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**BIOLOGY OF THE STRAWBERRY APHIDS,
PENTATRICHOPUS FRAGAEFOLII
(COCKERELL) AND
P. THOMASI HILLE RIS LAMBERS,
IN CALIFORNIA**

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GEORGE A. SCHAEFERS² and WILLIAM W. ALLEN³

INTRODUCTION

ALTHOUGH many aphid species occur on cultivated strawberries in California, members of the genus *Pentatrichopus* are by far the most important. These aphids cause considerable injury by direct feeding as well as by honeydew production, with the resultant development of sooty-mold fungi. They are of paramount importance, however, because of their capacity to transmit several serious virus diseases of strawberries. Plakidas (1927)⁴ and Vaughan (1933) were the first to transmit the "xanthosis" and "crinkle" viruses with a member of this genus. Massee (1935) proved that the species *Pentatrichopus fragaefolii* (Cockerell) was a vector of the strawberry virus, "yellow edge." Demaree and Marcus (1951) transmitted two virus types with the species *P. minor* (Forbes) and an "unnamed species" (probably *P. thomasi* Hille Ris Lambers). Although it does not occur on strawberry, *P. tetrahodus* Walker was reported as an experimental vector of "crinkle" by Whitehead and Wood (1941). Frazier and Posnette (1958) reported that *P. jacobi* (Hille Ris Lambers) was a potential vector of several strawberry viruses.

The most important members of the genus *Pentatrichopus* in California are *P. fragaefolii* and *P. thomasi*, with the former species occurring somewhat more commonly. *P. tetrahodus* is found primarily on rose, while *P. jacobi* occurs almost exclusively on thin-leaved wild *Fragaria* species. *P. minor* and *P. minor* forma *dorsalis* are known only from eastern North America.

In many areas, viruses become a limiting factor in the profitable culture of strawberries; since control of aphid vectors is one approach to virus control, it is essential to have as thorough knowledge as possible of these vectors. It is the purpose of this study to provide information on the biology

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⁴ See "Literature Cited" for citations, referred to in the text by author and date.

and field history of the strawberry aphids known to transmit viruses. Not only is there a paucity of information on these aphids, but most of the observations made in North America are of limited value because they were made prior to Hille Ris Lambers' (1953) taxonomic revision of the genus. Since the recently separated *P. fragaefolii* appears to be the most important species in the principal strawberry-growing areas of California, greatest emphasis has been placed on it.

SYSTEMATICS

Members of the genus *Pentatrachopus* may be readily separated from other aphids occurring on strawberry in California by the presence of capitate setae on the antennae, vertex, and tergites (fig. 1). *P. fragaefolii* was first described from cultivated strawberry in Arizona in 1901. *Myzus fragariae*, described in Europe by Theobald (1912), was placed in synonymy by Hottes and Frison (1931). Hodson (1937) disputed the synonymy because of differences between North American and European specimens. This confusion was clarified somewhat when Thomas and Jacob (1941) observed the existence of a complex in North America. Hille Ris Lambers (1953) examined the forms and concluded that the types of Cockerell are identical with the European species previously referred to as *M. fragariae*. The second species of Thomas and Jacob consisted of a light and a dark form which Hille Ris Lambers described as *P. thomasi* and *P. thomasi* ssp. *jacobi* respectively. More recently, Schaefers (1960) separated these two subspecies into distinct species.

The species *P. thomasi* (fig. 1) typically possesses a full complement of four pairs of second marginal setae on the first four abdominal tergites. In *P. fragaefolii*, on the other hand, the second marginal setae tend to be absent. Although some variation does exist in both species, when sufficient numbers of individuals are observed, populations of the two species can be separated. That is, *P. thomasi* tends toward the possession of eight setae in the second marginal rows, while *P. fragaefolii* tends toward the absence of a second marginal row. A certain amount of morphological overlap does occur which presents considerable difficulty, particularly since these two species frequently occur in the same area. Although *P. thomasi* and *P. fragaefolii* cannot be designated as distinct species with absolute certainty (Schaefers, 1960), the cautious approach of separate species has been used wherever possible in this paper for protection of biological information.

P. fragaefolii and *P. thomasi*, as they occur on the cultivated strawberry, are very fragile in appearance and vary in color from white to green to pale orange and finally buff, depending on age and the conditions under which they are reared. The "dark form" of Thomas and Jacob, *P. jacobi* (Hille Ris Lambers), has not been observed on cultivated strawberry by the authors. It possesses a number of setae in the second marginal rows which is intermediate with the above two species, and when mature has markedly blackened tergites. Its occurrence on the wood strawberry, *Fragaria californica* C. & S., as well as the darkened tergites, is sufficient to distinguish it from *P. fragaefolii* and *P. thomasi*. It was on the basis of these differences that Schaefers (1960) concluded that *P. thomasi* ssp. *jacobi* merited specific designation.

HOSTS

According to Dicker (1952a), *Pentatrichopus fragaefolii* in Europe has no important natural host other than cultivated strawberry. This is generally the case in North America. However, in certain instances various wild hosts,

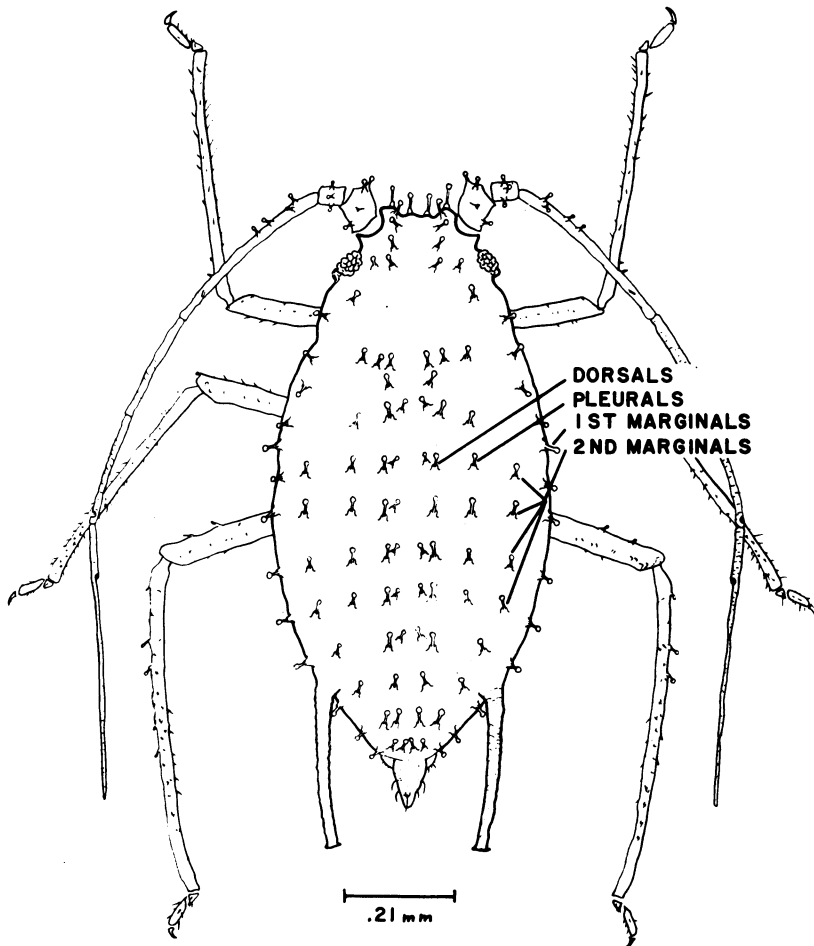


Fig. 1. The chaetotaxy of *Pentatrichopus thomasi*, showing the main character for separation from *P. fragaefolii*, i.e., the second marginal row of setae on the abdomen.

although not essential as alternate hosts, do sustain considerable populations of the *Pentatrichopus* species. A list of the hosts known to support various members of this complex is shown in table 1.

