an average of 64 and a maximum of 234 eggs from spring-brood moths and an average of 83 and a maximum of 208 from first brood moths at Vineland Station. Geier (1963) reported a much lower mean of 44 and a maximum of 198 eggs per female in the Capital Territory. Other early estimates of egg production ranged from a low of 8 to a high of 80. The greatest reported number laid by one moth was 345 (Isely, 1938). Much higher estimates of mean fecundity have been obtained for some lab-reared strains. Gehring and Madsen (1963) reported means per female over an 8 day period of confinement of 179.1 and 162.5 for two strains of codling moth. Under optimal conditions in a controlled environment chamber and extended length of the oviposition period (up to 15 days), Hagley (1972) obtained average fecundities of up to 236 eggs per female. Since the ability of researchers to accurately determine the number of eggs laid per female under natural conditions is limited, these estimates of fecundity have been made under artificial conditions in the field or insectary. Experimental artifacts associated with unnatural conditions may partially account for the discrepancies between different authors. Many investigators have found that confined moths, especially when confined in male/female pairs, oviposited irregularly or not at all (Putman, 1962). Differences in evening temperatures and other climatic factors have also been mentioned as sources of error. The reproductive capacity of a codling moth female in nature or under controlled conditions also depends on the potential fecundity, ability to mate, food supply, longevity, availability of favorable oviposition sites and other host properties.

Potential fecundity was found to be normally distributed (Zech, 1960, in Wearing, 1971). In addition, the number of oocytes per ovariole has been shown to increase as a function of total body weight (Geier, 1963). Newly emerged females usually contained 150-200 discernable oocytes; although a number of authors reported more than 300 oocytes or eggs in the ovaries of a single dissected female (Wiesmann, 1935, in Geier, 1963; Putman, 1962). Geier (1963) recorded a significant increase in body weight from spring brood to summer generations and inferred a slight increase in potential fecundity throughout the active season. However, he felt that these differences were too slight to affect rates of reproduction in the field, since most individuals produced more oocytes than could possibly develop even under optimal conditions.

Under natural conditions, the reproductive rate of L. pomonella is probably not limited by inability of the females to mate. In laboratory cage tests, males tended to mate with unmated females (Gehring and Madsen, 1963). Only under the extreme conditions of one male caged with five females was there a reduction in egg production. This may have been a result of some females not being mated until later in the test because of a time requirement for males to form more spermatophores.

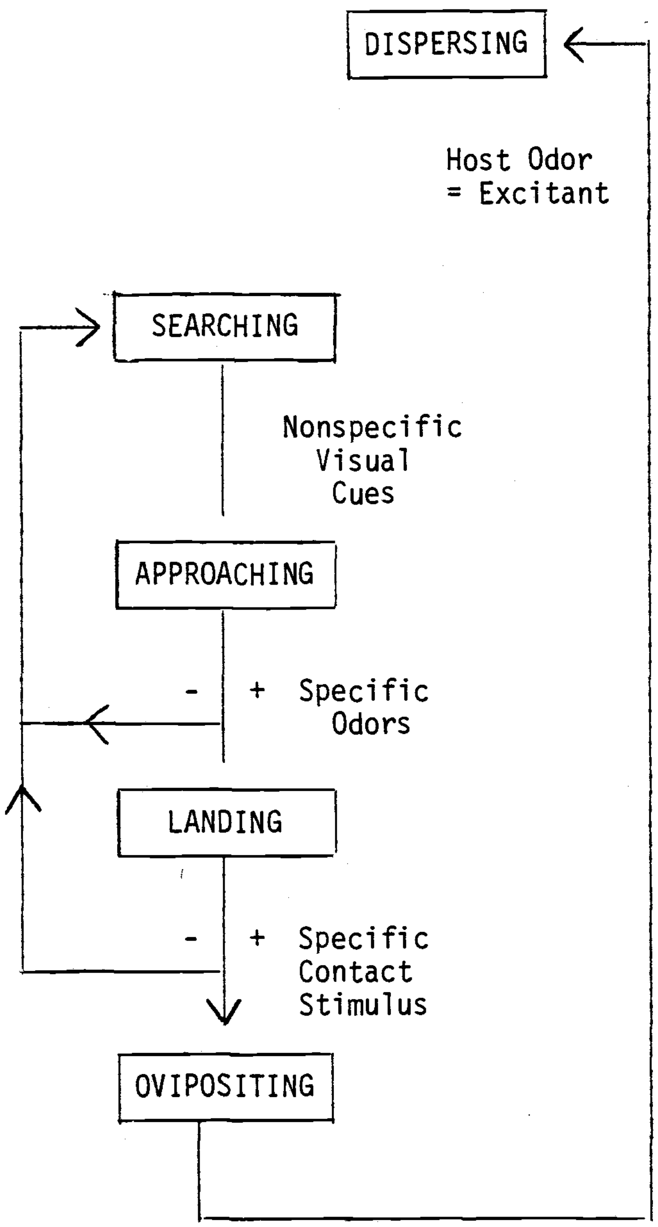
It has been suggested that moths find their foods on the host trees, mainly in the form of exudates from fruits (Geier, 1963). In the laboratory, adult codling moths feed readily on sugar solutions. Sugar-fed females laid twice as many eggs as unfed individuals (Wiesmann, 1935, in Geier, 1963). Hamstead and Gould (1950) noted that gravid females caged without water or food laid fewer eggs than did free-living moths. They suggested that lack of food may have caused the caged females to re-absorb part of their maturing oocytes. Discrepancies in published fecundity estimates, as well as interseasonal and intraseasonal differences may be partially explained by differences in the abundance of a food source.

In reviewing the early literature, Geier (1963) found that oviposition in the field began up to 3 days after emergence and most eggs were laid in about 10 days. Hall (1929) observed that the preoviposition and oviposition periods for spring and first generation moths were different. The pre-ovipositional period for the spring brood was 3.7, the maximum 11 and the minimum 0. The average oviposition period was 5.3 days, the maximum 16 and the minimum 1. For the first generation brood, the pre-oviposition periods ranged from 1 to 9 and averaged 2.6 days. The oviposition periods ranged from 1 to 13 and averaged 5.2 days. Under optimal laboratory conditions, no oviposition occurred until the second day with maximum reproductive effort in the 2 to 4 day period (Gehring and Madsen, 1963). Hagley (1972) reported that female longevity was highly correlated with the length of the oviposition period. There was also a significant correlation between female longevity and the number of eggs deposited. Contrary to this, Geier (1963) found no significant relation between fecundity and longevity and suggested, as did Isely (1938), ..."that in the absence of extrinsic mortality agents longevity seemed to depend primarily upon the rate at which females laid their complement of eggs: the faster the rate, the shorter a female's life."

Reproductive capacity has also been related to host suitability or preference. Wearing and Ferguson (1971) reported that moths caged on Red Delicious apple trees laid more eggs than those on Jonathan, Sturmer Pippin, Delicious, and King of Tomkin's County. These differences in fecundity were not related to the weight of the virgin females or the effects of the height and aspect of the cages in the trees.

The existence of host races may also influence moth longevity and oviposition capacity. Although there was no difference in longevity between walnut and apple races, Cisneros and Barnes (1974) did find that laboratory reared moths of the walnut strain oviposited 49 more eggs per moth than the apple strain.

Fig. 1. Scheme showing major behavioral components of oviposition behavior (from Yamamoto, et.al., 1969).



G. Oviposition Behavior and Host Selection

Oviposition involves a series of behavioral events which are regulated by different physical and chemical stimuli. A generalized scheme of oviposition behavior (taken from Yamamoto, et.al., 1969) is presented in Figure 1. The initial component of the oviposition behavior sequence is that of "recognition" and orientation to the host plant. This is followed by the selection of a specific plant part as an oviposition site. This is an especially important phase of host selection if the mobility of the progeny is severely limited. Larvae which at times may be much more polyphagous than the adult are restricted in their host range as a function of the ovipositing adult. Finally, the eggs are deposited and the insect departs from the oviposition site. Plant characteristics which influence the initiation and completion of these events are host "odor," visual cues, specific plant volatiles and specific contact stimuli. The latter two may either be stimulatory or inhibitory in nature. Oviposition may be prevented by the failure of the host to produce the appropriate releasing stimuli for one or more of the behavioral components or by providing stimuli that inhibit behavioral release.

Very little work has been done on the initial (long range) attractiveness of codling moth to a host. Visual as well as chemical factors may play a role in the initial orientation to a prospective plant. Codling moths were found to be attracted to light (Yothers, 1928). The degree of attractiveness may be influenced by intrinsic brilliance, the size of the luminous area and color of light (Marshall and Hienton, 1938). The shorter wavelengths from blue to ultraviolet have been found to be the most attractive (Peterson and Haeussler, 1928; Ellsworth, 1934; Headlee). However, the influence of color on the host selecting activity of the moth in the field has not been demonstrated.

It has been suggested that volatile substances released by pomaceous fruits, such as alpha-farnesene, may be attractive to female codling moths (Wearing and Hutchins, 1973; Wearing, et.al., 1973; Sutherland, et.al., 1974). Preliminary experiments by Russ (1976) indicated that gravid moths were more attracted to apples than pears. He found that the attractiveness of the fruit varied with fruit development and tentatively concluded that different stages of the fruit had different amounts of the attractant. He also felt that orientation of the females during oviposition to fruit odor was probable, and that females were able to distinguish between pears and apples on that basis. Wearing, et.al. (1973) were unable to demonstrate the upwind orientation of moths to apple odor. This along with the work by Wildbolz (1968) indicated that the greater damage suffered by heavier bearing apple trees was due to close-range stimulation of oviposition rather than the attraction of more moths over long distances.

