AN ABSTRACT OF THE THESIS OF

SATNAM LAL SETHI (Name) for the DOCTOR OF PHILOSOPHY (Degree)

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Title: ENVIRONMENTAL BIOLOGY OF ERIOSOMA PYRICOLA BAKER AND DAVIDSON

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A method of culturing Eriosoma pyricola on detached root pieces was developed to ensure a regular supply of aphids for experimental work. Another method was designed for studying the alate sexuparae formation in woolly pear aphid, whereby growing plants were infested so that the aphids or their progeny could be recovered later.

Sexuparae were produced in woolly pear aphid colonies on the roots of "Domestic Bartlett" seedlings treated to induce dormancy, indicating E. pyricola is holocyclic in Oregon. No sexuparae were found while shoot growth continued. Shoot growth of pear seedlings ceased when the plants were exposed to 10-hour photoperiods at a constant 24°C. Growth continued for a much longer time when plants were kept under 16-hour photoperiods at alternating day and night temperatures, 24°C and 18°C, respectively. However, aphids did not produce sexuparae when cultured on detached root pieces from

plants treated for four weeks under 10-hour photoperiods at a constant 24°C. Also, sexuparae were not found in aphid colonies on root pieces of dormant plants from the field.

All these results agree with our field observations. In the field, sexuparae are produced for about two months in late summer and early fall on the roots of infested plants. After this, no more sexuparae appear in the remaining aphid populations which continue as apterous virginoparae on pear roots until autumn of the following year.

Experiments on growth cessation in pear plants indicated that short day-length was not the critical factor responsible for the induction of growth cessation in pear seedlings. These experiments also showed that constant temperatures were more important in the regulation of growth in this pear variety.

The direct effect of photoperiods and temperatures on sexuparae production in this aphid was also investigated. Aphids on detached root pieces did not produce sexuparae when exposed to 10-hour photoperiods at alternating day and night temperatures, 24°C and 18°C, respectively. Aphid cultures on detached root pieces were kept under different combinations of 10- and 16-hour photoperiods and 15° and 18°C constant temperatures. But the treatments had no effect on sexuparae formation. No sexuparae were found in aphid colonies on root pieces kept in continuous darkness at constant temperatures of 15°, 18°, 21°, 24° and 27°C for periods of 14 to 49 days. Also, sexuparae

were not produced when aphid cultures on root pieces were alternated between 15° and 24°C every 12 hours for 47 days. Sexuparae were not found in our stock cultures maintained at 21°C for about three years.

Direct effect of different temperatures on the development and increase in numbers of woolly pear aphid was also studied. Apterous E. pyricola on detached roots developed and reproduced normally at 24°C, but failed to reproduce and died within two weeks when kept at 27°C.

Apterous from stock culture and alate virginoparae from elm galls were transferred to the detached roots of "Domestic Bartlett" pear, Amelanchier florida Lindl., Sorbus sitchensis, Crataegus species, Ribes sativum and Red Delicious apple. The aphids did not survive except on the pear roots.

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ENVIRONMENTAL BIOLOGY OF ERIOSOMA PYRICOLA BAKER AND DAVIDSON

INTRODUCTION

The research reported herein was conducted to determine the conditions responsible for form (morph) changes in the woolly pear aphid.

The woolly pear aphid, Eriosoma pyricola, was first described by Baker and Davidson (1917) in California, where they found that it alternated between cork elm (Ulmus suberosa Doud.) and pear (Pyrus communis L.). Some European workers considered it a synonym of E. lanuginosa Hartig, but Dr. Hille Ris Lambers disagrees and considers it a distinct species.[1]

Most aphids in temperate regions reproduce a succession of generations parthenogenetically and viviparously throughout the summer. Once a year alate sexuparae are produced on the secondary host which return to their winter (primary) host plant to deposit sexual forms, male and oviparous female. The oviparous female then lays wintering eggs on the primary host, thus completing the cycle (Figure 1). The production of wintering eggs in aphids is similar to diapausing response in other insects. It is a special adaptation in the seasonal cycle of the species for tiding over a period of unfavorable

[1] Personal communication to Dr. K. G. Swenson, August 17, 1965.

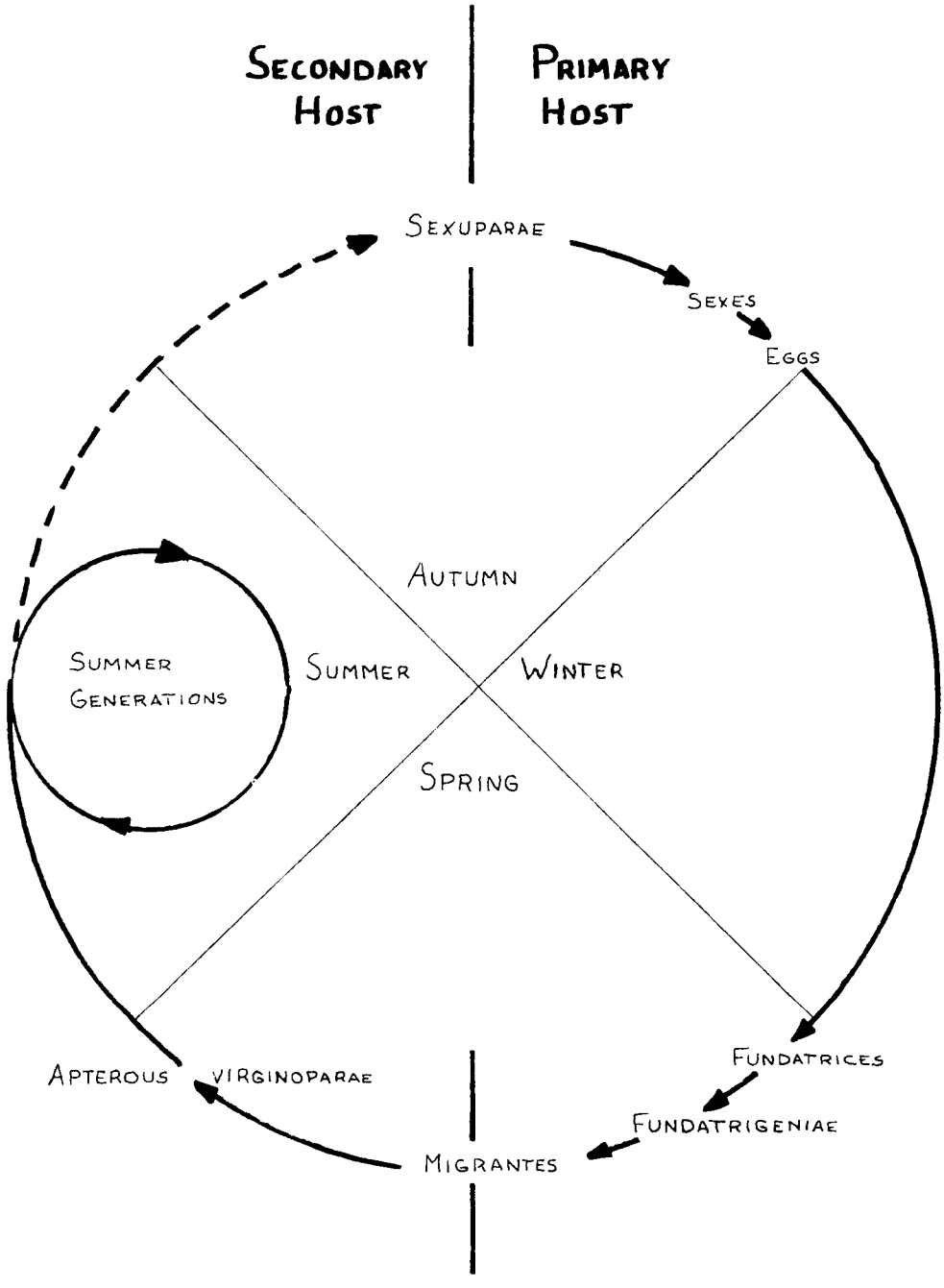


Figure 1. Typical life cycle of an aphid.

environmental conditions.

Diapause is a physiologically controlled arrest of development. The occurrence of a diapausing stage varies in different insect species. In some species it occurs during the egg stage. Other species diapause as larvae, pupae or adults. But the stage in which diapause occurs is characteristic of the species. For instance, the leafhopper, Colladonus clitellarius (Say) overwinters as eggs (George and Davidson, 1959) whereas in Nephotettix bipunctatus cinctipes Uhler diapause induction takes place in the fourth and fifth nymphal instars (Kisimoto, 1959). The European corn borer, Pyrausta nubilalis (Hübn.) diapauses as a full grown caterpiller (Babcock, 1927a and 1927b) whereas Heliothis armigera (Hübn) spends the winter as diapausing pupa (Ditman et al., 1940). Dickson (1949) reported that the oriental fruit moth, Grapholitha molesta (Busck) and the codling moth, Carpocapsa pomonella (L.) diapause as a fullfed larvae. However, the Colorado potato beetle, Leptinotarsa decemlineata (Say) diapauses as adults (De Wilde, 1954).

In temperate climates, the appearance of sexuparae in aphids and induction of diapause in other insects are regulated by short-photoperiod and low temperature (Danilevskii, 1965). However, tropical species do not produce sexuparae in response to day-length and temperature.

Of the factors known, seasonal changes in day-length have been

considered to be the most important in determining the sexuparae production in aphids and diapause induction in hibernating and aestivating insect species.

Diapause induction in most of the insects is the result of a certain combination of conditions (short days and low temperatures) experienced by the individuals of the preceding stages of that generation. For instance, the European corn borer, Pyrausta nubilalis (Hübn.) diapauses as a full-grown caterpillar when reared under short days. However, in aphids two complete generations elapse from the appearance of sexuparae to the production of wintering eggs. For example, the alate sexuparae of Myzus persicae Sulzer produced in response to short days, fly to peach to deposit oviparous females which in turn lay fertilized diapausing eggs after mating (Cottier, 1953).

Root aphids living in constant darkness cannot use light as a "timer" but they produce alate sexuparae in the autumn like the aphids living on the shoots of plants. It may be pointed out that the only form produced on pear roots is alate sexuparae which deposit beakless males and females.

During 1965-67, experiments were conducted to investigate: (1) the conditions responsible for the production of sexuparae in Eriosoma pyricola, (2) the conditions that induce cessation of growth in pear plants, (3) the direct effects of temperature and light on alate production in E. pyricola, (4) whether E. pyricola is holocyclic or anholocyclic in Oregon, and (5) the host range of E. pyricola.