Both *P. fragaefolii* and *P. thomasi* find certain varieties of cultivated strawberry to be highly favorable hosts. Under field conditions, both of the principal varieties of strawberry grown in California, the Lassen and the Shasta, are suitable hosts, but under greenhouse conditions, the former could

not be colonized. This observation agrees with Spinks' (1929) findings, whereby strawberry varieties which are highly susceptible to mildew are often resistant to the aphid. Although *P. jacobii* breeds freely on the Shasta variety under greenhouse conditions, it has not yet been collected from field plantings.

The sand strawberry, *Fragaria chiloensis* (Linnaeus), is one of the original parents from which all cultivated strawberry varieties were derived (Darrow, 1937). This species is frequently used as an ornamental ground cover, and on

TABLE 1
HOSTS OF THE *PENTATRICHOPUS* SPECIES OF APHIDS

Host	<i>Pentatrichopus fragaefolii</i>	<i>Pentatrichopus thomasi</i>	<i>Pentatrichopus jacobii</i>
<i>Fragaria</i> species			
Commercial strawberry varieties.....	Cockerell (1901)*	+	(Induced)
<i>F. chiloensis</i> (Linnaeus).....	+	+	(Induced)
<i>F. vesca</i> Linnaeus.....	? (See text)	-†	-
<i>F. moschata</i> Duchesne.....	Thomas and Jacob (1940)	-	-
<i>F. californica</i> C. & S.....	-	-	+
<i>Potentilla</i> species			
<i>P. anserina</i> Linnaeus.....	Massee <i>et al.</i> (1938)	+	-
<i>P. sterilis</i> Garcke.....	(Induced) Massee (1935)	-	-
<i>P. douglasi</i> Greene.....	+	-	-
<i>P. comarum</i> Nestler.....	Whitehead and Wood (1946)	-	-
<i>P. gracilis rigida</i> Douglas.....	-	+	-
Rose			
Cultivated roses.....	Thomas and Jacob (1940) (Induced) Hodson (1937)	+	-

* Plus sign or citation = "host under natural conditions unless noted."

† Minus sign = "no evidence."

several occasions has been observed to be heavily infested with both *P. fragaefolii* and *P. thomasi*. Both species have also been collected on this host in its natural habitat along the coastal beaches. *P. jacobii* has not been collected on this host under natural conditions, but it is a very successful host under laboratory conditions. In contrast to most other species of wild strawberry, the beach strawberry possesses fleshy leaves and can survive in more open and drier areas.

Although plant anatomy varies somewhat with the particular habitat in which the plant is grown, the other wild strawberries are thin-leaved plants. They most frequently occur in shaded, humid areas, such as under arboreal canopies or in meadows. In Europe, the common species of wild strawberry is *Fragaria vesca* Linnaeus. On few occasions, and these apparently exceptional, has *Pentatrichopus fragaefolii* been found to infest this host under natural conditions (Massee *et al.*, 1938; Dicker, 1952a). There are numerous reports, however, that *F. vesca* may be readily infested artificially or when

the host is removed from its natural habitat (Masse, 1935; Hodson, 1937; Thomas and Jacob, 1940; Greenslade, 1941; Hille Ris Lambers, 1953). Hille Ris Lambers suggested that the conditions of relative humidity under which the plant grows are responsible for a high mortality of the aphids at the time of molting. He felt that the high humidity, in conjunction with some plant characteristic, creates unfavorable conditions for the aphid.

Repeated collections from *F. californica* C. & S., the "wood strawberry" of California, have revealed the presence of *Pentatrachopus jacobii* only. Although this species has been observed on the wild strawberry on numerous occasions, it has never been collected in large numbers. Thomas and Jacob (1941) reported the collection of a strawberry aphid different from *P. fragaefolii* on wild strawberry, but it is not clear whether they were referring to *P. thomasi* or *P. jacobii*.

Pentatrachopus species have not been observed by the authors on the various *Potentilla* species, but it is apparent from the literature and from material in the collection of the California Insect Survey that both *P. fragaefolii* and *P. thomasi* infest this host genus. In view of the large number of species, and the paucity of aphid material from it, it would appear that the genus *Potentilla* is not a very favorable host for strawberry aphids.

P. fragaefolii was induced to breed on cultivated rose by Hodson (1937) and was found on one occasion to be naturally infesting cultivated rose by Thomas and Jacob (1940). Thomas and Jacob (1941) did not distinguish between the light and dark forms of *P. thomasi* when they reported its occurrence on rose. Small populations of both *P. fragaefolii* and *P. thomasi* have been observed in California on cultivated rose during the fall and winter. It is of interest to note that *P. tetrahodus* has been frequently collected in the same colonies with the above two species on cultivated rose. *P. tetrahodus* has not been observed on strawberry, however. Miller and Darrow (1954) reported the collection of *P. fragaefolii* and a species similar to it on wild rose in Oregon and Washington. The authors on one occasion observed wild rose in Oregon to be heavily infested with *P. thomasi* during July.

LIFE HISTORY OF *PENTATRICHOPUS FRAGAEFOLII*

On cultivated strawberry, the apterous viviparae of *P. fragaefolii* reproduce parthenogenetically throughout the year in California and are more abundant during the cooler seasons. Alate viviparae may be observed during most of the year, but peak dispersal periods occur in late fall and early spring in the central coast area of California. The alates disperse to other hosts, but alternate hosts are not essential to the annual cycle of this aphid. Alates are responsible for rapid long-distance dispersal and to a lesser degree for localized movements, while the apterae are primarily responsible for localized dispersal within the field. The apterae may move down the beds through the canopies of adjacent plants and over runners. Although they have been reported to move over bare soil for at least a yard (Thomas and Jacob, 1940), such dispersal probably occurs to a limited degree. The overwintering forms are apterous viviparae, and although sexuals do occur rarely, eggs have never been observed in the main strawberry-growing areas of California.

The adult generally feeds on one of the main veins on the ventral leaf surface. Almost invariably, she is observed with her head directed toward the base of the leaf. This species is, in general, rather inactive, and if temperatures are not too high, it may take a considerable amount of irritation with a camel's-hair brush to make an individual withdraw its mouthparts. The alates become positively phototropic on maturity and move to the upper leaf surface preparatory to flight.