The next step in the oviposition sequence is the selection of a specific plant part for egg deposition. Codling moth eggs are laid singly on the fruit or on the leaves near the fruit. More rarely they are laid on petioles or stems. Differences in the distribution of eggs have been noted between apple and pear trees, and between different varieties of each. In addition, egg laying patterns have been shown to vary with the seasonal development of the fruit. Differences in both physical and chemical factors have been proposed to explain the variation in the distribution of codling moth eggs. Hall (1929) made the general statement that early in the season most eggs were laid on the upper leaf surface, in mid-season on the underside and later after the pubescence wears off, chiefly on the fruit. Putman (1962) reviewed the early work and found in general that from 80 to 95% of the eggs laid on apple trees were on the leaves, mostly on the upper surface, 5 to 18% on the fruit and 0 to 2% on the twigs. He also found that the percentage of eggs laid on the fruit was somewhat greater late in the season. Geier (1963) reported that, within fruit clusters, approximately one-quarter of the eggs laid on Granny Smith and Delicious apple trees were on fruits, one-fifth on lower leaf surfaces and more than one-half on upper leaf surfaces. More specifically, the proportions of eggs remained relatively constant on lower leaf surfaces throughout the season, whereas the numbers of eggs on fruit were a low of 14% in the spring, rose to a maximum of 40% in midsummer and decreased gradually to 20% towards autumn. Wood (1965) found that about 40% of the eggs were laid on fruits, 40% on the upper surface of leaves and 20% on the lower surface of leaves, with some differences between the three apple varieties tested, Gravenstein, Delicious and Sturmer. The major difference was that approximately twice as many eggs were laid on the lower leaf surface of Delicious than the other two varieties, with proportionately fewer eggs also on the fruit and upper leaf surface. There was no seasonal change in the general distribution as was noted by Geier. VanLeeuwen (1939) also noted the position of eggs on three apple varieties. He found approximately 53% on the upper surface of primary leaves, 22% on the upper surface of secondary leaves, 4% on the lower surface of primary leaves, 2% on the lower surface of secondary leaves, 15% on the fruit, and 4% on the twigs and stems. On Jonathan and Winesap trees practically all eggs were on the upper surface of the leaf, whereas with Rome Beauty the majority of eggs were on the lower surface. In addition, the data showed that the moth had an oviposition preference for the Jonathan and Rome Beauty over the Winesap. VanLeeuwen speculated that this was one of the reasons why both Rome Beauty and Jonathan apples were more injured by the codling moth. In South Africa, Hattingh (1942) made detailed counts on three pear varieties (Beurre Bosc, Bon Chretien and Winter Nelis) and found that spring brood moths deposited the greatest number of eggs at full bloom. He suggested that this was the most attractive early season stage. As the season advanced and just at the time of fruit setting, most eggs were laid on the leaves of the fruiting points. The number of eggs deposited on the fruit increased throughout the season, with the fruit being in its most attractive condition for oviposition just prior to the normal harvest time. As the fruit neared the over-ripe stage its attractiveness progressively decreased. There appeared to be a tendency for more eggs to be laid on twigs and wood in the beginning of the season than later on for all varieties concerned. Hattingh (1943) also noted relative differences in the number of eggs laid on the lower and upper leaf surfaces. On the varieties Bon Chretien, Beurre Bosc and Winter Nelis more eggs were laid on the lower leaf surfaces. On the variety Glout Morceau, slightly more eggs were laid on the upper leaf surfaces than on the lower leaf surfaces for the whole season.

Westigard, et.al. (1976) reported that the favored site for oviposition by the codling moth on Bartlett pears was the underside of fruit cluster leaves (74% of the eggs found). Since moths prefer the upper surface of most apple varieties, he proposed that the difference between favored sites may be due to an avoidance by females of the normally pubescent underside of the apple leaf. The percentage of eggs found on a particular ovipositional site varied from year to year. For example, in 1970, 20% of the eggs were laid directly on the fruit, but only 3% in 1971. In either case, the number of eggs found on the fruit was somewhat lower than that reported for most apple cultivars.

Geier (1963) and Wood (1965) also made detailed analysis of egg distribution between fruit clusters. Geier's results showed that eggs were distributed at random with regard to individual fruits and that the frequency of oviposition within clusters of one, two and three fruits per cluster was also random. Geier concluded that each fruit had an equal instantaneous probability of being used for egg deposition. Unlike Geier's data, Wood's showed that the frequency of oviposition within clusters of one, two, and three or more fruits per cluster was not random. He found that this departure from randomness was only slightly accounted for by oviposition behavior of the female moths (i.e., multiple oviposition as a result of the impedement of movement by unfavorable weather before inhibiting oviposition). Aspect in the tree also had no effect on the distribution of eggs. However, in all three varieties more eggs per cluster were laid in the upper half of the trees than in the lower half. Geier also noticed more eggs in the upper parts of the trees but not to a significant degree.

The oviposition behavior of gravid codling moths is influenced by several naturally occurring "odorants." In an early review of moth "attractants and baits," Dethier (1947) concluded that essential oils such as citronellol, oil of cloves, and pine tar oil acted as codling moth oviposition stimuli. VanLeeuwen (1947) advocated the use of apple odor in the laboratory as a stimulant for oviposition by the moth. In the field, gravid codling moths were stimulated to oviposit by the odor of the apple (Wildbolz, 1958). Laboratory studies using an olfactometer confirmed that the moths lay more eggs when an apple source is present (Wearing, et.al., 1973). This may involve physical and/or contact stimuli or may be due to increased intensity of odorous stimulation. Apple odor not only stimulates oviposition but also affects the distribution of eggs laid. Moths which were exposed to an apple odor source consistently laid a greater proportion of their eggs on the front paper through which the airstream entered the olfactometer flight chamber (Wearing, et.al., 1973). This is consistent with the findings of several authors concerning the distance most eggs are laid from fruit. Geier (1963) and Wearing, et.al. (1973) found that most eggs were laid within 10 cm. of a fruit and MacLellan (1962) rarely found eggs more than 6 in. from fruit.

Mature apples of the cultivar "Sturmer Pippin" have been found to produce one or more volatile compounds which stimulate oviposition of gravid females in the laboratory (Wearing, et.al., 1973). Sutherland (1972) likewise found that the skin of these apples contained volatile substances which were highly attractive to neonate codling moth larvae and that some or all of these substances were present in an external chloroform extract of the apples. Further tests with fractions of this extract led to the identification of the sesquiterpene alpha-farnesene (Sutherland and Hutchins, 1972). Alpha-farnesene is present in large quantities, not only in the outer coating of Granny Smith, Sturmer Pippin, Delicious, Crofton and several other varieties of apples (Meigh and Filmer, 1967, in Sutherland, et.al., 1974; Murray, 1969), but also in that of some other fruits attacked by L. pomonella, such as pears (Packham and Winter Cole) and quinces (Murray, 1969). Most of the work on alpha-farnesene resulted from intensive interest in its association with the appearance of superficial scald, a disorder of stored apples (Murray, et.al., 1964; Huelin and Murray, 1966; Meigh and Filmer, 1967, in Sutherland, et.al., 1974; Huelin and Coggiola, 1968). (E,E)-and (Z,E)-alpha-farnesene, the two isomers which occur naturally (Anet, 1970) have been implicated as attractants for newly hatched codling moth larvae and oviposition stimulants for gravid female moths (Sutherland, 1972; Sutherland and Hutchins, 1972, 1973; Wearing and Hutchins, 1973; Sutherland, et.al., 1974). Both the number of eggs laid and the density of eggs near the odor source were greater in the presence of these compounds. Normal oviposition may also depend upon the presence of more than one olfactory stimulant. The oviposition response of gravid females to natural or synthetic alpha-farnesene was less intense than it was to whole apples or crude chloroform extracts. Sutherland, et.al. (1974) suggested that the terpenoids geraniol and citral may be important. They noted that both compounds have been isolated and identified from apples as well as implicated as positively influencing the sexual behavior of male codling moths.

Studies discussed previously have indicated that the egg-laying "preferences" may depend on the seasonal development of the fruit as well as the variety or type of fruit involved. Sutherland, et.al. (1977) reported that the total alpha-farnesene level in apple fruits (ten varieties were tested) steadily increased during fruit growth and maturation. Their study indicated that seasonal changes in alpha-farnesene production per apple may influence oviposition behavior of the moth, particularly the distribution of eggs.

Preliminary investigations in the areas of host selection, host preference and the stimulation of egg production by the codling moth have been spurred on by recent work concerning the stimulatory nature of host "odor," particularly the volatile compound alpha-farnesene. These studies have raised several questions concerning varietal or host type "preferences" and the possible relationship of alpha-farnesene to host "preference." The following study was conducted to investigate these aspects of codling moth oviposition behavior. The objectives of the study were: 1) to determine whether there is a significant difference in the number and location of eggs laid by the codling moth on several apple and pear cultivars grown in the Pacific Northwest. Tests were also designed to investigate intra-seasonal variation in the number and location of eggs on the various varieties. 2) to determine whether codling moths exhibit any ovipositional "preference" when given a choice between more than one variety of a single host type or several varieties of two different host types and to investigate any seasonal change in host "preference" for oviposition. 3) to investigate the possible role of alpha-farnesene in determining the number and distribution of eggs on different host types, as well as on several varieties of each. 4) to investigate the relationship of seasonal changes in the levels of alpha-farnesene to intra-seasonal changes in oviposition and 5) to determine if there is a relationship between the number of eggs laid and the concentration of alpha-farnesene.

II. Methods and Materials

A. Source of Insect Material

The adult moths used in these experiments were obtained from the USDA, ARS, SEA, Agricultural Research Laboratory at Yakima, WA. The strain was originally collected from apples in 1973 and has been continuously reared in the laboratory on Red Delicious apple thinnings (approximately 40 generations). The rearing method has been described by Hamilton and Hathaway (1966). Mature larvae which had spun cocoons in strips of corrugated cardboard were placed in styrofoam ice-chests and shipped to Medford by bus. Approximately 1,000 individuals were received every three weeks from mid-July to September, 1979. The strips were immediately placed in several glass jars (4 liter) whose lids had been replaced by cheesecloth to keep the moths from escaping when they emerged and at the same time allow for good ventilation. These holding cages were kept in a growth chamber which was set for a 16/8 hour light/dark cycle and maintained at 27 ± 1 degrees C and 75% R.H.