REVIEW OF LITERATURE

Mordvilko (1901) contended that the original hosts of aphids were woody plants. Host alternation (heteroecy) and change of hosts from trees and shrubs to herbaceous plants in aphids are secondary adaptations which resulted due to the seasonal changes in their host-plant conditions (Hille Ris Lambers, 1950; Kennedy, 1950; Kennedy and Booth, 1951 and 1954).

Generally, herbaceous plants constitute a secondary host in host alternating aphids, but both the hosts, primary as well as secondary, of the genus Eriosoma are woody plants. Also, one species, the woolly apple aphid, no longer uses the primary host in some parts of its range and does not produce sexual forms, thus is anholocyclic. Palmer (1952) reported that aphids will survive through the winter on secondary hosts if the climate is mild or if the plants having aphid colonies are protected in the greenhouse. Similarly the absence of sexual forms in tropical aphids has been attributed to mild winters and long days (Goot, 1917; Takahashi, 1931; Bodenheimer and Swirski, 1957).

Form changes in aphids have been the subject of speculation for over a century. Temperature and light were considered to be of major significance in the formation of sexupara, andropara and virginopara.

It is within the last few decades that day-length has been found to be the critical factor controlling the production of sexuparae in aphids. Marcovitch (1924) was the first to demonstrate that short-days determine the production of sexes in Aphis forbesi Weed. Effect of short photoperiods on sexuparae formation was later confirmed in Aphis chloris Koch (Wilson, 1938), Acyrthosiphon pisum Harris (Kenten, 1955), Macrosiphum euphorbiae Thomas (MacGillivray and Anderson, 1964), Aphis fabae Scopoli (De Fluiter, 1950), Megoura viciae Buckton (Lees, 1959 and 1960) and Brevicoryne brassicae L. (Kawada, 1967).

The role of photoperiod in the production of different forms has been thoroughly demonstrated in Megoura viciae (Lees, 1959). Response curves of apterous, M. viciae reared under different photoperiods from birth onwards are presented in Figure 2. It is interesting to note from the curves that the progeny of the aphids exposed to a range of 4 to 14-hour photoperiods became sexuparae, while proportion of sexuparae was much less in the colonies reared under 14 to 15-hour photoperiods per 24-hour day. Colonies kept under 16-hour photoperiods or longer, were all virginopara-producers. Thus the "critical photoperiod" at which this transition occurs in Megoura appears to be around 14 1/2 hours. But the individuals reared under critical photoperiods and in complete darkness produced mixed progeny. However, photoperiods have no influence on male production in

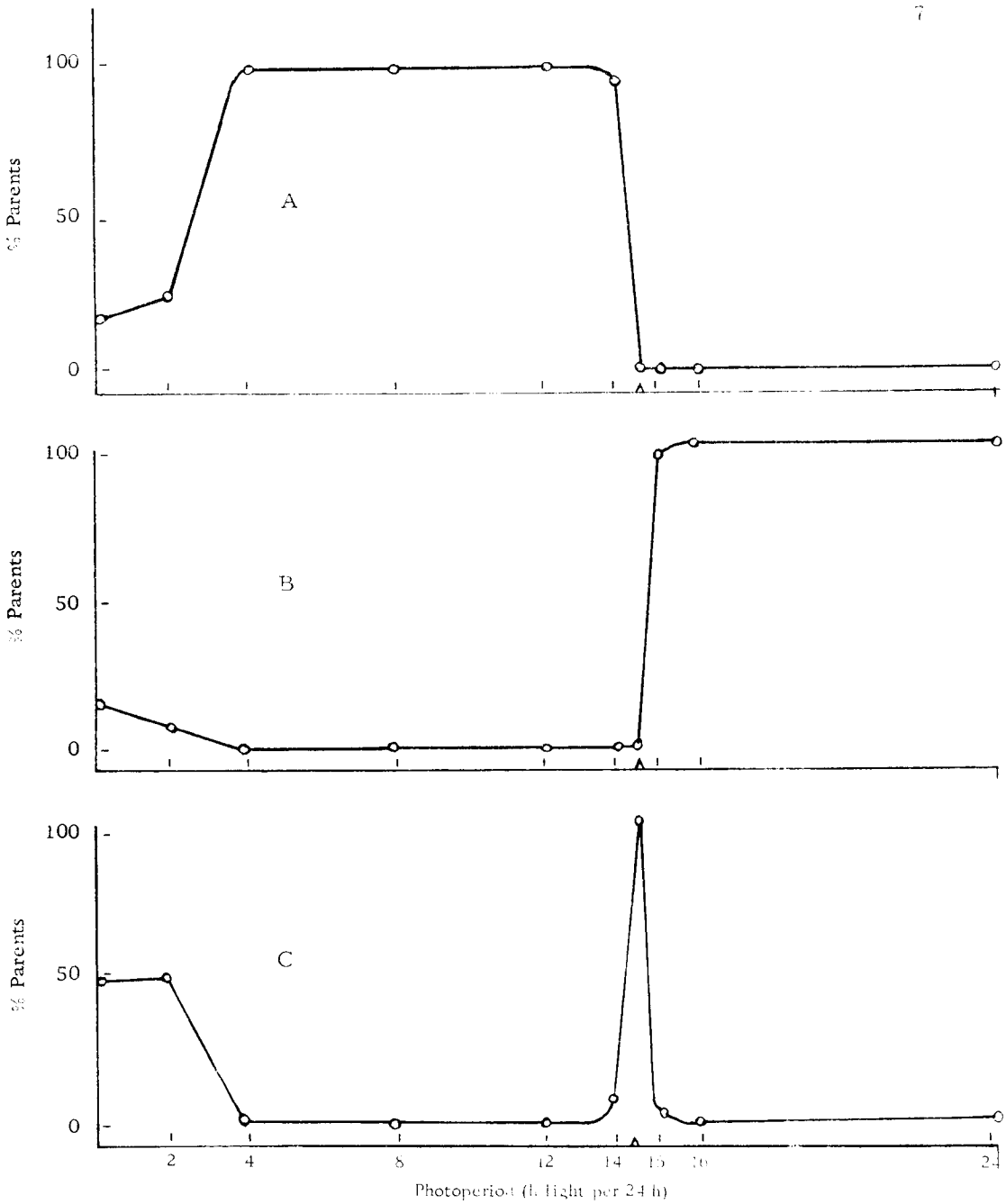


Figure 2. Photoperiodic response curves for apterae of Megoura viciae. Parents either produce oviparae only (A), virginoparae only (B), or mixed families (C). From Lees, 1959.

this aphid species. Bodenheimer and Swirski (1957) stated that a constant temperature of 22°C completely inhibited the formation of sexuparae in Brevicoryne brassicae L. and M. persicae in spite of simultaneous short-day treatments. Bonnemaison (1958) demonstrated that the short-day effect is readily cancelled by high temperatures. Bonnemaison (1964) reported the complementary influence of crowding together with short photoperiod on the production of oviparae in Dyaphis plantaginea Pass. Dyaphis apterous exposed to short days from birth onward produced less than five percent sexuparae when reared individually but 50 to 100 percent became sexuparae when crowded under the same conditions. The complementary effect of crowding on oviparous production was also demonstrated in the cabbage aphid, Brevicoryne brassicae (Kawada, 1967). However, crowding suppressed the formation of males in B. brassicae and M. persicae and isolation enhanced it (Bonnemaison, 1951).

The production of males in most aphids has been considered to be determined by the temperature conditions prevailing during the pre- and post-natal development period (i. e. before first moulting) of the mother. Temperature favoring the production of males in Acyrthosiphum pisum (Kenten, 1955) and Megoura viciae (Lees, 1963) seems to be in the range of 15 to 20°C. High (above 23°C) and low (below 11°C) temperatures completely suppress the formation of males. Shibata (1952 and 1954) demonstrated that the fluctuating temperature

favors the production of males in Myzocallis kuricola Mats. Wilson (1938) stated that a constant high temperature inhibited the production of males in Aphis chloris. The adverse effect of high temperature on male formation in B. brassicae and M. persicae was later confirmed by Bonnemaison (1951). He also stated that the proportion of males was greatly reduced in the colonies reared under long-days. No males were recorded in A. pisum cultures kept under long photoperiods (Kenten, 1955).

In most aphid species, males are produced late in the reproductive period of the aphid when reared under male-inducing conditions. However, the proportion of males is a species characteristic which can not be increased beyond that proportion by any means. But males can be readily suppressed by exposing the parents to high temperatures and long photoperiods (Kenten, 1955; Lees, 1959). Their sequence of appearance is also characteristic of the species. For instance in two species of Periphyllus some of the first born nymphs form males (Bückle, 1963) while in A. pisum males are the last born individuals (Kenten, 1955). In Megoura viciae, males appear in the middle of the reproductive period (Lees, 1959). Hille Ris Lambers (1960), however, reported that some of the individuals of Metopolophium dirhodum Wlk. produced males only.

In some species photoperiod can act directly on the aphids. Von Dehn, (1967) while studying the influence of light on morph changes in

Megoura viciae, found that it acted directly on the aphids as well as via the plant. She reported that the condition of food plant determined male production while oviparous female formation was controlled both by direct light and condition of the food plant if reared under complete darkness. Danilevskii (1965) stated that a number of studies show the influence of the composition of food plants on the seasonal cycle of aphids. He further pointed out that food condition cannot act as a critical regulator like the light because its biochemical composition varies with the species, age of the plant and with the fluctuating environmental conditions. However, nutrition may serve as a stimulant for the induction of diapause or sexuparae formation in monophagous sedentary insects (Danilevskii, 1965). Dunn (1959) reported that in Pemphigus bursarius sexual forms appeared in June on April-sown lettuce, but when plants were overwintered in the greenhouse, sexuparae appeared in March which coincided with the change in plant condition (nutrition). Hille Ris Lambers (1960) suggested that root aphids might react to changes in the host plant. Lees (1966) contended that photoperiods and temperature might play some role in the determination of sexual forms in subterranean aphids through their host-plant physiology. Induction of diapause in the cabbage maggot (Erioischa brassicae Bouche) infesting the roots of cabbage plants exposed to short days is probably the only demonstration to this effect (Hughes, 1960). Danilevskii (1965) did not agree with Hughes' conclusions

because the possibility of direct influence of light was not studied which might have affected the cabbage maggots under some circumstances.

The alate sexuparae of Eriosoma species that return to elm to deposit sexual forms in autumn are produced on the roots of their secondary hosts. It may be worthwhile to point out that the apterous form of the woolly pear aphid is always subterranean in habits. Root aphids living in constant darkness are not likely to respond to light as do the aerial aphids. Physical contact (crowding) is also unlikely because of restrictions on their movement in the soil.