Nymphs, which are deposited on the newly developing leaves, remain on the same leaf until the petiole is almost fully elongated. The young aphid, upon emergence from the parent, is enclosed in an embryonic sheath. While

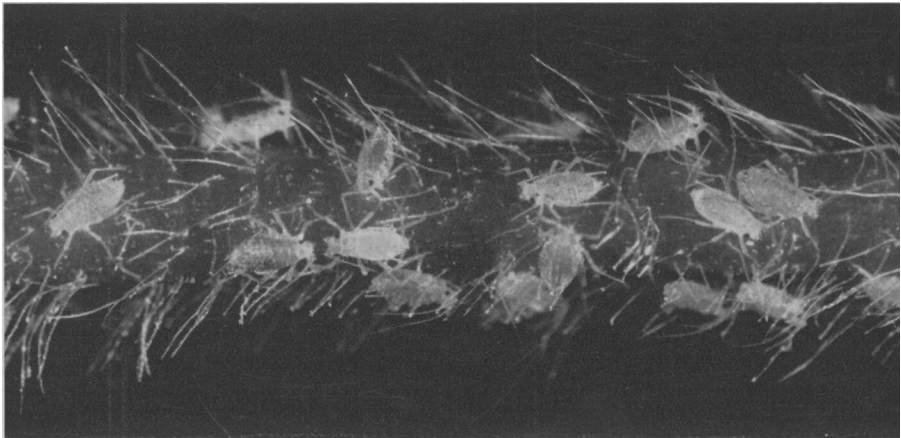


Fig. 2. The strawberry aphid, *Pentatrichopus fragaefolii*, on the petiole of cultivated strawberry.

still attached by its vertex to the genital plates of the parent, the nymph proceeds to discard the sheath by wavelike movements of its body. When the nymph is free of the embryonic sheath, the parent begins to move her abdomen vigorously up and down, and the nymph attaches itself to the leaf surface. This process, from emergence until reaching the leaf surface, lasts about fifteen minutes. The young nymphs feed anywhere on the ventral leaf surface, but the more mature nymphs and adults tend to feed on the larger veins. When populations become rather high and temperatures are not extreme, a small percentage of the individuals may move to the upper leaf surfaces and onto the older leaves.

The nymphs undergo four molts, generally on the same leaf on which they were deposited. While the aphids are maturing, the leaf is also growing; and in the last stadium or as an adult, depending on the relative growth rates of the aphid and the plant, they migrate down the petiole (fig. 2) to the next maturing leaf and repeat the cycle. If the growth rate of the plant is slow or inhibited, as during dormancy, then several generations may occur on the same leaf, and a considerable amount of honeydew and sooty-mold fungus may occur. During periods of rapid vegetative growth, relatively few young are deposited on the mature leaves. The dispersing adults and larger nymphs may frequently be seen attacking the flowering parts of the plant and also the runners.

TEMPERATURE RELATIONS

Materials and Methods

The aphids were obtained from adult apterous *Pentatrichopus fragaefolii* viviparae which were reared on Shasta variety strawberry plants in the greenhouse. These parents were transferred to a single Shasta leaf and confined within a plastic leaf cage which measured 29 mm. in diameter and 3 cm. in height. Observations were made every hour, and the nymphs deposited during that period were removed and the time was recorded. These nymphs were then transferred to smaller leaf cages on the laboratory host plants, *Fragaria chiloensis*. The cages were cut from plastic centrifuge tubes and measured 1.5 cm. in diameter and 1.5 to 2 cm. in height (fig. 3, *A*). The bottom of each cage was rimmed with pipe cleaner to prevent the edges from cutting into the leaf and blocking the flow in the leaf veins. The cage was closed with a cork in which a hole had been drilled and then covered with a fine-mesh cloth. The cage was fastened to the ventral leaf surface by means of clamps made from piano wire. The cages were then supported by six-inch lengths of seventeen-gauge steel wire with hooks formed on one end.

Three small leaf cages were attached to each plant, and four plants were placed in each constant-temperature cabinet. With one nymph per cage, twelve individuals could be reared at a time. Observations were made every twelve hours, and the molts, preoviposition time, number of young deposited, and total longevity were recorded. When any particular experiment exceeded three weeks, the aphids were transferred to new plants and returned to the cabinet.

The temperature cabinets used consisted of refrigerators of seven cubic feet, provided with six fifteen-watt fluorescent lights (fig. 3, *B*). Temperatures within the cabinets were thermostatically controlled, and the air was circulated with a small fan. Because of eddy currents in the cabinets, temperature variations were greater than desired. To reduce this variation, plastic boxes twelve inches square and fifteen inches in height were placed between the lights in each cabinet (fig. 3, *B*). This procedure reduced the temperature variation between leaf cages to $\pm 1.5^{\circ}$ F. Temperatures inside the leaf cages were measured with a recording potentiometer, and the cabinet temperatures were adjusted accordingly. Mercurial thermometers were maintained in each plastic box after the thermocouples were removed in order to give a periodic temperature check. The relative humidities in each box were not controlled, but hygrometer (Serdex HGS-HY-1) readings showed that the values ranged from 70 to 85 per cent. Leaf-surface humidities within the leaf cages were probably somewhat higher.

Developmental Rates

In these investigations, the developmental period refers to the interval between deposition and the completion of the fourth molt. Since this period consists of the major portion of the nonreproductive interval in the life history of the strawberry aphid, the time required for development critically affects the innate capacity for increase.