B. Selection and Location of Plant Material

The varieties used in these experiments were selected on the basis of availability, diversity of fruit types and a range of maturing dates. The five apple and four pear varieties selected and their approximate normal harvest periods in Southern Oregon were the Zielenski selection of Gravenstein, Aug. 10-20; Idared, Sept. 10-20;

Red Chelan, Oct. 1-15; Mutsu, Oct. 5-15; Granny Smith, Nov. 1-15; Bartlett, Aug. 15-25; Seckel, Aug. 31-Sept. 10; Comice, Sept. 10-20 and Bosc, Sept. 20-30. The parentages of Red Chelan, Mutsu, Idared and Granny Smith are, respectively, a sport of Red Delicious, a triploid of Japanese and Golden Delicious origin, a cross between Jonathan and Red Delicious, and a Newtown type (Lombard, personal comm.).

The trees used in these studies were located at the Oregon State University Southern Oregon Agrucultural Research Center in Medford, Oregon. Four young Granny Smith trees, two mature trees of each of the other four apple varieties, and six trees of each of the pear varieties were used.

C. Pre-experimental Handling of Adults

Adults were collected daily from the holding emergence cages and put into mating cages at a ratio of two males to one female. Each cage contained no more than 20 males and 10 females. Mating cages were 4-liter ice cream cartons (18 cm. high and 15 cm. dia.) from which the tops were removed and replaced with cheesecloth. A 60 ml. cup containing water-soaked cotton was placed at the bottom of each cage. The mating cages were placed in a growth chamber (27 degrees C and 75% R.H.) and left for 24 h to allow the moths time to mate. Females were then removed and weighed with a Mettler precision balance. A single weighed female and two males were then placed in small (120 ml.) ice cream cartons from which the tops had again been removed and replaced with cheesecloth. Moths were placed in a dark, temperature regulated chamber set at 55 degrees F in order to avoid any chance of egg-laying prior to their use in experiments that afternoon.

D. Laboratory Oviposition Studies

The experimental cages used to study codling moth oviposition on various pear and apple varieties under laboratory conditions were the same as the mating cages described above except that the side and bottom of the cartons were covered with waxed paper for ovipositional substrates and a glass vial was fastened to the bottom to hold the fruit spurs. Freshly cut fruit spurs from the varieties to be tested that day were placed in the water-filled vials.[1] At the beginning of each experiment, one weighed female and two males were released in each spur-containing cage. The cage was then placed in the same growth chamber as the holding and mating cages (27 degrees C and 75% R.H.). To help simulate lighting conditions at dusk, cardboard strips were placed over the fluorescent lights. Each cage was left in the chamber for 48 h. Water was added to each vial at 12 h intervals. The fruit spur was replaced with a freshly cut one after 48 h and the number of eggs counted. The number of eggs on

[1]Fruit spur samples were collected in the afternoon just prior to their use. In the context of these experiments, a fruit spur consisted of the leaves and woody material associated with two fruits which were located on a small enough branch to fit in the cage. After the spurs were removed from the trees they were cut underwater, to help insure water intake, and placed in an ice-chest for transport to the lab.

the fruit, upper and lower leaf surface and woody portion, as well as on the waxed paper and vial were counted under a 10X illuminated magnifying glass. The cage, now containing a fresh spur, was returned to the growth chamber and held there for 48 h at which time the eggs were again counted and the replicate terminated. Controls, which consisted of containers with no fruit spurs, were run concurrent with those containing spurs. The number of cages started each day (with and without fruit spurs) varied according to the number of available moths.

E. Laboratory "Choice" Experiments

Wooden flight cages measuring 45cm x 45cm were used for the choice experiments. A cheesecloth screen was stapled across the top to prevent the moths from ovipositing on the glass roof. A glass vial was secured in each corner. During the experiments, the cages were kept in a room that was maintained at 75±5 degrees F and exposed only to the natural light entering through the half-open door. Fruit spurs were collected, handled and placed in the vials as in the previous laboratory experiment. Two apple varieties (Gravenstein and Idared) and two pear varieties (Seckel and Bartlett) were used in the first "choice" experiment. Approximately one and a half months later in the season these varieties were tested again. In the other choice experiment three pear varieties (Bartlett, Bosc and Seckel) were used. After placing the varieties in each cage, ten female moths and twenty males were released. All experiments were terminated after three days and the number and location of eggs on each fruit spur recorded.

F. Field Oviposition Studies

Limb cages for use in the field were constructed using one inch mesh chickenwire, formed into a cylinder 23cm in height and 15cm diameter. Fiberglass screening (6.3 mesh per liner cm) covered the chickenwire skeleton. Cheesecloth (11 mesh per linear cm) was sewn to the screening to make a sleeve on each end of the cylinder. The sleeve was wired around the fruit bearing spur.

Initially, nine cages were to be placed in trees of each of the nine varieties. The lack of suitable fruit spurs, especially toward the end of the season when many of the fruits were infested with codling moth, made it necessary to vary the number of replicates from five to fifteen. One weighed female and two males were released in each cage. All releases took place between 16.00-18.00 hr. Although the number of releases each day depended on the availability of moths, both in early-July and late-August, all replicates were run within a four day period. After twelve days, the cages were removed and the initial sex ratio checked. Parts of the limb within the cage were removed and brought back to the lab to be examined for eggs. The number of eggs laid on the fruit, upper and lower leaf surface, and woody portion was counted under a 10X illuminated magnifying glass. This experiment was conducted twice with all nine varieties during the 1979 season (early-July and late-August). Bartlett, Red Chelan and Seckel were tested again in late September, after their normal harvest periods, in order to investigate the effect of fruit ripening on oviposition.

G. Alpha-farnesene Analysis

Samples of developing fruit were taken during the late afternoon and were weighed and extracted with solvent (Chloroform) within twelve hours. The fruits were transported from the field to the laboratory in ice-chests and stored at 36 degrees F prior to extraction. Nine samples were processed per day; three replicates for each of three varieties were completed each day for three consecutive days. Extraction of the cuticle for determination of alpha-farnesene was done by immersing intact apples in two successive two minute chloroform baths (250 ml $CHCl_3$ in a 1000 ml beaker). After a two minute immersion period each apple was withdrawn and rinsed with chloroform. The two baths were combined and concentrated by rotary evaporation under reduced atmospheric pressure at temperatures of 25-35 degrees C. The samples were quantitatively assayed by UV absorption methodology as described by Huelin and Coggiola (1968). Alpha-farnesene is readily determined, as its extinction from 215 to 500 nm gives a single peak at 232 nm with negligible extinction about 260 nm. Both the amount of alpha-farnesene per fruit and the amount per unit area of skin were determined. After extraction, each fruit was sliced in half and a profile[2] was traced. Measurements from the profiles were used to estimate surface area by assuming the shape of an apple to be a sphere and a pear to be a cone on top of half a sphere.

H. Alpha-farnesene Bioassay

This bioassay was designed to test for any relationship between the number of eggs laid and the different concentrations of alpha-farnesene associated with the apple and pear varieties used in these studies. Purified extracts obtained during the analysis of alpha-farnesene concentrations in the natural coating of the nine varieties of fruits were used to assess the response of gravid females to this compound. Samples of the extracts were pipetted into a 0.1 g ball of cotton wool 3 cm in diameter. The amount of material injected into the cotton ball was different for each varietal extract tested. Values were determined by calculating the amount of extract needed to give the same varietal ratio of $\mu g\,\alpha$-farnesene/ml of extract as was found in this study for μg of α-farnesene/cm^2. A control consisting of .2 ml of pure chloroform in the cotton ball was also prepared. After evaporation of the solvent, the balls of cotton were transferred to 9 cm diameter glass petri dishes. The test and blank cotton balls were placed against the inner wall of

[2]One-half of each fruit was placed cut-side down on the paper and the outline of the fruit traced. The height and diameter of each fruit could then be determined from its outline on the paper.

separate petri dishes which already contained one weighed female and one male moth. The petri dishes were placed in the 16/8 hr light/dark growth chamber. The eggs laid in each dish after 12 hours were counted. This procedure was repeated the following two evenings, for each pair of moths, with freshly treated cotton balls being used each evening. There were ten replicates for each varietal extract.