The appearance of alate sexuparae in the genus Eriosoma during fall seems to accompany the seasonal changes in their host plant physiology. It is very probable that the subterranean aphids use environmentally induced changes in the host plant as a "timer."

The seasonal changes in growth and dormancy induction in woody plants have been reported to be regulated by photoperiods in conjunction with certain temperature combinations (Downs and Borthwick, 1955; Wareing, 1956; Nitsch, 1957). However, environmental conditions responsible for growth cessation in woody plants are different in different species.

Photoperiod can hardly be the cause of cessation of growth in pear seedling by late summer or early fall in Oregon when photoperiod is still too long to be limiting. Reed (1939) recorded shoot growth

of loblolly pine in the field and concluded that seasonal trends in its growth were governed by the air temperature. Digger pine (Pinus sabiniana Dougl) grew better under constant 17°C than under 7° and 23°C, but its growth responses were significantly better when held at 17°C night with warmer days (Hellmers, 1962). Vegis (1956) claimed that under natural conditions the environmental temperature is of decisive importance in growth regulation of woody plants and the role of photoperiod in dormancy induction has been overstated. Kramer (1957) reported that the day-night temperature differential has a great bearing on the growth of loblolly pine seedlings. He also mentioned that warm nights of the summer probably caused the formation of resting buds in loblolly pine. Hellmers and Sundahl (1959) observed the favorable effect of day-night temperature differential in Douglas fir [Pseudotsuga menziesii (Mirb.) Franco]. However, day-night temperature differential has no significant effect on redwood (Sequoia sempervirens Endl.) growth, though day temperature was very important in its growth (i.e. growth increased with the rising day temperature from 7 to 23°C). Went (1948, 1953) recorded marked effects of day-night temperature differential on the growth of various herbaceous plants and postulated the theory of thermoperiodism in plants.

MATERIALS AND METHODS

Greenhouse Procedure

Investigations reported herein were carried out in the greenhouses of the Entomology Department at Oregon State University, Corvallis, Oregon. Studies were conducted throughout the year. Plants were held in the greenhouse rooms before and after the experimental treatment unless otherwise stated. A 16-hour photoperiod was obtained by supplementing the natural days with fluorescent lighting.

Greenhouse temperatures were regulated by the use of thermostats. Temperatures were recorded with a Leeds and Northrup multipoint recording thermograph throughout the experimental periods. Temperature in the experimental rooms varied between 65^{o} and 85^{o}F during summer months and between 68^{o} and 72^{o}F during winter months with occasional sharp fluctuations.

Greenhouse rooms were kept free from pests such as aphids, thrips and mites by the TEPP-fumigant and insecticidal as well as acaricidal sprays. Powdery mildew was often a problem on woody plants in the greenhouse, especially during late fall and winter, and was kept under check with Acti-dione sprays applied when required.

Experimental Plants

Plants used for these studies were raised from stratified seeds

of "Domestic Bartlett" pear (Pyrus communis L.). The seeds were sown (three per pot) in 6-inch clay pots filled with a mixture of loam and peat in the bottom two-thirds and with white sand in the upper one-third. Soil was supplemented with inorganic fertilizers at the rate of one cup of ammonium nitrate, one cup of 6-10-4, and one-half cup of lime per 25 gallons.

Most of the seedlings emerged between the 3rd and 6th day. After two weeks the seedlings were thinned to one plant per pot to obtain as uniform a group as possible. For experimental treatments, plants were kept in controlled-environment chambers. Both incandescent and high-intensity fluorescent lamps (Gro-Lux Sylvania, VHO) were the source of light in the chambers. Long days were of 16-hours duration and short days of 10-hours light at about 800-1100 f. c. intensity unless otherwise specified.

Handling of the Aphids

Stock cultures of woolly pear aphid, Eriosoma pyricola, were established from adult apterous virginoparae collected from the roots of pear seedlings at Forest Grove, Oregon during early July, 1965. The aphid cultures were maintained on detached pieces of pear roots according to the new methods described under Results. Aphids were transferred with the moist tip of a camel's hair brush. Every effort was made not to mix the species while transferring aphids to start

new cultures. One species was handled at a time and the working table in the head-house was cleaned before handling another species.

Experimental Procedure

Experiments reported in Section B were conducted to investigate the possibility of direct environmental effect on sexuparae formation in the woolly pear aphid. Aphid cultures on root pieces kept on moist sand in pint polyethylene boxes were kept at constant temperatures as well as at alternating day-night temperatures. The length of time required to complete a generation at different temperatures was also recorded (Section C). Some of these cultures were also exposed to different photoperiods at various temperatures. Aphids used in these experiments were taken from the stock culture. Nymphs produced within 24-hours were also used in some of the experiments.

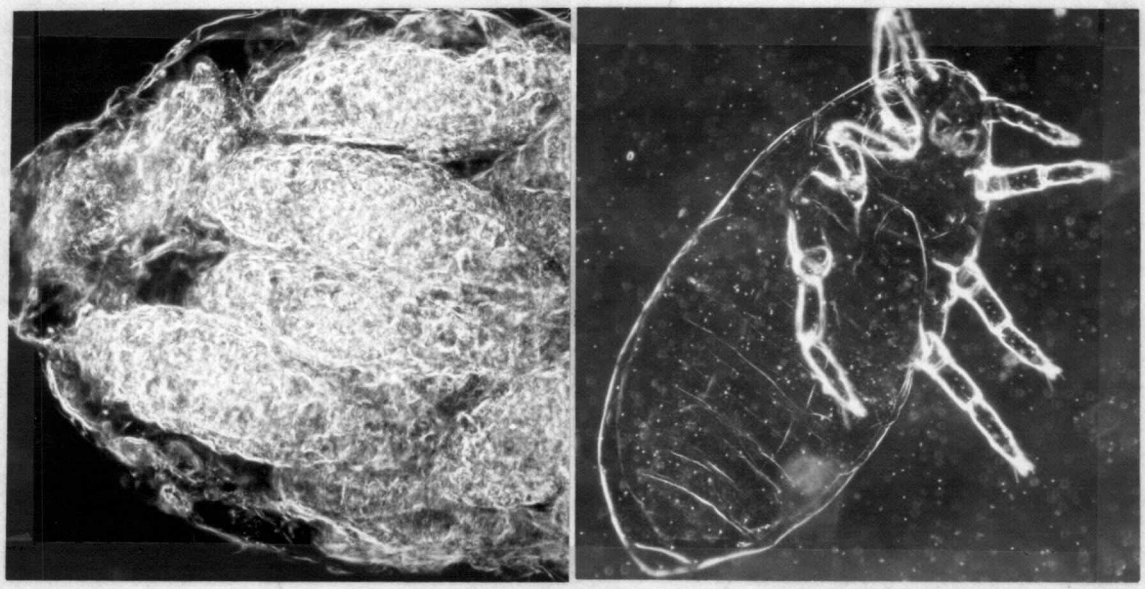
Experiments described in Section D were carried out to determine the conditions responsible for the initiation of growth cessation in pear seedlings. Bartlett pear seedlings grown in pots were treated under long- and short-photoperiods at different temperatures. The shoot length and duration of growth were recorded at the beginning of the treatments and each week thereafter until the plants ceased growth.

Pear seedlings having aphid colonies on their roots were exposed to various treatments of different temperatures and photoperiod combinations to determine the effect of environmentally induced cessation

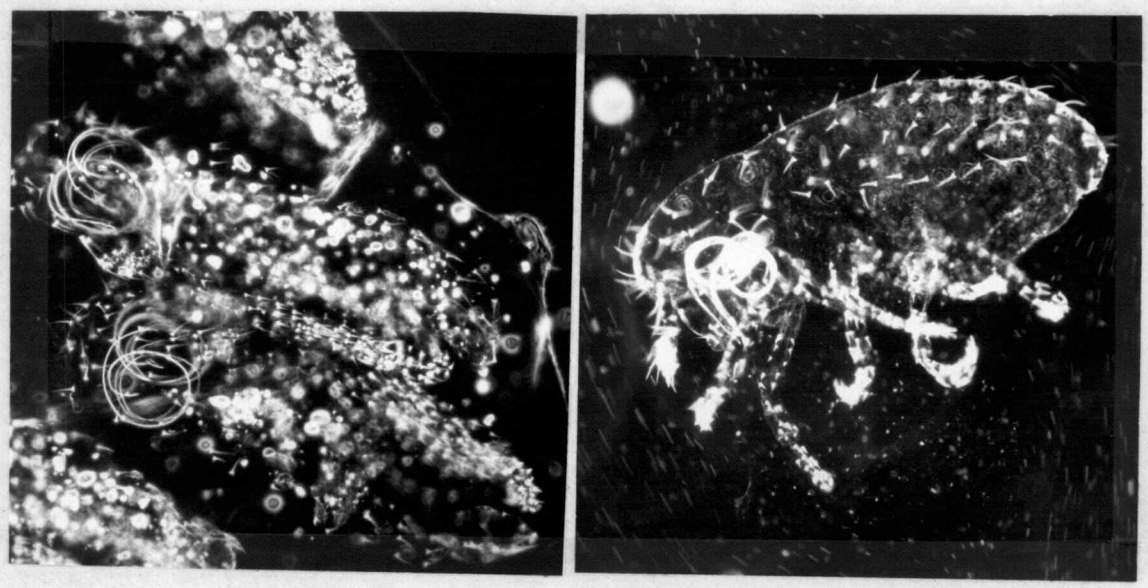
of shoot growth on sexuparae production (Section E). Apterous virginoparae used in these experiments were taken from the stock cultures. The percent sexuparae produced was recorded.

Examination of Sexuparae

A sample of 20 alates taken at random from the colonies on the roots of pear plants treated to induce dormancy were caged individually in glass petri dishes. The aphids readily deposited nymphs on moist filter papers in the petri dishes. The nymphs were collected in 70% ethyl alcohol for examination under the microscope at a later date. Some of the sexuparae aphids from experiments were also collected in lactophenol and were later cleared and mounted with embryos intact according to the method described by Richards (1964). Both nymphs and embryos were found to be beakless when examined under the microscope at 43x (Figure 3a). Also, the embryos dissected from a group of alate aphids taken from roots of pear seedlings at the Entomology Farm of Oregon State University on September 27, 1966, were found to be beakless. However, the nymphs produced by the alate aphids from elm leaf bladder gall had stylets and readily colonized on pear roots. A coiled stylet was clearly seen when the mounted alatae from bladder gall were examined under the microscope at 43x (Figure 3b).



(a)



(b)

Figure 3. Embryos of Eriosoma pyricola. (a) beakless embryo of sexupara (b) embryo of alate virginopara having coiled stylet.