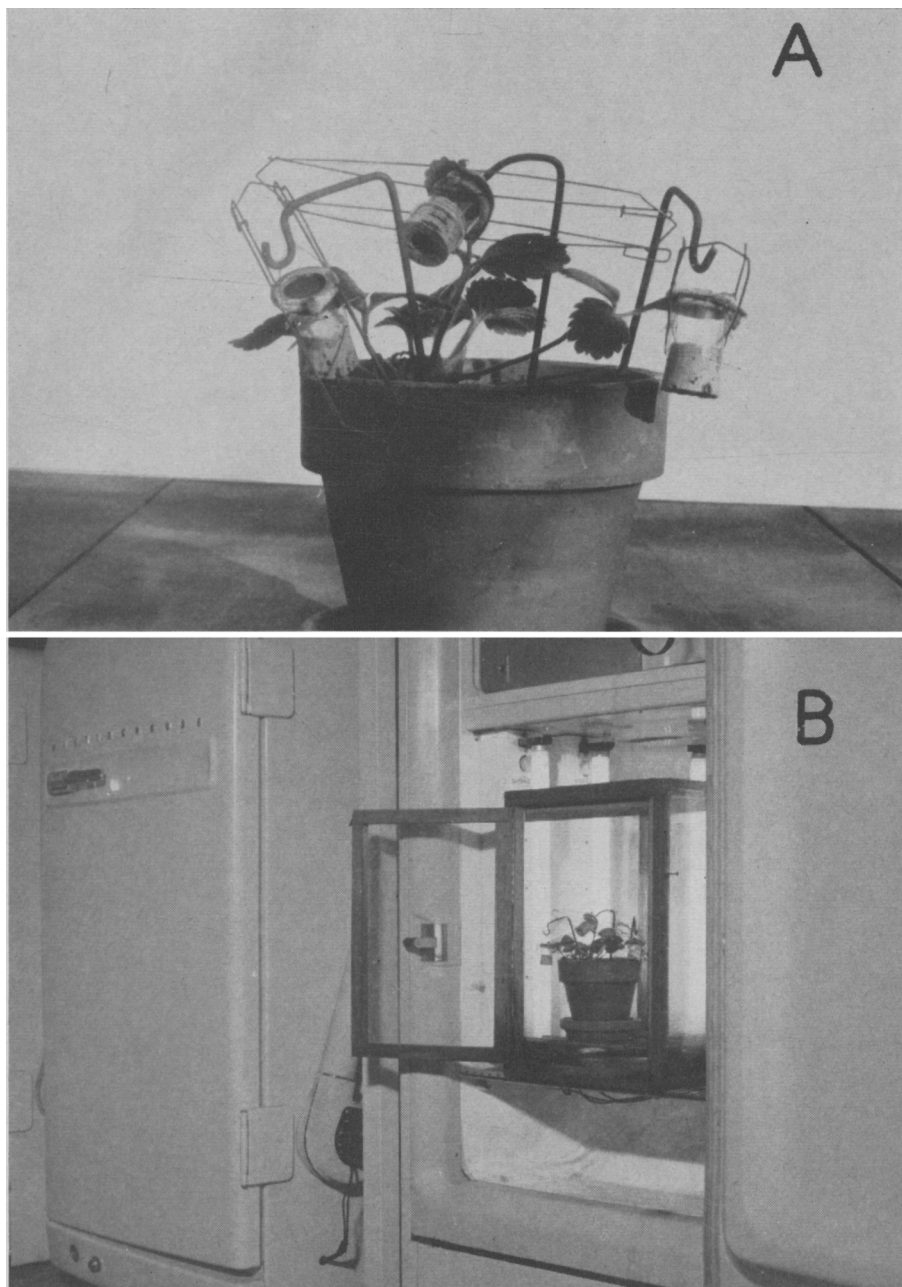


Fig. 3. Rearing methods for the strawberry aphid, *Pentatrichopus fragaefolii*. *A*: *Fragaria chiloensis* strawberry plant with plastic leaf cages attached. *B*: Temperature cabinets with lights and plastic box.

Newly deposited nymphs of *Pentatrachopus fragaefolii* were reared under nine different temperatures, ranging from 50 to 85° F. The single nymph in each cage was observed every twelve hours, the cast skins were removed with a camel's-hair brush, and the time of molting was recorded.

The times required for apterous viviparae to reach maturity when reared under various constant temperatures are shown in table 2. Since alates require a somewhat longer time to reach maturity than do the apterae, they were not included in the calculations for total developmental time. The total devel-

TABLE 2
PREMATURE MORTALITY AND TOTAL TIME OF DEVELOPMENT FOR
PENTATRICHOPUS FRAGAEFOLII AT VARIOUS CONSTANT
TEMPERATURES

Temperature (degrees F.)	Mortality in each stadium*				Number completing develop- ment	Developmental period (days)		
	First	Second	Third	Fourth		Mean ± Standard deviation	± Standard error _{0.05}	Range
85.....	0	0	10	13	1	12.0	—
82.....	1	1	1	2	16	8.4 ± 1.1	.6	6.6-10.6
80.....	7	0	1	0	12	7.3 ± .7	.5	6.5- 8.7
75.....	0	0	0	0	24	7.4 ± .7	.3	6.4- 8.7
70.....	0	0	0	0	19	7.9 ± .7	.3	7.0- 8.8
68.....	1	0	0	0	19	9.1 ± .8	.4	7.8-11.3
67.....	1	0	0	0	11	11.0 ± 1.2	.8	10.1-12.1
60.....	0	0	0	0	22	15.0 ± 1.8	.8	13.3-19.1
50.....	0	0	0	0	22	29.2 ± 2.5	1.1	24.6-33.2

* Exclusive of those killed and lost.

opmental times for each temperature are transposed to a time-temperature curve in figure 4. The developmental curve was calculated by means of the catenary formula devised by Janisch (1932). The formula for this curve is

$$t = \frac{m}{2} \left(a^T + \frac{1}{a^T} \right),$$

where t = time, m = developmental time required at the empirically determined optimum, a = empirically established constant which determines the slope of the curve, and T = the temperature in degrees Fahrenheit above or below the optimum. From the experimental data, m was estimated to be 7.1 days at 76.5° F. and $\log a$ provided the best fit at .035.

The maximum rate of development for *P. fragaefolii* occurs between 75 and 80° F. Within this temperature range, about 7.5 days are required to complete development. The most rapid development was exhibited by an individual reared at 75° F. which completed development in 6.4 days. Above 80°, the rate of development decreases. At 85°, which approaches the upper limit for development under constant temperatures, one out of twenty-four aphids reached maturity. The time required for this individual to complete development was twelve days. All the premature mortality at 85° occurred during the third and fourth stadia (table 2). At 82°, premature mortality was observed to occur in all stadia. Since mortality at 85° occurred in the

later stadia, the higher mortality observed in the first stadium at 80° appears inconsistent. This mortality would rather seem to be attributable to transfer injury or to some deposit on the leaf surface. Below 80°, unaccountable mortality was nearly absent. The rate of development below 70° decreased rapidly, and at 50°, the lowest temperature investigated, the mean time of development was 29.2 days, with a maximum time of 33.2 days.

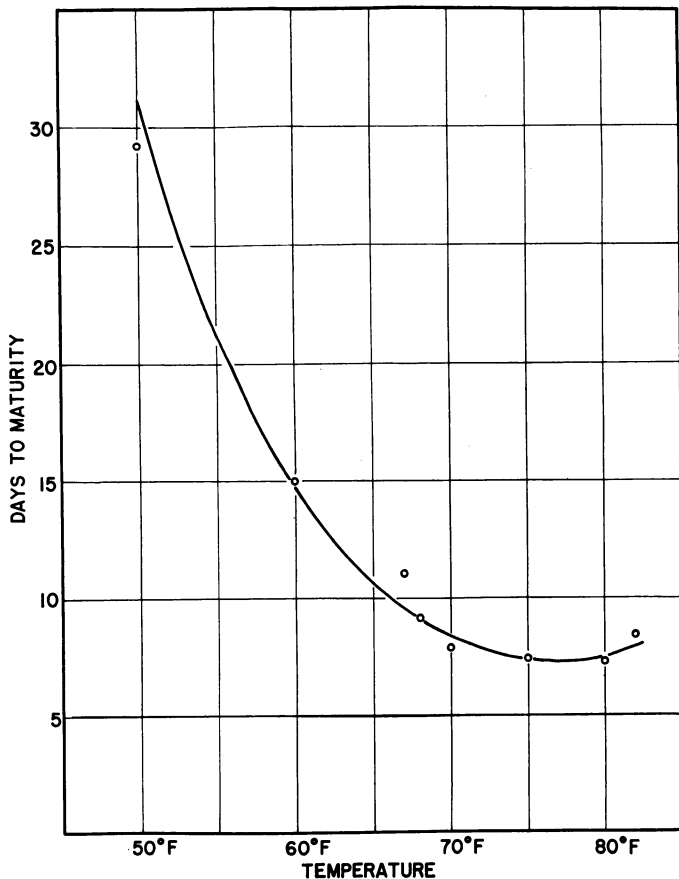


Fig. 4. Developmental rate of the strawberry aphid, *Pentatrichopus fragaefolii*, when reared under constant temperatures. Developmental curve has been calculated by means of the catenary formula devised by Janisch (1932).

The length of each stadium when *Pentatrichopus fragaefolii* was reared under various constant temperatures is shown in table 3. Under each stadium are listed the numbers of aphids included in the calculation and the mean time of development in days. At the optimum temperature for total development, i.e., 70 to 80° F., each of the first three stadia is about a day and a half, and the fourth is about a day longer. In general, the second and third stadia are shorter than the first and fourth. Each of the succeeding instars appears to have a lower optimum temperature for development. This observa-

tion may account for the mortality observed in the third and fourth stadia at 85° F., while none occurred in the first and second.

Hodson (1937) observed that *P. fragaefolii*, when reared on potted plants at a room temperature of 45 to 65° F., required from thirteen to twenty-five days for apterae to reach maturity, but that the alates took a few days longer. During the present investigations, four aphids formed wings when reared at 70° F. For these, the total time of development was 9.3 days, with a standard error $t_{.05}$ equal to ± 0.7 days. A single alate developed at 60° F. which required 17.3 days to reach maturity.