III. Results and Discussion

A. Field and Laboratory Evaluation of Codling Moth Ovipositional Behavior on Apple and Pear Varieties.

1. Field studies of oviposition on varieties of apple and pear.

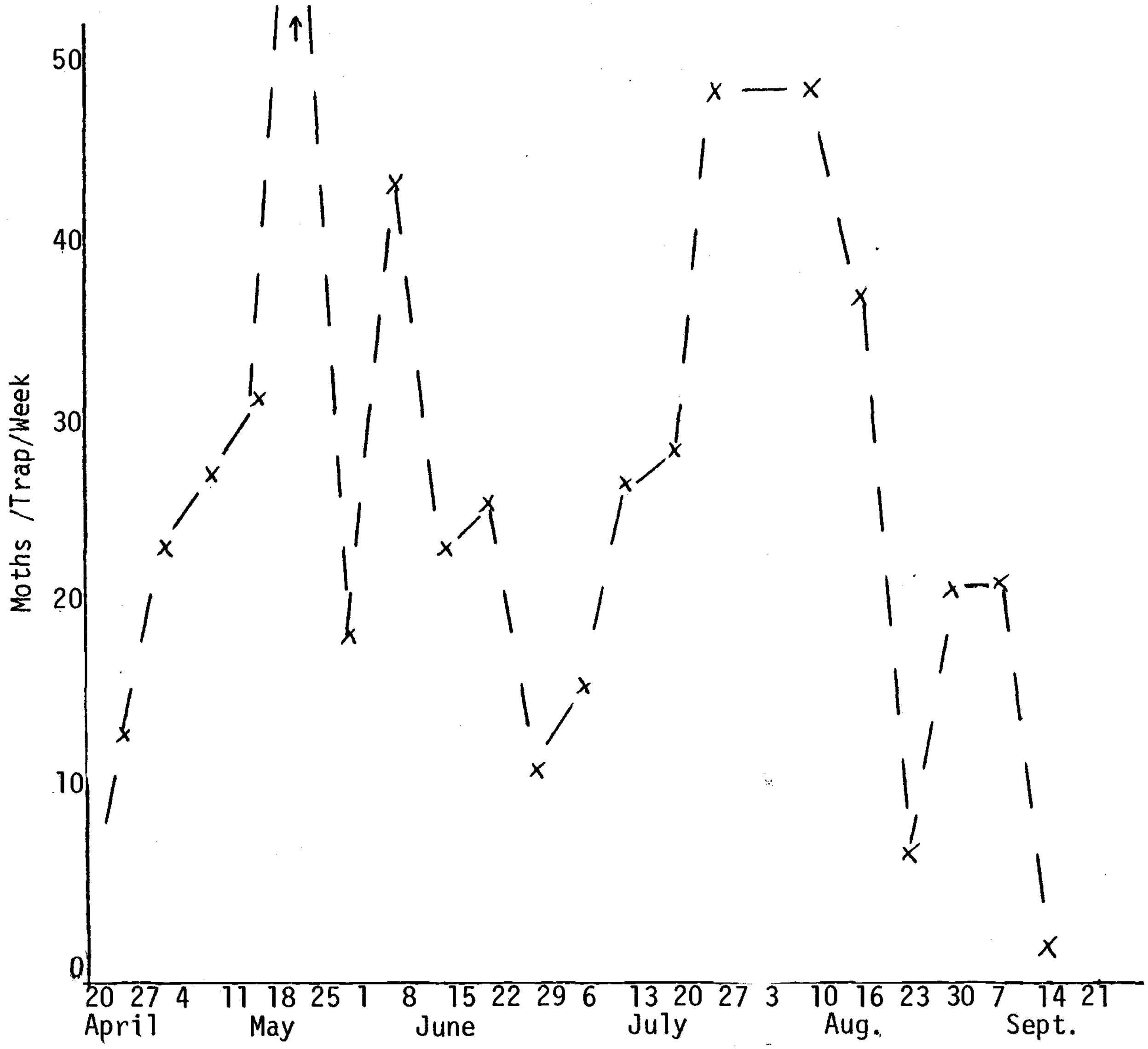
Comparison of varieties - Differences in the degree of codling moth injury on various apple and pear cultivars reported by several authors (e.g., Felt, 1910; Newcomer and Yothers, 1924; Cutright, 1935; Hall, 1929; Cutright and Morrison, 1935; Whitehead, 1944) may be partially due to their relative suitability for oviposition. Wearing and Ferguson (1971) reported a three-fold variation in the number of eggs laid on five apple varieties. They found that moths caged on Red Delicious laid significantly more eggs than those on Jonathan, Sturmer Pippin, Delicious and King of Tomkin's County. Table 1 presents the data on the number of eggs laid on various apple and pear varieties at three different periods during the spring/summer 1979 (late June/early July, late August, and late September/early October). In late June/early July (toward the end of first flight - see Figure 2) gravid females laid significantly more eggs on the Bosc cultivar than on Seckel, Bartlett, Idared, Granny Smith, Red Chelan, Comice, Mutsu and Gravenstein. The average number of eggs laid per female over the 12 day period ranged from a low of 53 for

Table 1. Oviposition of the codling moth on varieties of apples and pears in the orchard at three different time periods during the spring/summer, 1979. Medford, Oregon.

Variety	Normal Harvest Period	Period 1 (late June/early July) No of Cages	Wt of ♀♀* ($\bar{x}$ in mg)	No of Eggs* ($\bar{x}$)	Period 2 (late Aug.) No of Cages	Wt of ♀♀* ($\bar{x}$ in mg)	No of Eggs* ($\bar{x}$)	Period 3 (late Sept./early Oct.) No of Cages	Wt of ♀♀ ($\bar{x}$ in mg)	No of Eggs ($\bar{x}$)
Bosc	09/20-09/30	7	35.3a	127±42a	9	35.2a	155±70a	--	----	-----
Seckel	08/31-09/10	6	36.2a	82±22b	7	35.0a	147±57a	11	34.7	60±31
Bartlett	08/15-08/25	7	33.4a	77±23b	7	34.9a	114±45a,b	--	----	-----
Idared	09/10-09/20	7	36.1a	73±47b	7	36.0a	78±44a,b	--	----	-----
Granny Smith	11/01-11/15	7	35.1a	70±18b	8	35.3a	148±64a	--	----	-----
Red Chelan	10/01-10/15	7	36.7a	68±22b	7	34.7a	128±67a	7	34.9	69±36
Comice	09/10-09/20	7	36.4a	66±06b	9	34.1a	157±72a	--	----	-----
Mutsu	10/05-10/15	8	34.9a	62±30b	5	36.6a	83±36a,b	--	----	-----
Gravenstein	08/10-08/20	7	35.4a	53±24b	7	36.0a	41±40b	--	----	-----

* Means in each column followed by the same letter are not significantly different. Student-Newman-Keuls test (p 0.05).

Figure 2. Codling moth flight during the 1979 season. Medford, Oregon.



Gravenstein to a high of 127 for Bosc. In late August (toward the end of second flight - see Figure 2) females laid significantly fewer eggs on the Gravenstein apple variety than on Comice, Bosc and Seckel pears, as well as Granny Smith and Red Chelan apples. The range of mean number of eggs laid per female on the nine varieties was greater during this time of the season with a low of 41 for Gravenstein and a high of 157 for Comice. Two other pear varieties, Bosc and Seckel, were among the four most suitable varieties in terms of mean number of eggs laid on them, with averages of 155 and 147, respectively.

As was found by Wearing and Ferguson (1971), differences in the number of eggs laid on each variety were not related to female weight. The average weights of the females used in these experiments were not significantly different throughout the season (Table 1). In addition, there was no significant correlation between intravarietal differences in fecundity and the weight of the virgin females.

Wearing and Ferguson concluded that more eggs were found on the Red Delicious trees because they were located in a particularly protected part of the orchard, being protected from northerly winds by topography and southerly winds by trees. None of the trees in the present study were located in a more protected part of the orchard.

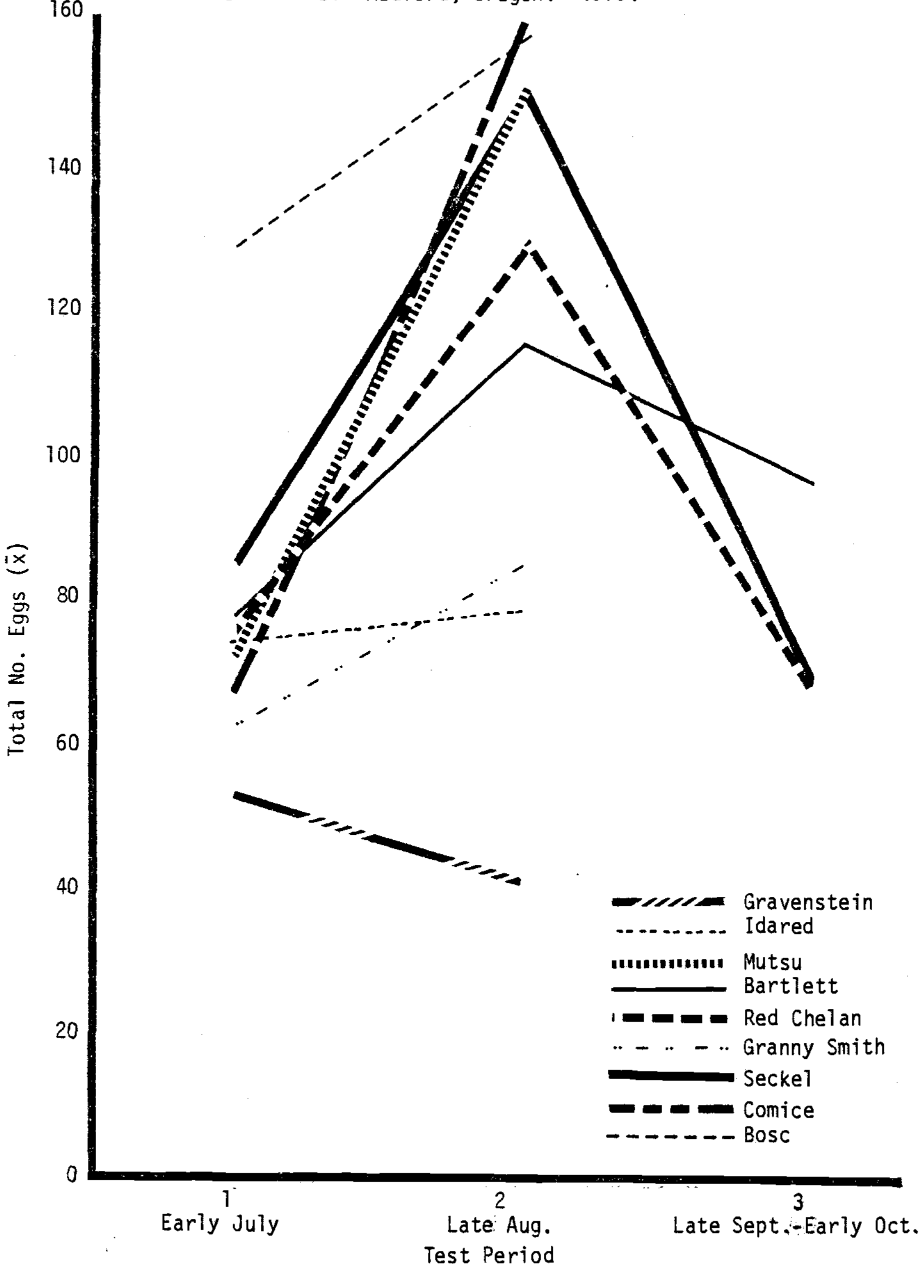
The significantly greater number of eggs laid on the Bosc cultivar during the first test period is probably due to physical and/or chemical factors which enhance its suitability or attractiveness for oviposition. Physical differences between the varieties studied were not quantitatively determined. Earlier studies indicate that codling moths "prefer" a smooth leaf surface (Westigard, et.al., 1979). Although Bosc leaves are generally less pubescent than leaves of the five apple varieties (the underside of the leaves in particular), the leaf surface texture of the other three pear varieties is more or less equal to that of Bosc. Since fewer eggs were laid on these pear varieties, as well as the apple varieties, leaf surface texture alone cannot account for the greater number of eggs laid per female on the Bosc cultivar. Other physical characteristics, such as leaf hardness, leaf surface area and fruit size, may be important. For instance, general observations indicate that Bosc leaves may have been larger than those of the other varieties early in the season. Also, leaf hardness (penetrability) has been shown to influence oviposition site selection and acceptance by other insect species (Clark, 1963; Moran and Buchan, 1975). The possible role of chemical factors in determining the increased number of eggs on the Bosc cultivar will be discussed in a later section.