DESCRIPTION OF EXPERIMENTS AND RESULTS

A. New Methods for Culturing Root Aphids

There was no known efficient method for rearing aphids on the roots of woody plants when this work was started. The method of rearing lettuce root aphid described by McClean and Kinsey (1961) is cumbersome and not very practical for culturing aphids of the genus Eriosoma.

Therefore, a practical method of culturing Eriosoma pyricola in the laboratory was an essential prerequisite to ensure the regular supply of aphids for experimental work. A method was also necessary by which aphid populations could be recovered from the roots of experimental plants for examination without any loss of aphids. With these objectives in mind, two methods were designed.

Rearing Aphids on Detached Roots

In this method, pieces of pear roots of various sizes were placed on wet sand in a polyethylene tray measuring 7 3/4 x 5 1/2 x 3 1/8 inches (Figure 4). The tray was covered with an airtight lid, and then kept in a controlled-temperature cabinet operated at 21°C. A colony of apterous root aphids could be maintained for two to three months on a given root piece under these conditions. A culture of the woolly pear aphid has been maintained on the root pieces of pear

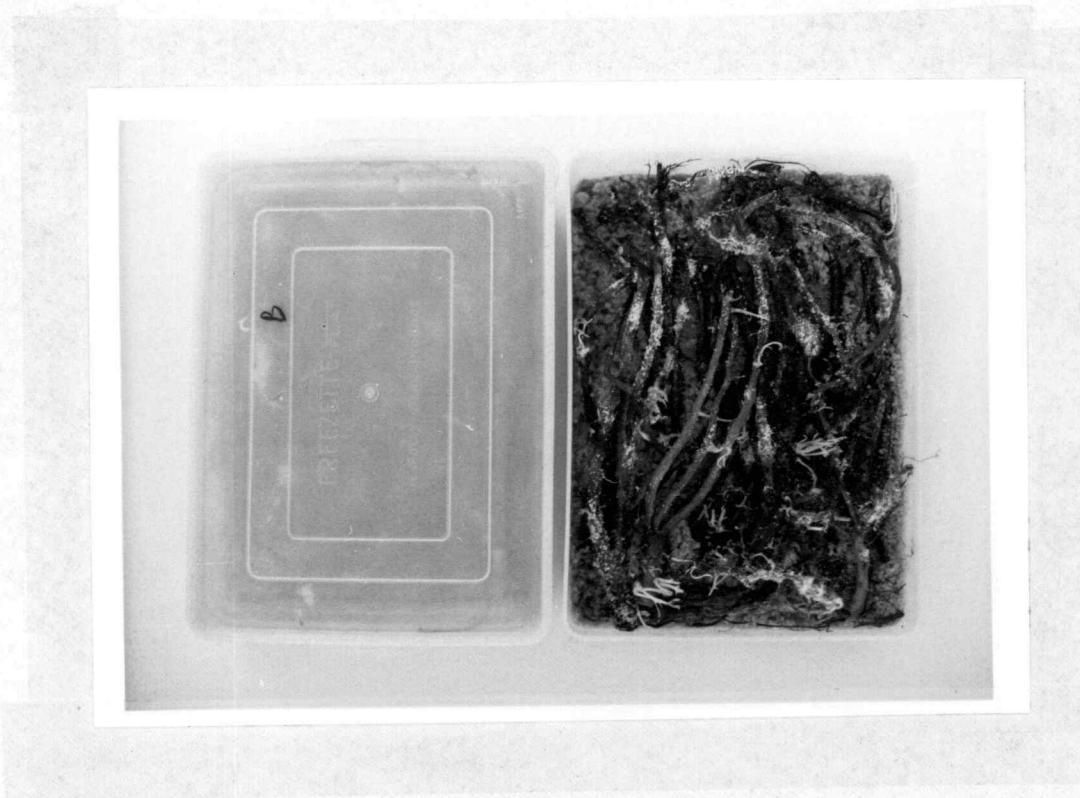


Figure 4. Aphids on detached roots.

seedlings in this way for about three years. Similarly E. americanum (Riley), E. ulmi L., E. herriotii (Börner), and E. lanigerum (Hausman) were cultured, respectively, on root pieces of Amelanchier florida Lindl., Ribes sativum, Crataegus species and Red Delicious apple for shorter durations of time. The roots for maintaining these stock cultures were obtained from the field and were held in polyethylene bags in cold-storage until they were required for starting a new culture. New cultures were started every 6th or 8th week by placing 20 to 30 aphids on uninfested root pieces.

This method is also useful for studying host relationships in aphids of the genus Eriosoma and may also have some use in the rapid evaluation of root-stocks for aphid resistance. Uniform infestation, which normally does not occur in the field trials, is possible by this method. This is important because root-stocks are generally seedlings and one might have to look for an individual resistant plant.

Rearing Aphids on the Roots of Growing Plants

This method was developed for studying the sexuparae formation in E. pyricola, whereby growing plants could be infested uniformly and all the aphids or their progeny could be recovered later.

For this purpose, a 6-inch clay pot was half-filled with soil. A band, made by removing the bottom of a pint polyethylene container (4 x 4 x 3 inches) sprayed with black paint was placed in the pot on top

of the soil (Figure 5). The band was filled with sterile white sand and soil was added around it in the space between the band and the side of the pot. Stratified pear seed was planted in the sand. The sterile sand also prevented damping-off among the germinating seeds. When the plants were ready for use in experiments, the sand was removed and aphids were placed on the exposed part of the roots. The lid of the pint container from which the band was made was also painted black, a small hole made in the center, and a slit cut from the hole to one edge. The lid was then placed on the chamber, with the plant stem through the center hole. The hole and the slit were sealed, providing a dark chamber with high humidity for the root aphids. All the experimental plants were examined the next day to ensure that aphids had established themselves and had started feeding.

B. Direct Temperature and Photoperiod Effects on Sexuparae Formation in Eriosoma pyricola

Experiment 1

This experiment was designed to determine the effect of different constant temperatures on sexuparae production in the woolly pear aphid. Adult apterous virginoparae (ten per box) were placed on detached root pieces on moist sand in pint polyethylene boxes. A group of five such boxes was placed at each of 18°, 21°, 24°, and 27°C on August 29, 1965. All the aphid colonies were examined every day at

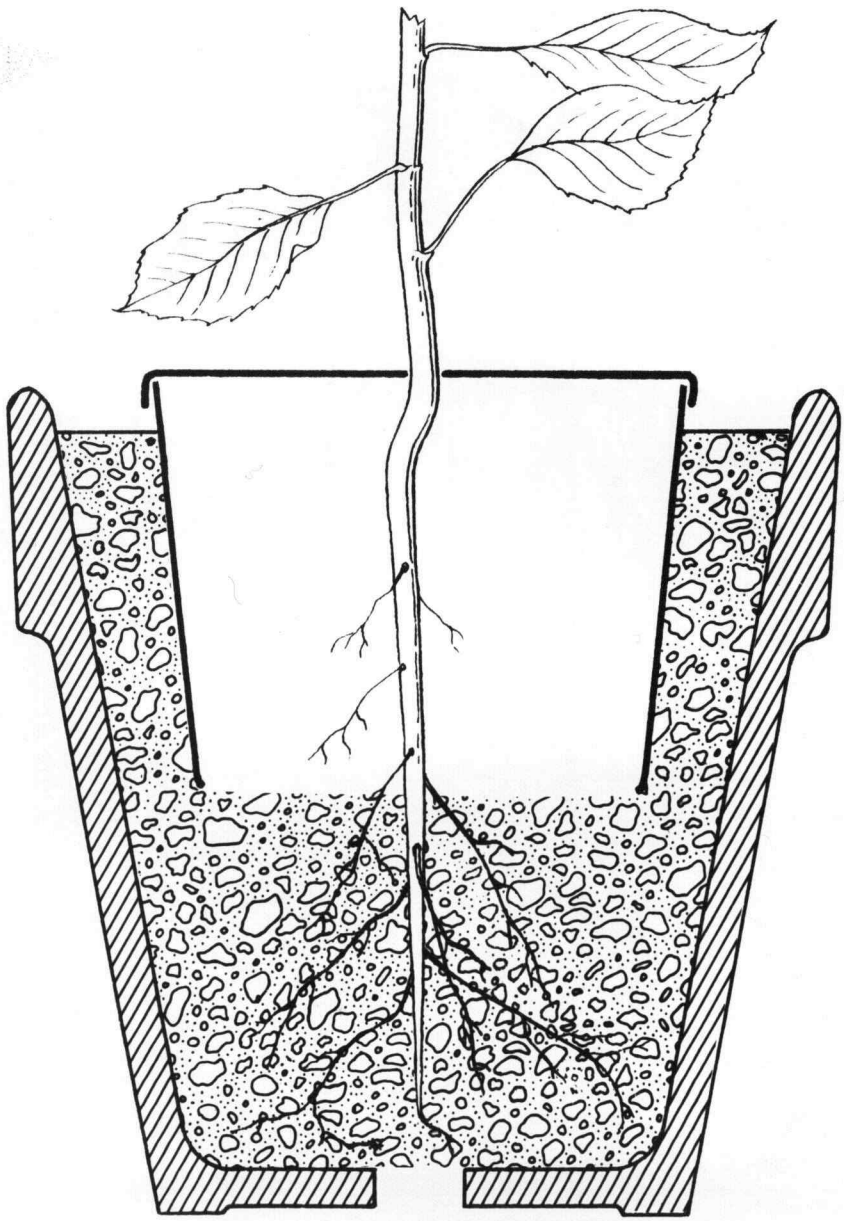


Figure 5. Apparatus for rearing Eriosoma pyricola on the roots of pear seedling.

8 A.M. and the number of sexuparae recorded (Table 1). The total number of aphids was also recorded (Table 2).

Table 1. Production of sexuparae of Eriosoma pyricola on pear root pieces at different constant temperatures. Ten apterous virginoparae were placed in each box on August 29, 1965. (Experiment 1).

Date of observation	18°C	21°C	24°C	27°C
1965				
Sept. 4,	0	0	2	0
Sept. 7,	0	1	0	0
Sept. 8,	0	1	2	0
Sept. 9,	0	0	1	0
Sept. 10,	1	1	0	0
Sept. 11,	0	0	1	0
Sept. 12,	0	0	2	0
Sept. 13,	3	1	0	0
Sept. 14,	1	0	0	0
Sept. 16,	1	1	0	0
Sept. 17,	2	0	0	0
Sept. 19,	1	0	0	0
Sept. 27,	0	2	0	0
Oct. 5,	0	1	0	0

Table 2. Growth of E. pyricola colonies at different temperatures. (Experiment 1).