TABLE 3
DEVELOPMENTAL TIME IN EACH STADIUM OF *PENTATRICHOPUS*
FRAGAEFOLII AT VARIOUS CONSTANT TEMPERATURES

Temperature (degrees F.)	First stadium		Second stadium		Third stadium		Fourth stadium	
	Number aphids	Mean days	Number aphids	Mean days	Number aphids	Mean days	Number aphids	Mean days
85.....	24	1.9	23	1.9	14	4.0	1	5.0
82.....	20	1.7	19	1.6	18	2.0	16	3.1
80.....	15	1.6*	14	1.6	13	1.8	11	2.4
75.....	24	1.8	24	1.5*	23	1.7	22	2.4
70.....	19	1.8	19	1.9	18	1.8*	17	2.4
68.....	21	2.5	20	2.2	20	1.7	18	2.3*
67.....	10	3.3	10	2.6	10	2.2	10	3.1
60.....	22	3.8	22	3.4	23	3.5	22	4.5
50.....	23	7.6	23	6.5	23	6.7	22	8.3

* Approximate optimum temperature for each instar.

The delay in development of the alates was not evenly distributed over the entire developmental period. At 70° F., the first stadium for the alates was 1.6 days and the second was 1.8 days. These times are not too different from the 1.8 days and 1.9 days required by the apterae. The third and fourth stadia for the alates, however, were 2.3 days and 3.6 days, while the apterae required only 1.8 days and 2.4 days. Similar results were obtained for the alates observed in the 60° F. replication. There were no differences from the apterae in the first and second instars, but the third and fourth stadia were 4 and 6.5 days, respectively, while the apterae required only 3.5 days and 4.5 days for each of the later instars. These observations indicate that development of the alates is retarded primarily in the third and fourth instars. Wing buds become apparent in the later instars, and it appears that this phenomenon occurs at the expense of other physiological processes, thus resulting in a decreased rate of development.

The studies just discussed were conducted under constant-temperature conditions. The results obtained under these conditions may be expected to differ from those occurring in the field, where there is a diurnal temperature cycle. A single experiment run under variable temperature conditions in the greenhouse, however, indicated that the differences between developmental times expressed under constant and variable temperatures are slight. During the course of the experiment in the greenhouse, the mean daily temperature was 78.8° F., with a mean maximum of 88.5° and a mean minimum

of 68.8°. Five aphids reared on *Fragaria chiloensis* required 8.5 days to reach maturity, or about one day longer than when reared under constant temperatures of 80°. The fact that the mean maximum greenhouse temperature was above the optimum for development would account for the increase in developmental time.

Longevity

These investigations were undertaken to determine the effects of temperature on the longevity of *Pentatrachopus fragaefolii*. It was of interest to ascertain the lethal effects of maximum temperatures on adult aphids as well as the ecological longevity at temperatures below those producing spontaneous lethal effects.

In determining the lethal temperatures, four cabinets without lights were adjusted to temperatures of 85, 90, 95, and 100° F. Two *Fragaria chiloensis* plants were placed in each temperature box after five plastic leaf cages were attached to each plant. Temperature ranges, measured with thermocouples, were as follows: 85 ± 1.5° F., 90 ± 2.5° F., 95 ± 1.5° F., and 100 ± 2° F. Pot saucers were placed under each plant in order to prevent wilting and also to maintain relatively high humidities in the cabinets. By means of a Serdex hygrometer, the relative humidities in the temperature boxes were found to range from 60 to 80 per cent. Again, humidities within the leaf cages were probably somewhat higher.

Adult aphids were collected on *F. chiloensis* from colonies in the greenhouse. The selection was made under a dissecting microscope to assure that the aphids were mature. The aphids were placed in a Petri dish and then transferred serially into forty vials. The serial accumulation of ten aphids per vial prevented any bias in selection of the aphids. The contents of each vial were then transferred to the individual leaf cages in the temperature cabinets.

Observations were made at four-hour intervals until 100 per cent mortality occurred in the 100° F. box. Mortality in the 95° box was at a slower rate, and observations were decreased to eight-hour intervals on the remaining boxes. After all the aphids in the 95° box died, the continuing observations on the 90 and 85° boxes were made at twelve-hour intervals.

An aphid was considered dead when no movement was observed under the dissecting microscope after one minute at room temperature. The number of dead aphids was recorded during each observation period, and the cumulative totals for each of the two plants in the four temperature cabinets were tabulated.

The cumulative mortality for the one hundred aphids observed at each temperature was calculated in percentages and plotted (fig. 5) on a probit scale (ordinate). The time required for the progressive mortality was plotted in hours on an arithmetic scale (abscissa).

As may be noted in figure 5, the longevity at 100° F. is very short. According to the results observed, 50 per cent mortality may be expected within four hours at this temperature if the relative humidity is close to 90 per cent. At constant temperatures of 95, 90, and 85° F., exposures of approximately 30 hours, 82 hours, and 215 hours respectively are required to bring

about 50 per cent mortality. Field temperatures in the area studied never persist for durations such as these, and it is unlikely that much mortality can be attributed directly to these temperatures. During the periods of observation, however, the aphids were frequently observed wandering over the side of the leaf cage at temperatures of 90 and 95° F. Although direct lethal effects at these temperatures are not severe, secondary mortality may occur as a result of restlessness. When temperatures are unfavorable, the adult aphids probably often leave the plants and are then exposed to other mortality factors.

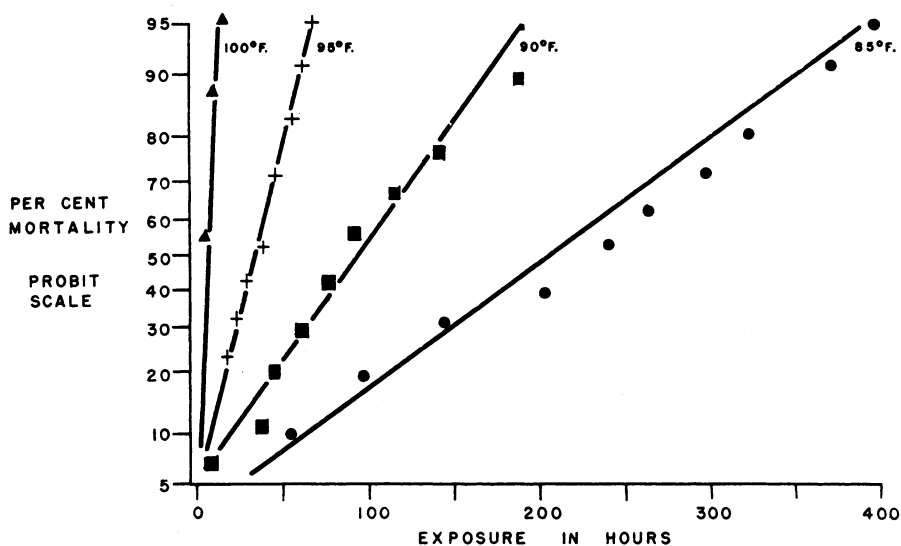


Fig. 5. Cumulative mortality of *Pentatrichopus fragaefolii* when exposed to various constant temperatures.

Information on aphid longevity at temperatures below those producing spontaneous lethal effects was obtained by a continuation of the developmental studies. After the aphids reached maturity, they were observed once each day for mortality.