In late August, the pattern of varietal attractiveness or suitability had changed. Bosc no longer had a greater number of eggs than the rest of the varieties. There was no significant difference in the number of eggs laid per female between eight of the varieties. However, the ninth variety, Gravenstein, had significantly fewer eggs laid on it than five of the other cultivars. At this time of the season, Gravenstein is the only variety of the nine tested that has passed the normal harvest period. Factors associated with fruit ripening probably account for the fewer number of eggs deposited on this variety.

Seasonal pattern - Further evidence for the effect of fruit ripening on egg laying is presented in Figure 3. Here, the seasonal change in the ovipositional pattern on all nine varieties is shown. This includes data on the number of eggs laid per female on varieties after/or at their normal harvest period (Gravenstein, Seckel, Bartlett, Red Chelan). All varieties except early ripening Gravenstein showed an increase in the number of eggs laid on them from the early July to the late August test periods. The most significant changes were found for the Comice, Seckel, Granny Smith and Red Chelan cultivars, all of which showed about a two-fold increase in the mean number of eggs laid. Two of these varieties, Red Chelan and Seckel, as well as the Bartlett cultivar, were tested in late September/early October and showed up to a two-fold decrease in the mean number of eggs per female laid on them.

Several authors have reported an increase in fecundity

Figure 3. Seasonal change in the oviposition pattern of codling moth on different varieties of apple and pear, under field conditions. Medford, Oregon. 1979.



from the spring to summer broods (Putman, 1963). The results of these early studies, as well as those of Wearing and Ferguson (1971) appear to support Geier's (1963) suggestion that intra-seasonal variation in fecundity is related to the number of evenings when environmental conditions (i.e., wind, humidity, precipitation and temperature) are most favorable for oviposition. Researchers have also proposed that a seasonal increase in potential fecundity, inferred from the known increase in body weight from spring brood to summer generations, may account for the increase in reproduction in the field throughout the active season. However, as noted by Geier, reported differences are probably too slight to affect fecundity in the field, since most individuals produce more oocytes than could possibly develop even under optimal conditions. The degree to which weather conditions account for intra-seasonal differences in reproductive rates is also questionable. Within a range of environmental conditions, differences in fecundity are slight (see, for example, Isely, 1938). More importantly, gravid females lay the majority of their egg complement in a short period (e.g., Hall, 1929, reported an average oviposition period of 5.3 days). Thus, even if extremely poor conditions exist during the reproductive period of a female's life, she only needs five or so days of good conditions to lay the majority of her eggs. Isely (1938) and Geier (1963) found that longevity seemed to depend primarily upon the rate at which females laid their complement of eggs: the faster the rate, the shorter a female's life. Under poor ovipositional conditions, fewer eggs are laid, but the length of the oviposition period is increased and the net reproduction effort may be the same as that achieved by gravid females under more favorable conditions.

Neither the weight of females nor differences in weather conditions account for the seasonal differences in total eggs/female in this study. As discussed earlier, female weights during the test periods were not significantly different. In addition, unlike previous studies where field collected spring and summer brood females were used, the moths used during all three times of the season were reared under the same conditions. Thus, other biological differences between broods can also be ruled out as sources of variation. Since differences in evening temperatures have been mentioned as a contributing factor to the large range of fecundities reported for the codling moth, their possible effect on these studies was examined. Following Hagley's (1976) finding that oviposition was highly correlated with the average hourly temperature during peak moth activity (5-11 p.m. at the Vineland Station in Ontario, Canada), the average temperature between 6-11 p.m. for the time periods relevant to these studies was calculated. These are presented in Table 2. The range of average temperatures between 6-11 p.m. for these 12-day intervals was

Table 2. Average temperature between 6-11 p.m. for the 12-day intervals the field oviposition experiments were run and the mean number of eggs laid on each of the varieties tested during those periods.

Time Period	Varieties Tested	No. of Eggs ($\bar{x}$)	Ave. Temp. 6-11 p.m. (°F)
June 22 - July 3	Granny Smith	70	69.54
	Red Chelan	68	69.54
	Seckel	82	69.54
	Idared	73	69.54
June 23 - July 4	Mutsu	62	69.31
	Gravenstein	53	69.31
June 24 - July 5	Bosc	127	69.04
June 25 - July 6	Bartlett	77	68.18
	Comice	66	68.18
August 16 - 27	Granny Smith	148	67.25
	Red Chelan	128	67.25
	Seckel	147	67.25
August 17 - 28	Idared	78	66.28
	Mutsu	83	66.28
	Gravenstein	41	66.28
August 18 - 29	Bosc	155	65.49
	Bartlett	114	65.49
August 19 - 30	Comice	157	64.68
September 19 - 30	Bartlett	96	64.64
September 20 - October 1	Red Chelan	69	64.64
September 29 - October 10	Seckel	60	65.72

64.6-69.5 degrees F (21.8-23.5 degrees C). This is very close to the optimal range of 23-25 degrees C reported by Hagley (1972, 1976). The effects of environmental factors other than temperature were not determined but it is assumed that they were minimal in these experiments, since even if female flight was negatively influenced by them the moths could oviposit within the confinement of the cages.

The increase in total oviposition in the field, which was nearly two-fold for several varieties, is probably due to an increase in the amount of stimulatory fruit volatiles produced as the season progresses and possibly a similar increase in the amount of foliage available for eggs to be deposited on. The latter would be especially important if the presence of an egg deters further oviposition as was suggested by Wood (1965). The decrease in total oviposition as the fruit ripens is probably also related to changes in fruit chemistry. The possible role of fruit volatiles will be discussed in a later section.

Distribution of eggs - Differences in the distribution of eggs have been noted between apple and pear trees, and between different varieties of each. In addition, egg-laying patterns have been shown to vary with the seasonal development of the fruit. Differences in both physical and chemical factors have been proposed to explain the variation in the distribution of codling moth eggs. However, to date, a great deal of conflicting information exists concerning the selection of an oviposition site by Laspeyresia pomonella.

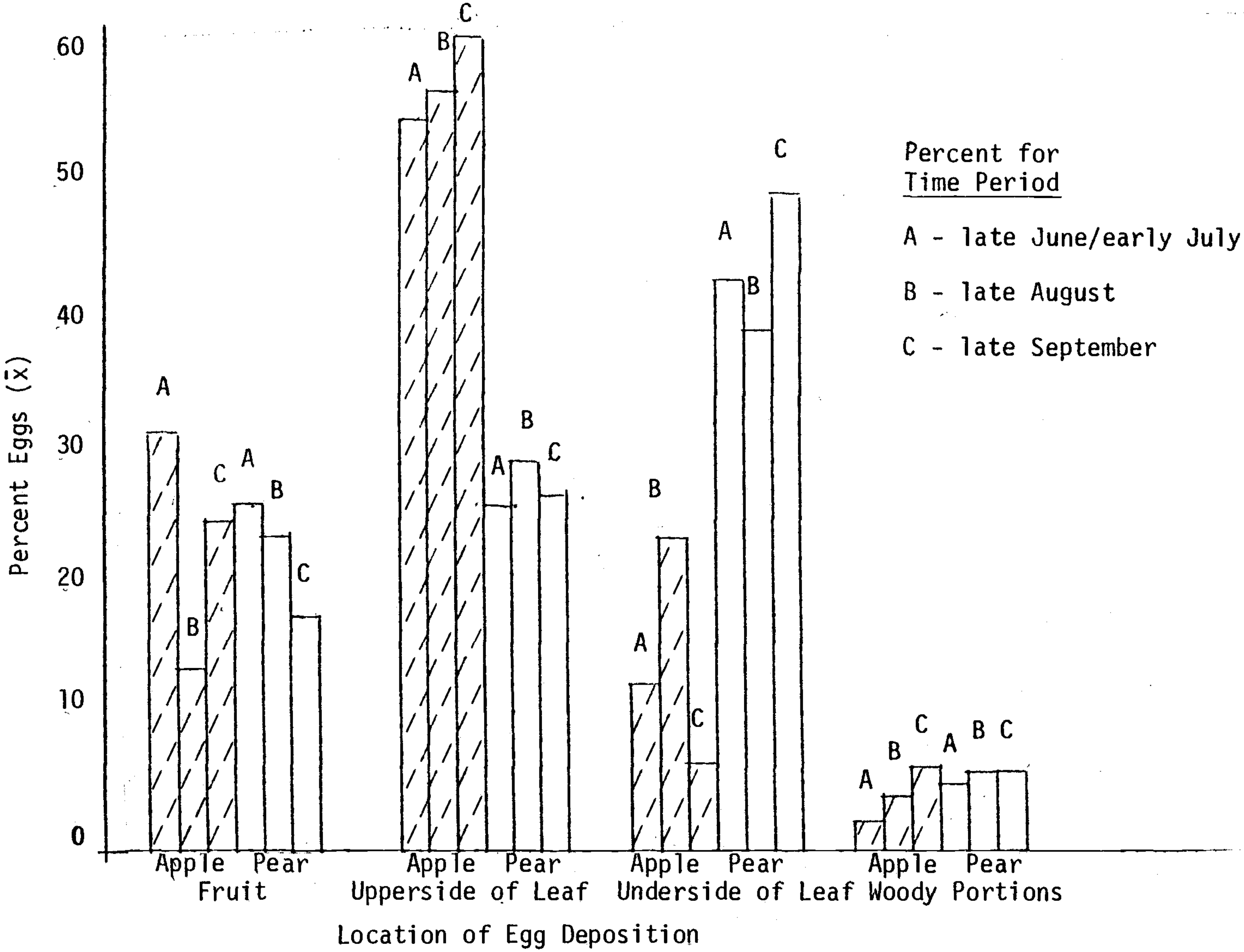
Differences in the location of eggs on the various plant structures of the nine varieties tested is presented in Table 3. In addition, these data, as well as some late season data, have been grouped into the more general classes of apple and pear and summarized for comparison in Figure 4. The general distribution of eggs for the whole season on apple varieties found in the present study (20% on fruits, 58% on upper-leaf surfaces, 20% on lower-leaf surfaces and 2% on woody portions) is in agreement with earlier works by Putman (1963), Geier (1963), VanLeeuwen (1939) and Wood (1965). The distribution of codling moth eggs on pears (22% on fruits, 28% on upper-leaf surfaces, 44% on lower-leaf surfaces and 6% on woody portions) is also in agreement with previous studies (Hattingh, 1942; Westigard, et.al., 1976). The pooled information in Figure 4 indicates that on apples the largest percentage of eggs are deposited on the upper-leaf surface, while on pears the largest percentage are laid on the under-sides of leaves. As was noted by Westigard and his colleagues, the differences in the location of eggs on apple and pear leaves may be due to an avoidance by females of the normally pubescent underside of the apple leaf.