Date of observation	Mean aphids per box (5 boxes)			
	18°C	21°C	24°C	27°C
1965				
Sept. 6,	25	35	32	3
Sept. 13,	62	83	56	0
Sept. 20,	115	194	126	0
Sept. 27,	148	225	168	0
Oct. 4,	197	260	180	0
Oct. 11,	204	240	207	0

None of the temperatures had any significant influence on sexupara production (Table 1). But there was an increase in aphid numbers through the 6th week at 18° and 24°C and up to the 5th week at 21°C (Table 2). The experiment was terminated at the end of the 6th week. At 27°C all the aphids died by the end of the second week indicating the lethal effect of high temperature. Similar effects of high termperature have been reported in other aphids (Kenten, 1955; Lees, 1959). Lees further stated that 25°C is near the upper limit for continuous reproduction in Megoura viciae Buckton.

It is also apparent that crowding has no effect on alate sexuparae formation in this aphid when reared on detached roots of pear plants (secondary-host). But the production of a few sexuparae (Table 1) indicated that E. pyricola is holocyclic in Oregon.

Experiment 2

As in Experiment 1, detached root pieces on moist sand in polyethylene boxes were infested with adult virginoparae (ten per box). A group of five such boxes was kept at each of 15°, 18°, and 21°C for 29 days. Once again the results showed that the temperature did not induce sexupara production in aphid cultures on detached roots.

Experiment 3

This experiment was performed to learn if the woolly pear aphid

would produce sexuparae when reared at alternating day-night temperatures.

Pieces of pear roots in polyethylene boxes on moist sand were infested with first-instar nymphs. A group of five such boxes having ten nymphs each was alternated between 15° and 24°C at 12-hour intervals, starting November 28, 1965. An equal number of such boxes were maintained at a constant 15°C and at a constant 24°C during the same time for comparison.

All the boxes were examined daily for sexuparae. No sexuparae were produced in any of the treatments in 65 days and then the experiment was terminated.

The duration of a generation from birth to reproduction under these temperatures was also recorded (Table 3).

Table 3. Duration of a generation of E. pyricola at different temperatures. (Experiment 3).

Treatment	Duration in days*
15°C	22.9 ± .07
24°C	13.3 ± .05
24°C & 15°C	16.3 ± .08

* Mean of 50 aphids.

Experiment 4

This experiment was designed to learn if brief (three hours)

exposure of aphid colonies on root pieces to high temperature (30°C) would result in sexupara formation.

Ten first-instar nymphs were placed on detached root pieces on moist sand in each of the ten polyethylene boxes used in this experiment. The treatments were: (1) constant 21°C; and (2) three hours at 30°C alternating with 21 hours at 21°C. Each treatment was replicated five times. No sexuparae were produced in any of the colonies under these treatments for a period of 32 days when the experiment was terminated.

Experiment 5

This experiment was conducted to investigate the direct effects of photoperiods on sexupara formation in the woolly pear aphid. Adult apterous virginoparae (ten per box) were placed on detached root pieces on moist sand in pint polyethylene boxes. A batch of ten such boxes was placed under 10- and 16-hour photoperiods at a constant 15°C and at a constant 18°C for 43 days. These treatments did not induce sexupara formation.

Experiment 6

In this experiment, adult apterous aphids were placed in polyethylene boxes (one per box) on detached root pieces and were exposed to 10-hour photoperiods at a constant 24°C and 16-hour photoperiods

at 24°C light and 18°C dark temperatures for 40 days. Each treatment was replicated 20 times. But the treatments did not result in sexupara production.

Summary of Experiments 1 Through 6

It may be concluded that environmental conditions studied in these experiments have no direct influence on sexuparae formation in woolly pear aphid.

C. Effect of Temperature on Generation Time in Eriosoma pyricola

Experiment 7

An experiment was conducted to study the duration of a generation, from birth to reproduction, at different temperatures. Twenty-five first-instar nymphs on detached root pieces in polyethylene boxes (one nymph per box) were kept at each of 12°, 15°, 18°, 21°, and 24°C. At 12°C, the first-instar nymphs did not establish themselves on the root pieces. To overcome this problem, nymphs on root pieces were placed at 15°C for three days and then were transferred to 12°C. The duration of a generation from birth to reproduction was recorded at each temperature (Table 4).

The results indicated that the duration of a generation decreased from 49 to 13.7 days when the temperature was raised from 12° to

24°C (Table 4 and Figure 6). However, the aphids kept at 27°C died within two weeks (Table 2).

Table 4. Duration of a generation of Eriosoma pyricola at different temperatures. (Experiment 7).

Temperature	Duration in days*
12°C	49.0 ± .36
15°C	26.4 ± .08
18°C	21.2 ± .08
21°C	16.6 ± .33
24°C	13.7 ± .05

* Mean of 20-25 nymphs.

D. Some Effects of Temperature and Photoperiod on the Growth of Pear Plants

Since direct temperature and photoperiod treatments failed to induce sexuparae formation in the woolly pear aphid, it was thought that the seasonal appearance of sexuparae may be associated with environmentally induced changes in its host-plant physiology.

There was no information on the growth of the pear plant in relation to environmental conditions. Therefore, a number of experiments were designed to determine the conditions which would induce cessation of shoot growth in pear seedlings. The experimental variables studied were different combinations of temperatures and photoperiods.

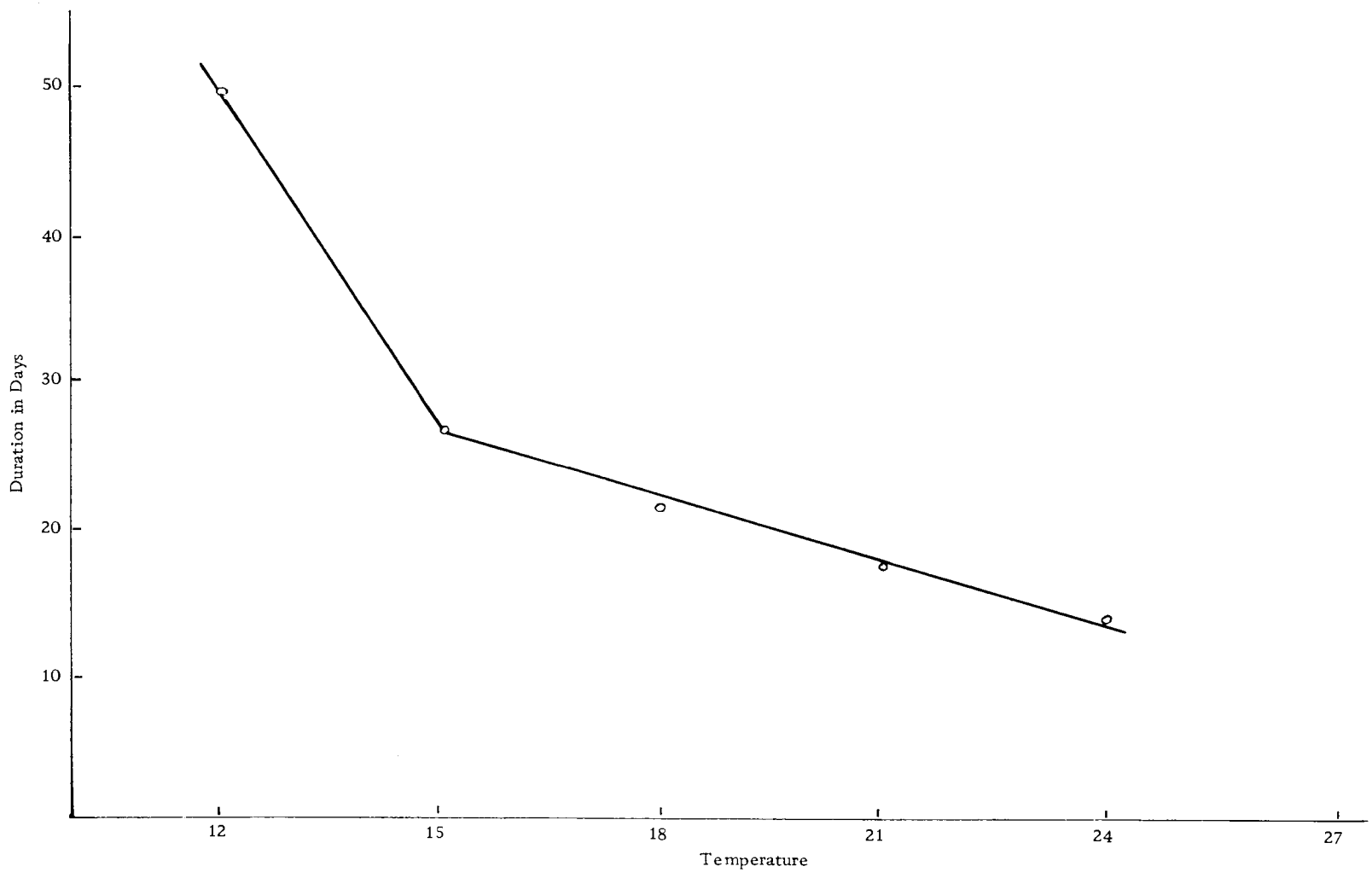


Figure 6. Duration of a generation of Eriosoma pyricola at different temperatures.

Experiment 8

The effect of long- and short-photoperiods on the growth of pear seedlings (with 2-3 nodes) was compared. Half of the plants were placed under 16-hour and the other half under 10-hour photoperiods at 24°C on March 31, 1965. Most of the plants under both the treatments ceased growth by May 21, 1965. They were moved to the greenhouse on May 25, 1965.

By June 1, 1965, all the plants stopped growing. None had resumed growth by July 21, 1965, when they were discarded. Thus the plants grew almost as long a time under 10-hour as under 16-hour photoperiods. The plants under long days attained an average of 30.8 ± 10.5 nodes as compared to 31.4 ± 1.7 nodes under short days. Apparently, at this temperature, photoperiods had no significant effect on the duration of pear growth.

Experiment 9

This experiment was essentially the same as Experiment 8 except that the seedlings exposed to short-day treatments were kept at 18°C instead of 24°C. Four groups of six seedlings (with 7-8 nodes except group four) each, were kept under 16-hour photoperiods at 24° for periods of 1, 2, 3 or 4 weeks, whereas four other groups were placed under 10-hour photoperiods at 18°C for corresponding time

intervals. The plants were placed in the greenhouse after experimental treatments. The shoot growth of each of the experimental plants was recorded at the beginning of the treatment and weekly following treatment periods. Duration of growth was also recorded. The data are presented in Table 5. Similar results were obtained when the experiment was repeated (Table 6).