In the section on developmental rates, it was shown that considerable nymphal mortality occurred at 85° F.; this amounted to about 96 per cent of the total nymphs observed. At 82°, 21 per cent of the twenty-four nymphs observed died. At temperatures below this, no significant mortality could be attributed to temperature. In table 4 are listed only those aphids which reached maturity. The single aphid which reached maturity at 85° lived for two days as an adult. Adult longevity for the viviparae increased as the temperature decreased, and at 50°, the lowest temperature investigated, the longevity was fifty-two days. The maximum longevity observed at this temperature was ninety-one days.

In addition to the observations made under constant temperatures, five aphids were reared on *Fragaria chiloensis* and six on Shasta variety strawberry under variable temperatures in the greenhouse. The temperatures re-

corded during this time ranged from a mean minimum of 68.8° F. to a mean maximum of 88.5°, with a mean of 78.8°. On *F. chiloensis*, the mean adult longevity was thirty-nine days, with a range of thirty-one to forty-five days. On the Shasta variety, the mean adult longevity was twenty-one days, with a range of eleven to forty-four days.

Dicker (1952a), in England, also investigated the longevity of *Pentatrachopus fragaefolii* under naturally fluctuating temperature conditions. During June, when daily mean temperatures were approximately 70° F., the longevity of the aphid was about thirteen days. This figure is somewhat lower than would be expected from the results discussed above. Interpolating from Dicker's temperature data, it appears that at mean daily tempera-

TABLE 4
LONGEVITY OF *PENTATRICHOPUS FRAGAEFOLII* ADULTS
WHEN HELD AT VARIOUS CONSTANT TEMPERATURES

Temperature (degrees F.)	Number of aphids	Longevity (days)	
		Mean	Range
85.....	1	2.0
82.....	16	8.1	2-19
80.....	8	12.8	9-18
75.....	11	21.3	10-29
68.....	10	31.4	17-42
60.....	12	37.4	7-71
50.....	11	52.0	2-91

tures of 40° F., the total longevity of the strawberry aphid may be as long as four months.

Hodson (1937) made observations on the longevity of aphids which were reared under room temperatures which varied from 45 to 65° F. He found that development required thirteen to twenty-five days, and that longevity of the adult was fifteen to twenty-five days. He observed the apterous males to have an adult longevity of eight to ten days, and oviparae to live for thirteen to eighteen days. Observations made by the authors on field-collected apterous males indicate that their adult life exceeds twenty days at a mean outdoor temperature of 50° F. A single oviparous female reared at a temperature of 60° lived as an adult for fifty-two days.

Fecundity

The results of the investigations on fecundity (table 5) were obtained in conjunction with the longevity studies which have been discussed above. Daily observations were made, and the nymphs deposited were removed from the cages. All the aphids reared to maturity at 85 and 80° F. failed to deposit young, and two of the sixteen aphids reared at 82° deposited one nymph each. At temperatures from 75° through 50°, all aphids deposited young readily. At 82°, the predeposition period was 4.5 days. The predeposition period decreased to a minimum of 1.7 days at 68°. Below this temperature, the predeposition period once again increased until 5 days were required at 50°. Since the deposition period is correlated with longevity, the increas-

ing deposition period with decreasing temperatures is to be expected. The mean number of nymphs deposited by each aphid throughout the deposition period was maximum at 68°, when each aphid deposited approximately fifty-six nymphs. The daily deposition rates also increased to 68°, when the rate was 2.1 nymphs per day. Further low-temperature studies indicated that the daily rate was 1.1 nymphs per day at 60°, and at 50° was less than 1 per day.

In addition to the constant-temperature studies, five aphids were reared on *Fragaria chiloensis* in the greenhouse under variable temperature conditions (mean: 78.8° F.). Of these aphids, five out of five deposited nymphs; they had a mean predeposition period of 2.6 days and a deposition period

TABLE 5
FECUNDITY RATES OF *PENTATRICHOPUS FRAGAEFOLII* WHEN REARED
AND HELD AT VARIOUS CONSTANT TEMPERATURES

Temperature (degrees F.)	Number of females	Number depositing young	Predeposition period (days)	Deposition period (days)	Mean nymphs per aphid	Mean nymphs per aphid per day
85.....	1	0
82.....	16	2	4.5	1.0	1.0	1.0
80.....	8	0
75.....	12	12	2.5	15.3	20.1	1.3
68.....	10	10	1.7	26.5	56.1	2.1
60.....	11	10	3.1	30.2	34.5	1.1
50.....	11	10	5.0	38.2	25.8	0.7

of 38 days. The mean deposition rate per day was 1 nymph, and the mean number of nymphs deposited by each adult was 39.2. It appears that although deposition is curtailed at 80° F. under constant-temperature conditions, such is not the case under variable temperatures.

Dicker's (1952a) observations on the fecundity rates of *Pentatrachopus fragaefolii* when reared under variable temperatures revealed that a rate of 2.1 nymphs per day occurred during June in England when the mean daily temperature was approximately 70° F. He further observed that the greatest total deposition occurred during this period. These results concur with those observed under constant-temperature conditions, although a greater total deposition of nymphs was noted in the laboratory. During the winter in England, when mean temperatures were about 40° F., Dicker observed the aphids to have a fecundity rate of about 0.4 nymphs per day. He reported that the interval between the final molt and the appearance of the first nymphs decreased from February (mean: 35–40° F.) to June (mean: 65–70° F.), and that in addition to a higher rate of reproduction in the summer, there was an indication that more nymphs were produced by each female.

Investigations were conducted to determine the effect that intermittent periods of high temperature have on fecundity. Adult aphids for this test were selected from the greenhouse colony. Ten aphids were placed in each leaf cage on a Shasta variety strawberry plant. Two plants with a combined total of four cages comprised a group. Five such groups were placed in a temperature box at 65° F. for eighteen hours, and were observed for relative

uniformity of deposition in the several cages. The different groups were then exposed to temperatures of 65, 80, 85, 90, and 95° F. for a period of six hours to simulate daily maximum temperatures as they might occur in the field. Following this exposure, the nymphs deposited were counted, and the deposition rates were calculated on the basis of number of young per female per hour. After removing the nymphs, the groups were again exposed to a temperature of 65° for eighteen hours, and the deposition rates were calculated as above. This procedure of exposing to high and low temperatures was repeated a second time, and the results were combined into a common mean (table 6).

TABLE 6
FECUNDITY RATES OF *PENTATRICHOPUS FRAGAEFOLII*
WHEN EXPOSED TO HIGH AND LOW (65° F.)
TEMPERATURES FOR SIX AND EIGHTEEN HOURS
RESPECTIVELY

Maximum temperature (degrees F.)	Mean deposition rate*	Mean rate at maximum temperature	Mean rate at low temper- ature (65° F.)
95.....	.058	.007	.074
90.....	.057	.048	.061
85.....	.048	.066	.042
80.....	.052	.044	.055
65.....	.048	.035	.055

* Calculated on the basis of number of young per female per hour.

The results indicate that deposition is not seriously affected until the aphids are exposed to a temperature of 95° F. At this temperature, the hourly deposition rate was .007 nymphs. This rate is substantially lower than those observed at other temperatures. When the aphids were returned to temperatures of 65° following the high-temperature exposure, however, there was an increase in the deposition rate for the 95° group over the groups exposed to lower maximum temperatures. The inhibition during the short exposure to 95° was apparently only temporary in effect, and the over-all deposition for the forty-eight-hour period was not different from those observed at the more favorable temperatures. It seems that prenatal development proceeds at a fairly rapid rate at the higher temperatures, but that deposition of the young is inhibited until lower temperatures are experienced.