Intra-seasonal changes in the percentage of eggs found on the fruit have been reported by Putman (1963), Geier (1963),

Table 3. Distribution of codling moth eggs on varieties of apples and pears in the orchard at three different time periods during spring/summer, 1979. Medford, Oregon.

	Period 1 (late June/early July)				Period 2 (late Aug.)				Period 3 (late Sept.)			
	No. of Eggs ($\bar{x}$)				No. of Eggs ($\bar{x}$)				No. of Eggs ($\bar{x}$)			
Variety	% on fruit	% on upperside of leaf	% on underside of leaf	% on woody portions	% on fruit	% on upperside of leaf	% on underside of leaf	% on woody portions	% on fruit	% on upperside of leaf	% on underside of leaf	% on woody portions
Bosc	24.3	26.0	46.5	3.2	36.2	21.5	34.0	8.3	----	----	----	----
Seckel	42.3	25.6	31.7	0.4	17.8	34.0	45.0	3.2	25.4	28.9	42.6	3.1
Bartlett	14.5	28.2	52.4	4.9	20.6	33.0	39.5	6.9	8.9	23.7	55.7	11.7
Idared	19.0	67.4	13.5	0.1	11.3	63.6	24.6	0.9	----	----	----	----
Granny Smith	29.8	55.0	6.9	8.3	8.4	60.0	26.6	5.0	----	----	----	----
Red Chelan	42.0	57.5	0.4	0.1	18.1	68.1	6.7	7.1	24.9	63.0	6.0	6.1
Comice	24.8	21.6	46.6	7.0	21.7	30.4	42.8	5.1	----	----	----	----
Mutsu	29.1	50.4	19.1	2.4	11.3	49.5	37.3	1.9	----	----	----	----
Gravenstein	42.0	44.5	11.6	1.9	20.9	50.1	28.0	1.0	----	----	----	----

Figure 4. Distribution of codling moth eggs on apples and pears at three different times during spring/summer, 1979. Medford, Oregon.



Wood (1965) and Hattingh (1942). Putman noted that the percentage of eggs found on apple fruit was somewhat greater late in the season. While Geier reported that the number of eggs on apple fruit reached a low of 14% in the spring, rose to a maximum of 40% in midsummer and decreased gradually to 20% toward autumn, Wood found no seasonal change in the distribution of eggs on apples. The present study is in agreement with Geier, with a greater percentage of eggs being laid on the fruit toward midsummer (33%) and then decreasing later in the season (14%). Intra-seasonal changes in the percentage of eggs found on pear fruit were slightly different from those reported by Hattingh. He found that the number of eggs deposited on the fruit increased throughout the season, with the fruit being in its most attractive condition for oviposition just prior to normal harvest time. In the present study, the percentage of eggs laid on the fruit did not differ from mid- to late season and decreased after the normal harvest time. The number of eggs laid on apple fruit appears to increase from late August to late September but this is based on data for a single variety (Red Chelan). The percentage of eggs laid on the fruit in late September for this variety (25%) is not significantly different from the corresponding value in late August (18%).

Intra-seasonal differences in the distribution of eggs between various plant surfaces may be due to physical changes associated with plant growth, such as leaf surface texture or the average surface area of fruit relative to that of leaves. Glen (1977) found that a greater percentage of eggs was laid on the fruit when the mean surface area of fruit was large relative to that of leaves. Surface areas of fruit and leaves were not determined for these studies. Decreased pubescence on the lower surface of apple leaves later in the season may play a role, since a greater percentage of eggs were laid there during the late August time period than the early July test period. This increase in eggs on the lower surface of apple leaves corresponds with a decrease in the percentage of eggs on apple fruit from early July to late August. Egg distribution may also be influenced by one or more fruit volatiles which are involved in fruit maturation. These will be discussed in a later section.

Because of the large intra-varietal variation in the location of eggs, as well as a great deal of inter-seasonal variation (see, for example, Westigard, et.al., 1979), differences in the location of eggs within varieties of the same host type (apple and pear) must be noted with caution. In these studies, one significant difference that is evident is the very low percentage of eggs laid on the underside of Red Chelan leaves. Upper to lower-leaf surface ratios for this variety during the three test periods are 145 to 1, 10 to 1, and 12 to 1, while the ratios on the other apple varieties are closer to 3 or 4 to 1. Also, the Mutsu variety has the largest percentage of eggs on the undersides of leaves for the apple cultivars in both period 1 and period 2. In period 2 the percentage is similar to the four pear varieties. Similar varietal differences in egg location have been noted by Hattingh (1942) and VanLeeuwen (1939). General observations indicate that the Mutsu variety has the least pubescent leaves of all the apple varieties tested. The extreme "preference" for the upper surface of the Red Chelan leaves may also have been due to greater pubescence on the lower-leaf surface, but any difference in the degree of pubescence on this variety was not noted. Leaf curling was suggested to explain the difference in the number of eggs laid on the upper and lower leaf surface of one of four pear varieties studied by Hattingh. On the variety Glout Morceau, slightly more eggs were laid on the upper leaf surfaces than on the lower leaf surfaces for the whole season. Early in the season, more eggs were laid on the lower than on the upper-leaf surface but as the season progressed the position was reversed. Hattingh ascribed this varietal difference in surface "preference" to the "spiral" tendency of the leaves of Glout Morceau. The leaves of this variety curled in such a way that more or less equal areas of lower and upper-leaf surfaces in any one plane were exposed, whereas the leaves of the other three varieties tended to fold upwards from the mid-rib to expose the lower and close the upper-leaf surfaces. Although a great deal of leaf curling was observed on Red Chelan it was not determined if it was in such a way as to provide greater access to the upper-leaf surface.

2. Laboratory studies of oviposition on apples and pears.

Comparison of varieties - The number and location of eggs on varieties of apple and pear under laboratory conditions is presented in Table 4. There were no significant differences in the mean number of eggs laid over the four-day test period for any of the varieties or the control. The means ranged from 140.0 to 196.5 eggs/female. It should be noted, however, that the mean number of eggs laid for all of the varieties were much greater than the corresponding data obtained under field conditions. There were also no significant differences in the percentage of eggs laid over the first two-day period compared to the second two-day period. The ratio was about 60% for days 1 and 2 to 40% for days 3 and 4 for all of the varieties and the control. The distribution of eggs was similar to the results of the field tests except that the majority of the eggs (70-80%) were laid on the waxed paper lining the side and bottom of the cages. The ratio of eggs laid on the upper surface to eggs laid on the lower-leaf surface was about 1 to 1 for all of the pear varieties. Very few or no eggs were laid on the lower surface of the apple varieties. However, the total percentage of eggs laid on the leaves was

Table 4. Oviposition of the codling moth on different varieties of apple and pear, under laboratory conditions. Mid-July, 1979. Medford, Oregon.[a]

Variety	Wt. of ($\bar{x}$) (g)		No. of Eggs ($\bar{x}$)						
			% on fruit	% on upperside of leaf	% on underside of leaf	% on woody portions	% on waxed paper	% Days 1 & 2	% Days 3 & 4	Total for Days 1-4[b]
Seckel	.030	.004	6.6	7.9	6.7	0.4	78.4	62.0	38.0	196.5±59.5
Bartlett	.032	.004	5.6	5.5	7.0	0.4	81.5	57.3	42.7	165.5±34.8
Red Chelan	.034	.005	8.3	13.3	0.0	0.0	78.4	67.3	32.7	165.2±31.9
Bosc	.033	.006	4.5	9.6	13.3	1.1	71.6	59.5	40.5	161.4±31.0
Mutsu	.032	.004	5.1	18.2	6.5	0.1	70.1	61.7	38.3	161.3±29.8
Idared	.030	.004	6.5	23.5	0.5	0.0	69.5	63.0	37.0	156.0±31.2
Gravenstein	.033	.003	3.8	17.0	1.1	0.0	78.1	63.1	36.9	154.3±29.3
Granny Smith	.032	.004	7.0	13.7	0.7	0.0	78.6	59.5	40.5	146.4±35.9
Comice	.033	.003	4.5	5.5	6.6	1.0	82.4	57.5	42.5	140.0±25.6
Control	.035	.005	---	----	----	---	----	59.5	40.5	150.7±28.0

a - n=10 for all varieties, n=15 for the control
b - no significant differences at p 0.05

about equal for apples and pears, since twice as many eggs were laid on the upper-leaf surface of all the apple varieties as on the upper-leaf surface of the pear varieties. There were no significant differences in the percentage of eggs laid on the fruit. The only significant difference in the location of eggs within varieties of apple or within varieties of pear was the greater percentage of eggs deposited on the lower-leaf surface of the Mutsu apple variety. The moths deposited an equal percent of their eggs on the lower-leaf surface of this variety as on the four pear varieties.