Plants exposed to 16-hour photoperiods at 24°C ceased growth earlier than those placed under 10-hour photoperiods at 18°C (Tables 5 and 6), the difference being significant at the 1% level. Since the plants treated under short days at a constant 18°C grew relatively longer than those kept under long days at a constant 24°C (Tables 5 and 6), the difference must have been due to temperature. This also implies that in this pear variety short-photoperiod is not the critical factor responsible for the cessation of shoot growth.

Experiment 10

Effect of Alternating Day-Night and of Constant Temperatures on Pear Growth: It is apparent from the foregoing experiments that the plants placed under 10-hour photoperiod at 18°C grew relatively longer than those plants kept either under 10-hour or 16-hour photoperiods at 24°C. However, under field conditions pear seedlings continued to grow, if they were provided with adequate water, even when the day temperature was 24°C or higher, but the night temperature was

Table 5. Response of pear seedling to different temperatures and photoperiods. (Experiment 9).

Treatment duration	Plant no.	Treatments: 24°C and 16-hours light: Initial nodes	Nodes produced	Duration of growth in days	18°C and 10-hours light: Initial nodes	Nodes produced	Duration of growth in days
1 week	1	8	13	30	7	17	43
	2	7	16	37	7	19	43
	3	8	16	44	7	21	50
	4	7	16	44	8	22	50
	5	7	23	51	7	24	57
	6	7	29	51	7	26	57
Mean		7.3	18.8	42.8	7.2	21.5	50.0
2 weeks	1	7	13	30	7	16	30
	2	7	13	37	8	15	43
	3	7	14	30	7	14	43
	4	7	17	37	6	20	50
	5	8	18	37	7	27	57
	6	7	20	37	8	28	57
Mean		7.2	15.9	34.7	7.2	20.0	46.7
3 weeks	1	7	10	30	7	16	43
	2	8	12	30	7	16	43
	3	7	13	30	8	16	50
	4	6	16	30	7	17	50
	5	8	18	30	8	22	64
	6	7	21	37	7	23	64
Mean		7.2	15.0	32.7	7.2	18.8	52.3
4 weeks	1	12	7	24	13	4	23
	2	13	7	24	12	5	23
	3	12	9	31	12	4	30
	4	11	17	37	12	4	37
	5	12	13	37	11	11	57
	6	11	10	43	12	17	57
Mean		11.9	10.5	31.2	12.0	7.5	37.8

Table 6. Response of pear seedling to different temperatures and photoperiods. (Experiment 9).

Treatment duration	Plant no.	Treatments: 24°C and 16-hours light — Initial nodes	Nodes produced	Duration of growth in days	18°C and 10-hours light — Initial nodes	Nodes produced	Duration of growth in days
1 week	1	9	11	36	9	9	29
	2	9	11	36	9	18	50
	3	9	14	36	9	19	50
	4	9	16	43	9	23	50
	5	10	21	50	9	23	57
	6	9	22	50	9	27	64
Mean		9.2	15.8	41.8	9.0	19.8	50.0
2 weeks	1	7	8	15	7	5	22
	2	7	9	22	7	6	36
	3	7	13	29	7	16	43
	4	7	12	36	7	15	57
	5	7	19	50	7	9	57
	6	7	19	50	7	26	57
Mean		7.0	13.3	33.7	7.0	12.8	45.3
3 weeks	1	7	9	24	8	8	30
	2	9	10	24	9	14	45
	3	7	11	31	7	15	45
	4	7	13	31	8	16	52
	5	9	11	38	7	16	52
	6	9	8	38	9	22	59
Mean		8.0	10.3	31.0	8.0	15.3	47.2
4 weeks	1	8	4	16	8	5	30
	2	8	7	23	8	8	37
	3	8	8	23	8	8	37
	4	8	9	30	8	14	50
	5	8	10	30	8	14	58
	6	8	14	37	8	23	58
Mean		8.0	8.7	26.5	8.0	12.0	45.0

lower. The purpose of this experiment was to determine whether the low night temperature or the day-night differential temperature is the determining factor in the growth of pear plants.

Thirty-six pear plants with 10-14 nodes (except plants 7, 11 and 13) were divided into two groups of 18 plants each and kept under two different controlled environments for three weeks. One group of plants received 16-hour light at 24°C and 8-hour dark at 18°C while the other group was maintained under 10-hour light and 14-hour dark at a constant 18°C. The data on shoot growth and growth durations are presented in Table 7.

The shoot growth and duration of growth were longer under alternating day-night temperatures ($P < 0.01$) whereas both were significantly less under 18°C constant day-night temperatures (Table 7).

Experiment 11

Growth of Pear Plants Under Long and Short Days at Differential Day-Night Temperatures: This experiment was designed to determine if photoperiod has any significant role in pear growth under differential day-night temperatures. Thirty-six plants of 9-12 nodes (except plants 1 and 17 of 10-hour) were used for this experiment. Eighteen plants were placed under 16-hour photoperiods with an equal number under 10-hour photoperiods at 24°C light and 18°C dark temperatures for three weeks. The data on growth responses were

recorded before and weekly after the treatment till the plants stopped growing (Table 8).

At these temperatures, there is little difference between the effect of short- and long-photoperiods on pear growth. Mean duration of growth was 46 days for 16-hour plants and 42 days for the 10-hour plants. The mean number of nodes for the two groups of plants differed by less than one.

Table 7. Response of pear seedlings to alternating day-night and constant low temperatures. (Experiment 10).

	16-hours light at 24°C and 8-hours dark at 18°C			10-hours light and 14-hours dark at 18°C		
Plant no.	Initial nodes	Nodes produced	Duration of growth in days	Initial nodes	Nodes produced	Duration of growth in days
1	13	5	20	14	1	27
2	10	7	20	12	3	27
3	14	9	27	13	4	27
4	13	10	27	14	5	27
5	12	21	48	13	6	27
6	13	21	48	13	6	27
7	14	21	55	13	7	27
8	16	22	55	13	7	34
9	12	23	55	13	18	34
10	12	32	55	14	7	48
11	12	32	55	12	13	55
12	15	26	69	13	51	55
13	10	29	69	12	21	55
14	15	27	76	13	21	55
15	11	35	76	13	21	55
16	12	36	76	13	26	69
17	12	36	83	11	27	69
18	13	39	83	12	33	69
Mean	12.16	23.9	55.4	13.0	13.4	43.9

Table 8. Growth of pear plants under long- and short-photoperiods at alternating day-night temperatures. (Experiment 11).

	24°C day and 18°C night					
	16-hour light and 8-hour dark			10-hour light and 14-hour dark		
Plant no.	Initial nodes	Nodes produced	Duration of growth in days	Initial nodes	Nodes produced	Duration of growth in days
1	9	5	29	10	9	22
2	11	10	36	8	13	22
3	12	11	36	12	10	29
4	12	12	36	10	11	29
5	12	14	36	11	11	29
6	11	14	36	11	15	36
7	10	13	43	13	13	43
8	11	16	50	11	15	43
9	9	17	50	9	19	43
10	11	18	50	10	21	43
11	10	21	50	11	10	50
12	11	21	50	9	15	50
13	9	22	50	12	19	50
14	10	25	50	11	21	50
15	11	21	57	10	24	50
16	10	23	57	10	21	57
17	9	24	57	10	27	57
18	11	29	57	12	30	57
Mean	10.5	17.6	46.1	10.6	16.9	42.2

Summary of Experiments 8 Through 11

It may be concluded that high night temperatures (constant 24°C) might be responsible for the cessation of growth in pear plants. The results are similar to those obtained for loblolly pine and northern red oak for which warm nights were found to be unfavorable for continuous growth, and for which the difference between day and night temperatures appeared more important than the actual temperatures

(Kramer, 1958). It may be pointed out that these results are of limited application. But this information was enough to enable regulation of plant growth for studying effects of host plant conditions on woolly pear aphid.

E. Effect of Cessation of Plant Growth on Sexuparae Formation in E. pyricola

A series of experiments were conducted to test the hypothesis that the production of sexuparae in E. pyricola was associated with cessation of shoot growth in pear plants.

Experiment 12

This experiment was performed to determine if the aphids reared on the roots of pear seedlings would produce sexuparae when environmental conditions induced dormancy in the plant. The experiment was done in two controlled-environment chambers. Thirty-six pear plants (with 7-8 nodes) grown in the greenhouse were divided into two groups of 18 each. One group was placed under 16-hour light at 24°C and 8-hour dark at 18°C while the other group was kept under 10-hour light and 14-hour dark at a constant 24°C. After one week of treatment, one adult virginopara was placed on the roots of each plant on April 1, 1966, according to the procedure described in the beginning of this section (Figure 4). On April 15, 1966, the plants were

removed from the controlled-environment chambers and were returned to the greenhouse. The aphids recovered from the roots of experimental plants were separated into two groups i.e., (1) 1st and 2nd instars, and (2) 3rd instar and older. Then the percent sexuparae found in the second group was recorded (Table 9).

On April 22, three plants from each of the long- and short-day plants were removed and aphid colonies on their roots were examined for sexuparae. All the plants were growing on April 22,and no sexupara was found in the aphid colonies on roots of the plants examined. By May 8, 1966 all the short-day plants ceased growth and alate sexuparae were present in the aphid colonies on their roots (Table 9). But most of the plants kept under long-days at alternating temperatures during the corresponding period continued to grow and aphid colonies on their roots did not have any sexuparae. The only sexuparae on the roots of plants exposed to 16-hour photoperiods at alternating temperatures were on the plants which had stopped growing by the time they were examined. Cessation of shoot growth in some of these long-day plants two weeks following the treatment period was perhaps hastened by the high night temperatures prevailing in the greenhouse during that time.

Experiment 13

This experiment was essentially a repetition of Experiment 12

Table 9. Production of sexuparae by Eriosoma pyricola on roots of seedlings given different environmental conditions. (Experiment 12).

16-hour photoperiod: light 24°C dark 18°C			10-hour photoperiod: constant 24°C				
Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Approximate day growth ceased**	Day examined
1	9	None	1	16	None	----	29th
2	14	None	2	21	None	----	29th
3	11	None	3	No infestation		----	29th
4	32	None	4	45	5	----	36th
5	43	20*	5	47	20	----	36th
6	50	None*	6	48	50	28th	36th
7	30	None	7	112	90	28th	43rd
8	80	None	8	23	10	35th	43rd
9	26	None	9	82	90	28th	43rd
10	87	None	10	87	85	28th	45th
11	47	None	11	67	95	28th	45th
12	59	None	12	54	70	28th	45th
13	71	None*	13	66	65	42nd	45th
14	62	None*	14	60	95	35th	45th
15	63	5	15	53	40	35th	45th
16	86	5	16	63	90	35th	45th
17	53	5*	17	70	85	35th	45th
18	65	8*	18	56	95	35th	45th

* These plants stopped growing on the 35th day. All others were still growing when the aphids were examined.