Dicker (1952a) presented information on the lower temperatures at which deposition ceases. He observed that development of the nymph within the aphid continued when temperatures approached the freezing point, but that a rise to over 40° F. was necessary for the deposition of nymphs. Observations made during the present investigations indicate that deposition is still largely inhibited at temperatures up to 44°.

SEASONAL HISTORY OF *PENTATRICHOPUS* *FRAGAEFOLII* AND *P. THOMASI*

The seasonal history of the strawberry aphid, *Pentatrichopus fragaefolii*, has been studied by several workers, with an excellent comprehensive study

conducted by Dicker (1952a). Because the investigations by these workers were carried out almost exclusively in Europe, where both climate and strawberry varieties differ from those in California, a detailed study on the seasonal history of the strawberry aphids in California was needed for a better understanding of the spread of strawberry viruses.

An immediate difficulty encountered in the study of the *Pentatrachopus* species in the central coast regions of California was the sympatric occurrence of *P. fragaefolii* and *P. thomasi*. Because no reliable macroscopic method could be found to distinguish between these species (Schaefers, 1960),

TABLE 7
RELATIVE ABUNDANCE OF *PENTATRICHOPUS FRAGAEFOLII* AND *P. THOMASI* ON CULTIVATED STRAWBERRY AT SANTA CLARA, CALIFORNIA, 1955-1957

Sample date	Sample size	<i>Pentatrachopus fragaefolii</i> (per cent)	<i>Pentatrachopus thomasi</i> (per cent)
March 20, 1955.....	52	56	44
March 9, 1956.....	57	81	19
April 13, 1956.....	48	69	31
July 3, 1956.....	16	81	19
August 16, 1956.....	31	55	45
September 9, 1956.....	36	53	47
October 9, 1956.....	52	48	52
November 12, 1956.....	34	38	62
December 4, 1956.....	53	47	53
June 1, 1957.....	66	68	32
June 14, 1957.....	37	73	27
July 22, 1957.....	33	64	36
November 19, 1957.....	62	42	58

there was no alternative but to treat them as a population unit. The species composition of various samples observed throughout the three-year period is shown in table 7. It was concluded that the combined samples observed over the three-year period consisted of approximately 60 per cent *P. fragaefolii* and 40 per cent *P. thomasi*. Although the differences were not striking, there was some indication that the ratio favored *P. thomasi* during the fall months. Just what factors were responsible for this slight change in ratio are not known, and until further biological differences in these species are revealed, the seasonal history considered here must be viewed as an expression of population trends of a strawberry aphid complex.

Materials and Methods

The three plots selected for the seasonal history study were located at the University of California Deciduous Fruit Station near Santa Clara. These noncommercial plots were selected because only in such fields could the use of insecticides be restricted. The Santa Clara Valley is characterized by long, dry summers, with daily maximum temperatures occasionally exceeding 95° F. Heavy rains occur during the winter and early spring, with minimum temperatures rarely reaching 30°.

The station is located in one of the principal strawberry-growing areas of California. The climate differs slightly from the more coastal strawberry-growing areas. Along the coast, lower summer temperatures result from the ameliorating offshore breezes, and higher humidities are produced by frequent morning fogs. The seasonal trends in strawberry aphid densities appear quite similar in both areas, except that slightly higher densities persist through the summer in the coastal area.

The two principal varieties of strawberries grown in California were sampled. The Lassen variety is a vigorous plant which has a longevity of several years and is very susceptible to *Verticillium* wilt. It is also susceptible to mildew. It is a long-stemmed plant with smooth, up-cupped leaves and has a medium-dense crown. The Shasta variety has a somewhat shorter longevity than the Lassen, is less vigorous, and is less susceptible to *Verticillium* wilt and to mildew. It is a smaller plant than Lassen and has wrinkled, down-cupping leaves.

Plot A was planted in May, 1956, and consisted of approximately one-twentieth of an acre of the Lassen variety. Sampling commenced in the late summer of 1956 and continued through the late fall of 1957, when the planting was removed. This plot, which was being used for *Verticillium* wilt control studies, was somewhat more protected from the wilt than was plot C, because of preplanting treatments.

Plot B covered about one-tenth of an acre and was planted in May, 1957, with the Shasta variety. Although it would have been desirable to follow population trends on both strawberry varieties simultaneously, such a procedure was impossible because suitable plots were not available. Sampling commenced in plot B in the middle of the summer of 1957 and continued through early August, 1958. This plot was also somewhat protected from *Verticillium* wilt by preplanting treatments.

The studies on plot C consisted of second-year samples only. This plot comprised approximately one-twentieth of an acre of the Lassen variety. Sampling commenced in March, 1955, and continued through October of the same year. This plot was generally in a much poorer condition than plots A and B, due to *Verticillium* wilt and several insect and mite infestations.

In general, the sampling procedures used in each plot were identical. The use of the young, unfolding leaves seemed to provide the most descriptive measurement of the population trends and was selected for the sampling unit. This leaf age was also used by Greenslade and Pearce (1940), Thomas and Jacob (1940), and Dicker (1952a); consequently, a basis of comparison was provided by this sampling method. The leaves in this stage of growth represent a sheltered habitat which is cooler (about 1.5° F. in midday sunlight) and more humid than that provided by the leaves comprising the upper canopy. In order to detect whether any real differences in aphid densities on leaves of different ages occurred throughout the year, fifty leaves from the upper canopy were also sampled in plot A. These leaves represented the growth stage between the opened leaves with fully elongated petioles and those older leaves which had become prostrate. Since the aphids were

frequently found in considerable numbers on the petioles, the mature leaf sample was further standardized by restricting the petiole length to one inch.

In sampling leaves of both ages, fifty units were taken in such a manner as to cover the entire plot and to include any gradient which might exist as a result of gradual infestation from adjoining plots. In plot B, the sample size was increased to one hundred leaves during March, and beginning on August 2, in plot C, because of continued low aphid densities.

The leaves were collected in pint-sized paper cartons and returned to the laboratory for counting. The aphids were removed from the leaves by means of the "aphid-shaker" described by Gray and Schuh (1941). The young leaves were run through the shaker in sets of fifty. Because of the bulk of the older leaves, they were separated into sets of fifteen, fifteen, and twenty. Methyl isobutyl ketone was added to the canisters, and they were allowed to sit for ten minutes. They were then shaken vigorously but uniformly seventy-five times, and the aphids were removed from the bottom of the funnel. The aphids were transferred to a Petri dish subdivided with grid lines and with the aid of a dissecting microscope were counted under several classifications. These consisted of adults, both apterous and alate, apterous nymphs, third- and fourth-instar nymphs with prominent wing pads, and sexual forms.

The use of alatoid nymphs as indices of the true alate populations was necessary, since, as was pointed out by Dicker (1952*a*), the alates depart rapidly from the plants after reaching maturity. Additional error would have been introduced by adult counts because conditions suitable for flight varied greatly. Dicker pointed out that this method of sampling alates anticipates their actual production by a few days, but this does not introduce any appreciable error.

After the leaves had been collected on each sampling date, approximately one hour was spent searching through the planting. Observations were made on the occurrence of natural enemies, sexual forms of the aphid, and growth characteristics of the strawberry plants.

Temperature and rainfall data were obtained from standard weather station equipment located on the station grounds.