The greater number of eggs under laboratory conditions than under field conditions, as well as the lack of any difference in total oviposition between varieties in the laboratory, seems to indicate that certain conditions associated with the laboratory experiment were highly conducive to egg-laying. The greater number of eggs per female may be due to the more favorable overall environmental conditions in the laboratory, as well as the presence of the wax substrate which was a highly favorable surface for egg laying. The lack of varietal differences in the number of eggs laid per female may also be due to the presence of the "preferred" wax substrate in all of the cages. It is also possible that the effect of fruit volatiles was negated by the confining nature of the cages and the growth chamber. Concentrations of compounds which affect oviposition may have been different from those encountered in the exposed conditions of the field.

Again, the greater percentage of eggs laid on the lower-leaf surface of the Mutsu apple variety was probably due to the less pubescent nature of the lower-leaf surface of this variety compared to the other apple varieties.

Studies on host preference - Table 5 presents the data on the oviposition "preference" of codling moth when given a choice between two apple and two pear varieties. In early July there was no significant difference in the percentage of eggs laid on each of the varieties. In mid-August the two pear varieties, Seckel and Bartlett, were "preferred" over both the Gravenstein and Idared varieties of apple. Almost two-thirds of the eggs were laid on the pear varieties, with the largest percentage (36) being deposited on the Bartlett cultivar.

Table 6 presents the data on the oviposition "preference" of the codling moth when given a choice between three pear varieties in mid-August. Again, a significantly greater proportion of the eggs were deposited on the Bartlett variety (44%). There was no significant difference in the "preference" for either the Bosc or Seckel varieties.

The "preference" for pear cultivars over apple cultivars in mid-August but not in early July indicates that it is a result of factors associated with the seasonal growth of the plants. The "preference" probably reflects physical differences in host suitability rather than differences in plant

Table 5. Oviposition preference of the codling moth when given a choice between two apple and two pear varieties under laboratory conditions. Early July and Mid-August, 1979. Medford, OR.

Variety	% of Total Eggs ($\bar{x}$) Early July (5 reps)[a]	% of Total Eggs ($\bar{x}$) Mid-August (10 reps)[a]
Gravenstein	18.40 ± 2.30 [b]	21.10 ± 5.11 [b]
Idared	27.20 ±11.92	15.90 ± 4.41
Seckel	24.40 ± 3.21	27.00 ± 7.92
Bartlett	28.00 ±10.89	36.00 ±11.51

[a] 10 females per replicate.

[b] Bars encompass non-significantly different means. Student-Newman-Keuls test (p 0.05).

Table 6. Oviposition preference of the codling moth when given a choice between three pear varieties under laboratory conditions. Mid-August, 1979. Medford, Oregon.

Variety	% of Total Eggs ($\bar{x}$) (10 reps)[a]
Bartlett	44.40 + 15.40[b]
Bosc	31.60 + 8.44
Seckel	24.00 + 10.02

[a] 10 females per replicate.

[b] Differs significantly from values below. Student-Newman-Keuls test (p 0.05).

volatiles (see section B on the role of alpha-farnesene). For instance, it may be a result of the increased amount of smooth surface area available on the pear cultivars. The fact that this "preference" does not result in increased total oviposition on single caged pear varieties as opposed to single caged apple varieties may reflect the general nature of the moths to lay their egg complement even if the more suitable substrate is not available. The results of the choice experiment involving three varieties of a single host type (pear) indicate that other physical characteristics are also involved in the selection of a site for oviposition. A significantly greater percentage of the eggs were laid on the Bartlett variety even though all three pear varieties have smooth leaf surfaces. Plant characteristics, such as leaf hardness, leaf size or leaf or fruit surface ratios could be important.

B. Relationship of Alpha-farnesene to Ovipositional Behavior

1. Concentration of alpha-farnesene in apple and pear varieties.

The amount of alpha-farnesene present in the cuticle of the nine varieties of fruit tested was determined prior to the first two field oviposition experiments. Concentrations of alpha-farnesene per fruit and per surface area are presented in Table 7. In early June the amount of the sesquiterpene per fruit and per cm^2 was greater in all four of the pear varieties than the five apple cultivars. The highest

Table 7. The amount of alpha-farnesene found in the epicuticular wax of nine varieties of fruit in early June and late July, 1979. Medford, Oregon.[a]

Variety	June 4-6			July 25-27		
	Surf.[b] area ($\bar{x}$) (cm^2)	Conc. (μg/frt.) ($\bar{x}$)	Conc. ($\mu g/cm^2$) ($\bar{x}$)	Surf.[c] area ($\bar{x}$) (cm^2)	Conc. (μg/frt.) ($\bar{x}$)	Conc. ($\mu g/cm^2$) ($\bar{x}$)
Seckel	11.04	95.2	8.62	27.51	146.08	5.31
Comice	13.21	78.4	5.93	50.02	135.46	2.78
Bartlett	18.27	104.5	5.72	62.31	187.55	3.01
Bosc	18.51	104.5	5.65	57.94	198.15	3.42
Gravenstein	27.50	67.6	2.46	128.68	124.81	0.97
Mutsu	17.30	62.1	3.59	95.03	130.19	1.37
Red Chelan	16.51	57.5	3.48	69.40	115.90	1.67
Idared	18.80	49.9	2.66	84.95	96.84	1.14
Granny Smith	14.51	45.3	3.12	75.43	139.55	1.85

a - n=3 for each variety on both dates.
b - n=45 (3 replicates per variety X 15 fruits per replicate).
c - n=15 (3 replicates per variety X 5 fruits per replicate).

concentration per fruit was 104.5 μg for Bosc and Bartlett while the highest concentration per cm^2 was 8.62 for Seckel. The lowest concentrations for the five apple varieties were from 45.3 μg/fruit to 67.6 μg/fruit and 2.46 μg/cm^2 to 3.59 μg/cm^2 while for the four pear varieties the ranges were from 78.4 μg/fruit to 104.5 μg/fruit and 5.65 μg/cm^2 to 8.62 μg/cm^2. In late July the amount of alpha-farnesene per fruit had almost doubled for all of the varieties. However, fruit surface area had increased by a factor of four or more, resulting in a decrease in the amount of alpha-farnesene per cm^2. Seckel still had the highest concentration per cm^2 with with 5.31 ug and Bosc and Bartlett still had the highest concentrations per fruit with 198.15 ug and 187.55 ug, respectively. Concentrations ranged from 96.84 ug/fruit to 139.55 μg/fruit and 0.97 μg/cm^2 to 1.85 μg/cm^2 for the apple varieties and 135.46 μg/fruit to 198.15 μg/fruit and 2.78 μg/cm^2 to 5.31 μg/cm^2 for the pear varieties. The lowest concentrations per fruit and per cm^2 were found in Idared and Gravenstein, respectively.

2. Laboratory bioassay of alpha-farnesene as an ovipositional stimulant.

This bioassay was designed to test for any relationship between the number of eggs laid and the different concentrations of alpha-farnesene associated with the apple and pear varieties used in these studies. The concentrations of alpha-farnesene involved in this bioassay (3-9 µg) are close to those Wearing and Hutchins (1973) found to have a positive influence on codling moth oviposition (4-16 µg). These values also correspond fairly well with the concentrations of alpha-farnesene per cm^2 found in the varieties tested in this study. Sutherland, et.al. (1977) speculated that the amount of alpha-farnesene per unit area was probably the important value when considering the close range stimulatory nature of the sesquiterpene. Table 8 presents the data on the number of eggs laid by female codling moths in response to extracts of the cuticle of nine varieties of apples and pears over a three-day period. General observations indicated that the majority of eggs were laid within the first six hours. There were no significant differences in the number of eggs on any of the varieties or the control.

3. Discussion of the role of alpha-farnesene.

Sutherland, et.al. (1977) attempted to correlate varietal susceptibility with the concentration of the larval attractant and oviposition stimulant, alpha-farnesene, but were unable to do so. Linear regression analysis of the relationship between oviposition of the codling moth under field and laboratory conditions and the concentration of alpha-farnesene is presented in Table 9. The mean number of eggs laid per female in the field was positively correlated with the concentration of alpha-farnesene per fruit and per cm^2. The highest r^2 (.48)

Table 8. The number of eggs laid under laboratory conditions by gravid female codling moths in response to extracts of the epicuticular wax of apple and pear varieties[a].