**The first 5 plants had not stopped growing when the aphids were examined.

except that the plants were grown and maintained in the controlled-environment chambers instead of the greenhouse before and after the treatment periods. Germinating seeds were planted in pots kept in controlled-environment chambers operated at 16-hour photoperiods with a light temperature of 24°C and a dark temperature of 18°C. On June 18, 1966, 32 of these plants (with 6 nodes each) were selected for experimental treatments. Sixteen of these plants were then continued in this environment while the rest of the 16 plants were transferred to a chamber set at 10-hour photoperiod with a constant 24°C. One adult apterous virginopara taken from the stock culture was placed on the roots of each experimental plant on June 25. On July 9, short-day plants were transferred back to the chambers set at 16-hour photoperiods with 24°C day temperatures and 18°C night temperatures and were held there until data were recorded (Table 10).

These results agree with those of the previous experiment in which sexuparae were produced in woolly pear aphid colonies on the roots of plants treated to induce growth cessation. Sexuparae did not appear in any of the colonies on the roots of pear seedlings as long as their shoot growth continued. Since only one long-day plant ceased growth in this experiment as compared to six plants in Experiment 12, it is clearly indicated that high night temperatures in the greenhouse during the pre- and post-treatment periods did influence the growth of plants in Experiment 12.

Table 10. Production of alate sexuparae by Eriosoma pyricola on roots of pear seedlings treated under different environmental conditions. (Experiment 13).

16-hour photoperiod: light 24°C dark 18°C			10-hour photoperiod: constant 24°C				
Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Approximate day growth ceased	Day examined
1	20	None	1	37	10	29th	36th
2	23	None	2	36	5	29th	36th
3	27	None	3	33	8	29th	36th
4	21	None	4	24	15	36th	36th
5	53	None	5	86	29	22nd	45th
6	43	None	6	94	75	22nd	45th
7	40	None	7	21	85	36th	45th
8	23	None	8	111	80	22nd	47th
9	22	None	9	12	65	22nd	47th
10	29	None	10	11	10	**	47th
11	24	None	11	99	85	29th	47th
12	23	None	12	93	74	29th	47th
13*	44	35	13	4	100	29th	47th
14	24	None	14	45	70	29th	47th
15	25	None	15	12	30	22nd	47th
16	20	None	16	48	65	22nd	47th

* Only plant that stopped growth on 48th day when the experiment was terminated.

**Only plant that was still growing on 48th day when the experiment was terminated.

Experiment 14

Both Experiments 12 and 13 demonstrated that environmentally induced cessation of pear growth was accompanied by the production of alate sexuparae in aphid colonies on the roots. An experiment was designed to learn if short-day treatments given to pear plants having aphid colonies on their roots would result in sexupara production.

Plants for this experiment were grown in the greenhouse until 7-8 nodes were produced. On July 12, 1967, five groups of eight plants each were exposed to 16-hour photoperiods with similar numbers held under 10-hour photoperiod at a light temperature of 24°C and a dark temperature of 18°C. One adult apterous virginopara, taken from the stock culture, was placed on the roots of each plant about four hours prior to treatment. A group of eight plants were removed from each of the two treatments following 28, 35, 42, 49, and 56 days of treatment and the aphids on their roots were examined for sexuparae (Table 11).

These results indicate that sexuparae were produced on the roots of pear plants when exposed to environmental conditions that resulted in cessation of their shoot growth. The data also revealed that photoperiod was not the critical factor responsible for the production of sexuparae in Eriosoma pyricola (Table 11).

Table 11. Production of alate sexuparae by Eriosoma pyricola on roots of pear seedlings treated under different environmental conditions. (Experiment 14).

24°C day and 18°C night						
16-hour photoperiod			10-hour photoperiod			
Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Plant no.	No. aphids 3rd instar or older	Percent alate sexuparae	Day examined
1	4	None	1	11	None	28th
2	20	None	2	12	None	28th
3	7	None	3	29	None	28th
4	4	None	4	30	None	28th
5	3	None	5	6	None	28th
6	4	None	6	7	None	28th
7	1	None	7	42	None	28th
8	12	None	8	16	None	28th
9	No infestation		9	86	None	35th
10	9	None	10	7	None	35th
11	No infestation		11	1	None	35th
12	18	17	12	3	None	35th
13	10	None	13	No infestation		35th
14	1	None	14	67	3	35th
15	6	None	15	12	None	35th
16	1	None	16	84	12	35th
17	27	37*	17	2	None	42nd
18	11	9	18	4	None	42nd
19	No infestation		19	No infestation		42nd
20	9	33*	20	36	22*	42nd
21	2	None	21	36	14*	42nd
22	45	36*	22	6	17	42nd
23	2	50*	23	6	None	42nd
24	7	72*	24	14	29*	42nd
25	50	78*	25	40	45*	49th
26	1	None	26	3	67	49th
27	2	None	27	4	75*	49th
28	2	None	28	No infestation		49th
29	61	22*	29	4	None	49th
30	1	100	30	7	None	49th
31	No infestation		31	41	None	49th
32	6	None	32	No infestation		49th
33	13	46	33	22	None	56th
34	No infestation		34	71	80*	56th
35	No infestation		35	5	None	56th
36	3	None	36	35	None	56th
37	10	10	37	13	None	56th
38	26	73*	38	No infestation		56th
39	5	None	39	98	65*	56th
40	67	69*	40	30	30	56th

*These plants had stopped growing when the aphids were examined.

Experiment 15

Experiments described in the previous pages demonstrated that cessation of shoot growth of plants resulted in production of sexuparae in the aphid colonies on their roots, and sexuparae were not produced as long as plants continued to grow.

An experiment was conducted in an attempt to learn if the aphids reared on detached root pieces from pear seedlings treated to induce cessation of shoot growth, would produce sexuparae. The plants were treated for four weeks under 10-hour photoperiods and a constant temperature of 24°C. Then, their roots were detached and were infested with apterous virginoparae. Sexuparae were not produced in aphid colonies on these roots. Aphids cultured on detached root pieces of dormant plants from the field did not produce sexuparae either. Occasionally one or a few alate sexuparae were found in stock cultures which constituted less than one percent of the aphids in the culture.

Results of Experiment 15 suggest that the aphids had to be on the roots of growing plants for certain periods of time before they could produce sexuparae in response to environmentally induced changes in host plant conditions which resulted in the cessation of shoot growth.

Experiment 16

An attempt was made to determine how long aphids need to be on the roots of pear seedlings, treated under conditions that stop growth, to produce sexuparae. Pear seedlings were grown in the greenhouse under long-day and fluctuating day-night temperatures until 7-9 nodes were produced. Forty of these plants were exposed to 10-hour photoperiod at a constant 24°C for three weeks. Adult apterous virginoparae taken from the stock culture were then placed on the roots of each of the experimental plants (five per plant) on April 29, 1967 (22nd day of treatment). On May 2, 1967, all the adult apterous virginoparae were removed without disturbing their progeny. A group of ten plants was removed from the treatment chamber after 3, 6, 9, and 12 days of infestation, starting May 2, 1967, and the aphids recovered from the roots of each of these plants were transferred to detached root pieces kept on moist sand in polyethylene boxes. These boxes were then placed at a constant temperature of 21°C until two complete generations had elapsed. But the treatments had no effect on sexuparae formation.

Experiment 17

Field Observations on Sexuparae of Eriosoma pyricola. The production of sexuparae in woolly pear aphid was related to physiological changes in its host plant (Experiments 12, 13, 14). In the field,

sexuparae were not found in the aphid colonies on the roots of pear seedlings examined on September 19, 1966, while about 80% of the population on the roots of seedlings examined on September 27, 1966 was found to be sexuparae. No sexuparae were observed on the roots of plants examined on October 29, 1966.

This experiment was designed to determine if sexuparae production in the field was associated with cessation of plant growth. Population records were taken from pear seedlings at the Entomology Department Farm near Corvallis, starting June 15, 1967. Five plants (about two years old) were dug every week and the aphids present on their roots were carefully removed with a camel's hair brush for sexuparae examination in the laboratory. The total number of aphids as well as percent sexuparae were then recorded (Table 12). By August 11, 1967 some of the plants stopped growing. They were separated into two groups: (1) growing, and (2) non-growing, which were then marked with red and yellow labels respectively. After that date, five plants from each of the groups were dug every week and the total number of aphids as well as alate sexuparae were recorded for both the groups separately (Table 12).

These results (Table 12) further substantiate our laboratory findings that sexuparae production in Eriosoma pyricola on the roots of pear seedlings was related to cessation of shoot growth.

Table 12. Records of the aphid, Eriosoma pyricola on roots of pear seedlings at the Entomology Farm, Corvallis, in 1967. (Experiment 17).

Date of observation	Condition of plant					
	Growing			Non-growing		
	No. aphids	No. alates	Percent alate	No. aphids	No. alates	Percent alate
June 15,	65	0	0	---	--	----
June 23,	57	0	0	---	--	----
June 30,	27	0	0	---	--	----
July 7,	106	0	0	---	--	----
July 14,	91	0	0	---	--	----
July 21,	253	0	0	---	--	----
July 30,	---	--	----	614	10	1.6
Aug. 4,	---	--	----	264	22	8.3
Aug. 11,	430	19	4.4	319	32	10.0
Aug. 20,	385	6	1.6	241	49	20.3
Aug. 25,	220	9	4.1	353	72	20.4
Sept. 1,	387	9	2.3	242	44	18.9
Plants stopped growing						
Sept. 8,	387	21	5.6	248	44	17.3
Sept. 15,	166	25	15.1	239	9	3.8
Sept. 22,	199	75	37.7	195	17	8.7
Sept. 29,	149	21	14.1	---	--	----
Oct. 4, *	---	--	----	201	31	15.4
Oct. 12,	139	4	2.9	103	1	1.0

*Aphids floated out by placing the samples material in buckets full of water.

F. Host-Relationships in E. pyricola

Experiment 18

Baker and Davidson (1917) reported that in California the woolly pear aphid produced a bladder-like gall on elm and infested the roots of pear plants. Alate sexuparae, which return to elm are produced

on pear roots during late summer. In the field, alate sexuparae were recorded on the roots of pear seedlings during late summer and early fall every year (Experiment 17), but we failed to find any bladder-like gall on elm trees in and around Corvallis in spite of our extensive search. However, bladder galls (Figure 7) were frequently observed during spring on elm trees grown around Medford, Oregon.

The purpose of this trial was to ascertain if the aphids causing bladder leaf gall formation on elm in Medford would infest pear grown in the Willamette Valley. This would also indicate that in Oregon at least some population of E. pyricola utilizes elm as a primary host.

Bladder galls containing alate virginoparae were obtained from elm trees at Medford on July 22, 1966. The alate virginoparae taken from these galls were transferred to detached roots of "Domestic Bartlett" Pyrus communis L., Amelanchier florida Lindl. and Red Delicious apple. At that time the identity of the aphid taken from bladder galls was not certain. But it was later identified as E. pyricola by Dr. Hille Ris Lambers. Table 13 summarizes the response of the alate virginoparae of E. pyricola to the roots of woody plants to which it was transferred.

Of the plants tested, colonies of E. pyricola could be reared on pear roots continuously as long as the transfers were made before the root pieces decayed or became severely overcrowded (Table 13).

Figure 7. Bladder gall on elm caused by Eriosoma pyricola.

Table 13. Response of alate virginoparae of E. pyricola to roots of various plants. (Experiment 18).

Host	No. of aphids	Replication	Aphid response
	Date aphid transferred, July 22, 1966		
Domestic Bartlett Pear	20-40	3	Population increased steadily and colonies persisted as long as fresh roots were provided.
Red Delicious Apple	20-40	3	Nymphs deposited but died within 24 hours
Amelanchier florida Lindl.	20-40	3	Nymphs deposited but died within 24 hours

Apterous virginoparae from the stock cultures (started from aphids obtained from Forest Grove in July, 1965), were also transferred to Pyrus communis L., Amelanchier florida Lindl., Sorbus sitchensis, Crataegus species, Ribes sativum and Red Delicious apple roots but they did not survive except on the pear roots, indicating that perhaps pear is the only secondary host.

DISCUSSION

Alate sexuparae of the woolly pear aphid were produced in colonies on the roots of pear seedlings exposed to 10-hour photoperiods at a constant 24°C (Tables 9 and 10). These environmental conditions induced cessation of growth in most pear seedlings. However, a few sexuparae were found in the colonies on the roots of plants that continued to grow under these environmental conditions. Production of sexuparae on the roots of plants that did not stop growth under dormancy-inducing conditions indicated that physiologically growth cessation may have been initiated. On the other hand, sexuparae were not found in the aphid colonies (Tables 9 and 10) on the roots of pear plants, treated under 16-hour photoperiods at 24°C light temperature and 18°C dark temperature, which were growing vigorously at the time they were examined. But some of the plants exposed to long days and alternating temperatures stopped growth, thereby resulting in sexuparae formation in the aphid colonies on the roots. These results clearly demonstrate that environmentally-induced cessation of pear growth was accompanied by the production of alate sexuparae in aphid colonies on the roots. Conversely, no sexuparae were produced on the roots of pear plants as long as their shoots continued to grow. This phenomenon had not so far been observed in other species of aphids except Von Dehn's (1967) statement that the male formation in

Megoura viciae was regulated by the host plant conditions while oviparous female production could be induced by either short photoperiods or host plant conditions when reared in darkness. However, extensive researches by Lees (1966) did not show any effect of host plant conditions on the production of sexes in Megoura viciae.

Results of our laboratory experiments are in conformity with our field observations. Sexuparae are produced for over a month on the roots of infested plants in the field. After this, no more sexuparae appear in the remaining populations which continue as apterous virginoparae on pear roots till the autumn of the following year. For instance, no sexuparae were found on the roots of plants in the field examined on July 21, 1967 (Table 12) and all the plants were growing until that time. By July 30, some of the plants stopped growing thereby resulting in 1.6% sexuparae in the aphid colonies on the roots. Aphid colonies on the roots of non-growing plants examined on August 25, had 20.4% sexuparae. But on September 1, 18.9% of the population on the roots of non-growing plants was found to be sexuparae. By October 12, the sexuparae decreased to 1% only. Hence, unlike most of the aerial aphids, the woolly pear aphid uses environmentally induced changes in the host as a "timer."

Little is known about the nature and mode of action of this physiological mechanism (timer) except that the virginoparous aphid colonies on pear roots "switch over" to sexuparae production when shoot

growth stops. Results, however, suggested that the proportion of sexuparae in aphid colonies on the roots of pear is related to the stage of dormancy in the plant even when treated under dormancy-inducing conditions. For example, the percent sexuparae found on the roots of plants that completely stopped growth was significantly higher than those which did not stop growth under the same conditions at the time they were examined (Table 9).

Aphids reared on root pieces from pear seedlings treated to induce cessation of shoot growth did not produce sexuparae. Aphids cultured on root pieces of dormant plants from the field did not result in sexuparae either. However, sexuparae were produced by aphids provided they were on the roots of plants prior to cessation of shoot growth (Tables 9, 10 and 12). Thus, production of sexuparae in aphids on the roots of pear must have been in response to physiological changes in the plant during transition from the growing to dormant condition.

Cessation of shoot growth in pear seedlings was induced by a constant temperature of 24°C under both 10-hour and 16-hour photoperiods (Experiment 8 and 9). However, plants treated at alternating day-night temperatures grew for a much longer time regardless of the photoperiods. For instance, plants treated under 16-hour days at a light temperature of 24°C and a dark temperature of 18°C grew for an average of 55.4 days (Table 7) while plants exposed to 16-hour

photoperiods at a constant 24°C, for a similar duration, grew for an average of 32.7 days only (Table 5--three weeks treatment). However, there was little difference in the growth of plants under 16-hour and 10-hour photoperiods while both kept at alternating day-night temperatures (Table 8). Apparently, short days are not the critical factor responsible for the induction of growth cessation. But in these experiments constant temperatures appeared to be the critical factor responsible for cessation of shoot growth in this pear variety. This hypothesis tends to support Vegis' (1954, 1964) views that the temperatures are more important than short days in the regulation of growth in woody plants. Obviously, 24°C is a high night temperature, but it does not seem to be high day temperature for the growth of Pyrus communis seedlings. These results are in conformity with those obtained for loblolly pine and northern red oak for which warm nights were unfavorable for continued growth and for which difference between day and night temperatures appeared more important (Kramer, 1958). The significance of differential day-night temperatures on the growth responses of many other plants was confirmed by Went (1957).

Present studies also revealed that in all the experiments pears went into complete dormancy because once the plants ceased growth, subsequent long-day treatments at temperatures not above the optimum failed to initiate growth. Gardner (1929) reported that in Bartlett pears winter chilling is essential for the initiation of growth in

the following spring. He further stated that plants kept in the warmer greenhouse in October without previous chilling, remained practically dormant around the year even when the temperature and moisture conditions were favorable for their growth at all the times.

Apterous Eriosoma pyricola on detached root pieces developed and reproduced normally at 24°C but failed to reproduce and died within two weeks when kept at 27°C (Table 2). It appeared that the upper threshold limit for woolly pear aphid perhaps was very close to 24°C. This may be likely in view of the fact that the root feeding apterous woolly pear aphid seldom experiences such high temperatures in its natural abode where the temperature often fluctuates between 20° and 24°C during July to September, the period of its abundance. Ehrenhardt (1940) reported that Eriosoma lanigerum (Hsm.) could develop at 30°C but did not reproduce, while Fenjves (1945) found that Myzus persicae even failed to develop at this temperature. Apparently E. pyricola is slightly less heat resistant than E. lanigerum. Lees (1958) found that the upper limit for continuous reproduction in Megoura viciae was near 25°C. Injurious effects of high temperature (29-30°C) were also reported in Acyrthosiphon pisum (Kenten, 1955). Rattan Lal (1951), however, reported the normal development and reproduction in A. pisum at 30°C while working in India, indicating a wide ecological variation between two different geographical populations of the same species.

SUMMARY

A method of culturing Eriosoma pyricola on detached root pieces was developed to ensure a regular supply of aphids for experimental work. Another method was designed for studying the alate sexuparae formation in woolly pear aphid, whereby growing plants were infested so that the aphids or their progeny could be recovered later.

Sexuparae were produced in woolly pear aphid colonies on the roots of "Domestic Bartlett" seedlings treated to induce dormancy, indicating E. pyricola is holocyclic in Oregon. No sexuparae were found while shoot growth continued. Shoot growth of pear seedlings ceased when the plants were exposed to 10-hour photoperiods at a constant 24°C. Growth continued for a much longer time when plants were kept under 16-hour photoperiods at alternating day and night temperatures, 24°C and 18°C, respectively. However, aphids did not produce sexuparae when cultured on detached root pieces from plants treated for four weeks under 10-hour photoperiods at a constant 24°C. Also, sexuparae were not found in aphid colonies on root pieces of dormant plants from the field.

All these results agree with our field observations. In the field, sexuparae are produced for about two months in late summer and early fall on the roots of infested plants. After this, no more sexuparae appear in the remaining aphid populations which continue as

apterous virginoparae on pear roots until autumn of the following year.

Experiments on growth cessation in pear plants indicated that short day-length was not the critical factor responsible for the induction of growth cessation in pear seedlings. These experiments also showed that constant temperatures were more important in the regulation of growth in this pear variety.

The direct effect of photoperiods and temperatures on sexuparae production in this aphid was also investigated. Aphids on detached root pieces did not produce sexuparae when exposed to 10-hour photoperiods at alternating day and night temperatures, 24°C and 18°C, respectively. Aphid cultures on detached root pieces were kept under different combinations of 10- and 16-hour photoperiods and 15° and 18°C constant temperatures. But the treatments had no effect on sexuparae formation. No sexuparae were found in aphid colonies on root pieces kept in continuous darkness at constant temperatures of 15°, 18°, 21°, 24° and 27°C for periods of 14 to 49 days. Also, sexuparae were not produced when aphid cultures on root pieces were alternated between 15° and 24°C every 12 hours for 47 days. Sexuparae were not found in our stock cultures maintained at 21°C for about three years.

Direct effect of different temperatures on the development and increase in numbers of woolly pear aphid was also studied. Apterous E. pyricola on detached roots developed and reproduced normally at

24°C, but failed to reproduce and died within two weeks when kept at 27°C.

Apterous from stock culture and alate virginoparae from elm galls were transferred to the detached roots of "Domestic Bartlett" pear, Amelanchier florida Lindl, Sorbus sitchensis, Crataegus species, Ribes sativum and Red Delicious apple. The aphids did not survive except on the pear roots.

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