Variety	Vol. of Extract (ml)	Approx. Content ∝-farn. (µg)	Wt.♀♀ ($\bar{x}$) (mg)	Day 1	Day 2	Day 3	Day 4
Granny Smith	0.23	3.13	36.7	55.4±12.2	33.4±16.3	20.3± 9.1	110.1±25.8
Red Chelan	0.20	3.46	36.5	49.6±16.7	48.6±18.8	17.3± 5.6	115.5±25.5
Idared	0.18	2.70	35.1	59.5±15.9	42.2±10.6	17.2± 8.3	117.7±17.3
Mutsu	0.19	3.54	36.0	54.6±14.7	41.4± 6.5	24.4± 8.7	119.4±12.3
Gravenstein	0.12	2.43	34.3	67.2±18.0	37.9± 5.9	17.2± 8.0	122.3±18.1
Seckel	0.30	8.57	33.1	63.8±27.8	37.4±20.0	21.6±11.5	122.8±20.1
Bartlett	0.18	5.59	34.7	77.6±16.2	28.8±10.6	17.5± 7.2	123.9±16.8
Comice	0.25	5.88	35.4	55.9±18.8	50.4±12.9	19.8± 6.3	126.2±20.9
Bosc	0.18	5.59	36.6	66.8±20.1	44.1±10.8	19.9± 8.1	130.8±18.6
Control	0.20	0.00	35.9	67.4±18.8	42.1±15.2	17.7± 6.3	127.2±22.2

[a]n=10 for all varieties, n=15 for control.

Table 9. Linear regression analysis of the relationship between oviposition of the codling moth under field and laboratory conditions and the concentration of alpha-farnesene. Spring/summer, 1979. Medford, Oregon.

Oviposition (y)	Alpha-farnesene Concentration (x)			
	µg/fruit		µg/cm^2	
	r^2	slope	r^2	slope
Field Studies				
Mean No. Eggs/ (Period 1)	0.37	0.56	0.20	4.61
Mean No. Eggs/ (Period 2)	0.22	0.59	0.45	19.75
Mean No. Eggs/ (Periods 1 & 2)	0.48	0.60	0.0015	0.73
% Eggs on Fruit[a] (Period 1)	0.05	- 0.07	0.002	0.15
% Eggs on Fruit[a] (Period 2)	0.44	0.12	0.18	1.79
% Eggs on Fruit[a] (Periods 1 & 2)	0.09	- 0.05	0.17	1.49
Laboratory Studies				
Mean No. Eggs/	0.15	- 0.03	0.0005	- 0.02
% Eggs on Fruit[a]	0.21	0.31	0.39	4.86
Laboratory Studies (moths enclosed in petri dishes)				
Mean No. Eggs/ (Days 1-4)	---	---	0.30(0.12)[b]	1.67(0.05)[b]

[a] - Percentage data transferred (are sin $\sqrt{\text{percentage}}$) for regression analysis

[b] - Values in parentheses are for analyses which include a 0.00 level of alpha-farnesene.

was found for the relationship between mean number of eggs per female in periods one and two and ug of alpha-farnesene per fruit. Thus, the concentration of alpha-farnesene in apple and pear fruits may account for up to half of the variation in the number of eggs laid per female on different cultivars. The remainder of the variation may be accounted for by other physical and/or chemical factors, as well as biological variations in fecundity not associated with the plant host.

Wearing and Hutchins (1973) and Sutherland, et.al. (1974) reported that moths laid significantly more eggs in petri dishes when exposed to alpha-farnesene levels of 4 to 16 ug than in dishes containing none of the sesquiterpene. In the present study, although moths exposed to alpha-farnesene levels of 2.5 to 8.5 ug did not lay significantly more eggs than moths that were not exposed, there was a positive correlation between the level of alpha-farnesene and the number of eggs laid per female ($r = .12$ if the control is included in the analysis and $r = .30$ if it is not included). The failure to reproduce the more dramatic differences found in earlier studies may be a result of the rapid evaporation of alpha-farnesene during the bioassays as well as its high susceptibility to oxidation.

As was found by Sutherland, et.al. (1977), the total level of the known oviposition stimulant, alpha-farnesene, per fruit increases during fruit growth and maturation. Thus, there seems to be a relationship between an increase in the concentration of this sesquiterpene and the number of eggs laid. Changes in the concentration may also account for the decrease in oviposition on fruit spurs after the normal harvest dates. However, neither Sutherland's nor the present study determined the concentrations of alpha-farnesene in the field post-harvest. Sutherland and his colleagues did report that the concentrations leveled out as harvest approached. Brown, et.al. (1966) also indicated an increase in fruit volatiles to just past the climacteric peak; the compounds, however, were not identified.

Other fruit volatiles associated with ripening may also influence oviposition. The major volatile compound given off by ripe pear and apple fruits is ethylene, which may appear in amounts more than twice that of all the other volatiles added together (Fidler, 1950). It is possible that this olefin may act as an oviposition inhibitor. Other volatiles associated with fruit flavor, such as the main constituents of apple odor 2-hexanol, 1-hexanol, and ethyl-2-methyl (Flath, et.al., 1967) should also be investigated as possible oviposition inhibitors.

Preliminary experiments by Russ (1976) indicated that gravid moths were more attracted to apples than to pears. He found that the attractiveness of the fruit varied with fruit development and suggested that different stages of the fruit had different amounts of the attractant. This has been confirmed both in this study and that of Sutherland, et.al. (1977). However, Russ also tentatively concluded that females distinguished between apples and pears on this basis and suggested that apples were "preferred" because they contained more of the attractant. In the present study, pears were found to contain a greater amount of the attractant or stimulant, alpha-farnesene. Also, females caged separately on several apple and pear varieties showed no consistent pattern of greater egg deposition on either pear or apple cultivars. When given a choice between apple and pear fruit spurs in early July, the moths did not "prefer" one host over the other. However, when given the same choice in late August they did "prefer" pear. This "preference" seems to be partially related to the higher levels of alpha-farnesene in pears. However, because of inconsistencies with field data on singly caged pears and apples, as well as the confining nature of the choice experiments on potential levels of the sesquiterpene, it is thought that the "preference" for pears later in the season also reflects physical differences in host suitability (see section A-2 on host preference).

The concentration of alpha-farnesene, as well as other fruit volatiles associated with fruit maturation may also influence the distribution of eggs on apple and pear. Sutherland, et.al. (1977) proposed that increasing alpha-farnesene levels influence seasonal patterns in egg location. Although the distribution of eggs on apples and pears was fairly consistent throughout the season, regression analysis (see Table 9) indicates that the percentage of eggs laid on the fruit may be partially related to the concentration of alpha-farnesene.

IV. Conclusion

Oviposition behavior of the codling moth is influenced by a wide array of physical and chemical factors. Variation in these factors may affect the number and location of eggs. Host type, varietal and seasonal differences may all be associated with variation in these important oviposition modifying cues. There is little doubt that leaf pubescence has a negative effect on oviposition. This accounts for much of the difference between the number of eggs laid on the upper or lower-leaf surfaces of apples and pears, as well as on specific varieties of each host type which are more or less glaborously leaved. Other physical characteristics which are known to influence oviposition by other insect species, such as leaf hardness, may have an effect on codling moth egg laying behavior and need to be addressed in future studies.

This study, as well as earlier studies, supports the role of alpha-farnesene as an oviposition stimulant. They suggest that the seasonal increase in total oviposition on apple and pear hosts is related to an increase in the concentration of this sesquiterpene during fruit maturation. Varietal differences in total oviposition per female are partially related to differences in the levels of alpha-farnesene. A reduction in reproductive capacity on trees with mature fruit may be related to alpha-farnesene levels or may be due to other volatiles which are involved in fruit ripening, such as ethylene, acting as oviposition inhibitors. Important fruit volatiles such as ethylene, 2-hexanol, ethyl-2-methyl, citral and geraniol must be assayed for their possible stimulatory or inhibitory influence on codling moth oviposition. Further work is needed to determine the extent to which differences in the concentration of alpha-farnesene affect oviposition. Attempts to determine this are limited by the volatility and susceptibility of the sesquiterpene to oxidation. The apparent ability of lab-reared moths to lay their complement of eggs on petri dishes without the presence of an oviposition stimulant also presents a problem. Experiments to determine the influence of alpha-farnesene on the oviposition behavior of codling moths should be conducted with field collected individuals. In order to determine if differences in oviposition are related to alpha-farnesene concentrations, the sesquiterpene must be presented in such a way as to reduce the rate of evaporation. The inability to reproduce the work of Sutherland, et.al. (1977) may be a result of the rapid evaporation of alpha-farnesene during the bioassays. Since the concentration of alpha-farnesene increases with fruit storage, it is possible that this could be overcome by using fruits which had been in storage for different lengths of time as the source of stimulant. The concentration of alpha-farnesene could be determined for each of these varieties prior to their use in the bioassays.

A close look at reported differences in oviposition, whether related to host type, variety, or seasonal physiology, indicates that several factors acting at the same time are important. Past studies have placed too much emphasis on the role of a single factor. For example, weather conditions have been heavily implicated as the major cause of seasonal changes in fecundity. The present study indicates that this is not the case. Laboratory studies, under controlled conditions are still needed to confirm this. These studies could be conducted in a manner similar to those reported here except that the laboratory cages should be lined with a "non-preferred" substrate. Physical and chemical factors associated with oviposition have been limited to leaf pubescence and alpha-farnesene. Other factors must also be examined. More importantly, the possible inter-relationships of two or more factors must be considered. Some plants produce a multiplicity of physical and chemical stimuli which must be integrated by the insect nervous system to produce the observed behavioral response. Oviposition by other insect species has been reported to be regulated by a combination of stimulatory and inhibitory chemical factors as well as by tactile factors such as surface characteristics (Mehta and Saxena, 1970; Coaker and Finch, 1973). The relative roles of several factors which affect codling moth oviposition could be studied by manipulating the level of one (i.e., removing leaf hairs or supplementing alpha-farnesene levels) and then comparing oviposition behavior before and after the manipulation. Alternatively, several factors thought to influence oviposition could be quantitatively measured at the same time on three or four varieties which are known to differ in their suitability for oviposition and then analyzed by regression procedures.

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