Population Trends

A comparison of the population trends on young, unfolding leaves and on mature leaves in plot A is illustrated in figure 6. The aphid densities on mature leaves were consistently lower than on young leaves throughout the entire year. This selection of the younger leaves might have been caused by the nutritional qualities of the leaves or by the creation of a more suitable microclimate. However, since it was found in a laboratory experiment that young leaves were selected much more frequently at both high and low humidities, the selection, at least in part, must have been caused by nutritional qualities of the leaves. This does not preclude that at certain times of the year, unfavorable temperatures and humidities may stimulate a more rapid migration from the old leaves to the young ones.

During the period from September through November (fig. 6) in both of the years observed (1956-1957), the population on the younger leaves in-

creased, while that on the older leaves continued at a low level. At this time of year, the young leaves are in adequate supply, and the older leaves are still upright with long petioles. In December and January, the differences in density on leaves of the two age groups became less pronounced. During this period, the plants are dormant, and there is negligible leaf growth. At this time, the mature leaves have shortened petioles, and the older leaves have become prostrate.

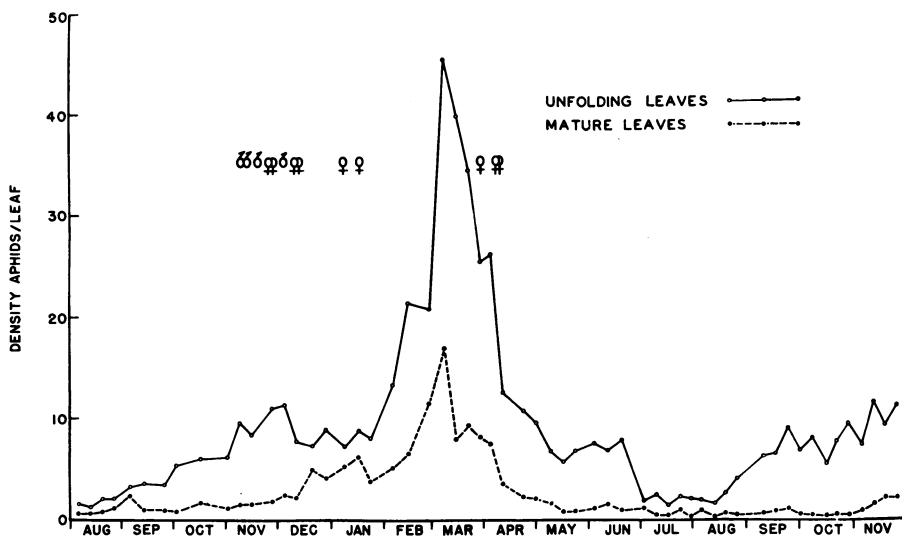


Fig. 6. A comparison of the seasonal population trends of *Pentatrichopus* species on young and mature strawberry leaves in plot A, with symbols (♀ = oviparous females and ♂ = apterous males) illustrating the collection dates of sexual forms. (1956-1957.)

The higher aphid density on the young leaves during the fall apparently reflects a nutritional preference, but the downward migration from the older leaves may be stimulated by a somewhat unfavorable microclimate. The relative increase in aphid density on the older leaves during the winter is undoubtedly due to the lack of young leaves, thus forcing the population to remain on the same leaf past maturity. At the same time, the leaves are all occupying the same strata, and the differences in microclimate are less.

Although the aphid density on the mature leaves increased during the period from February until April, the differential in aphid density on young and mature leaves also increased. The increasing proportion of aphids on the new leaves may be attributed primarily to the increased growth rate of the leaves. In addition, however, the leaves are again occupying different strata, and environmental differences may be stimulating a downward migration.

Although young leaf growth may decrease slightly during the period from May until September, it seems likely that the continued low density on the older leaves is primarily due to the microclimatic differences between the strata occupied by leaves of the two ages.

The seasonal population trends on the young, unfolding leaves in plot A are shown in figure 7. The density recorded on each sampling date includes the total number of adults, nymphs, and alate nymphs, as well as alates per

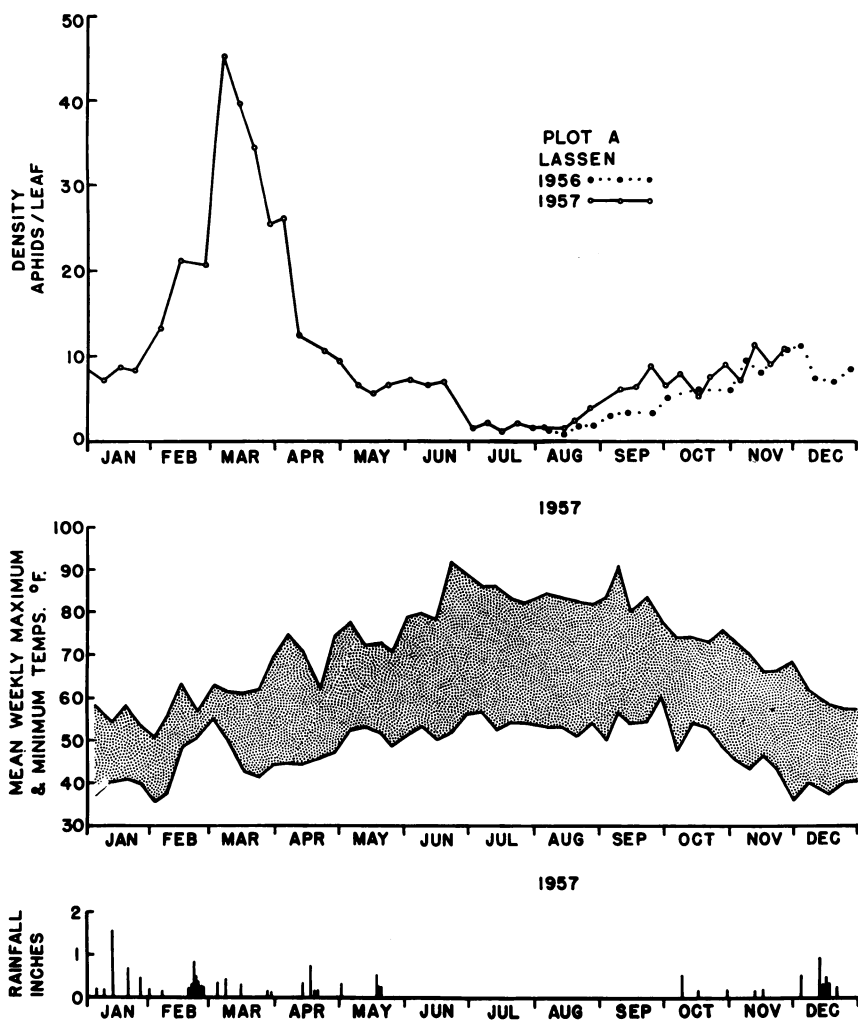


Fig. 7. (Plot A.) Seasonal population trends of *Pentatrichopus* species on cultivated strawberry at Santa Clara, California, during 1956 and 1957, with temperature and rainfall data for 1957.

leaf. The dotted line indicates the densities observed in the fall of 1956 following planting, and the solid line indicates the population trends during the second year of planting.

The aphid density in 1956 began increasing in late August and reached a peak of eleven aphids per leaf in early December. The density dropped off slightly during the winter and then began to increase rapidly in February.

Following the annual high of forty-five aphids per leaf in early March, the population declined rapidly. After the sharp decline in March and April, the density leveled off until a further reduction occurred in late June. As

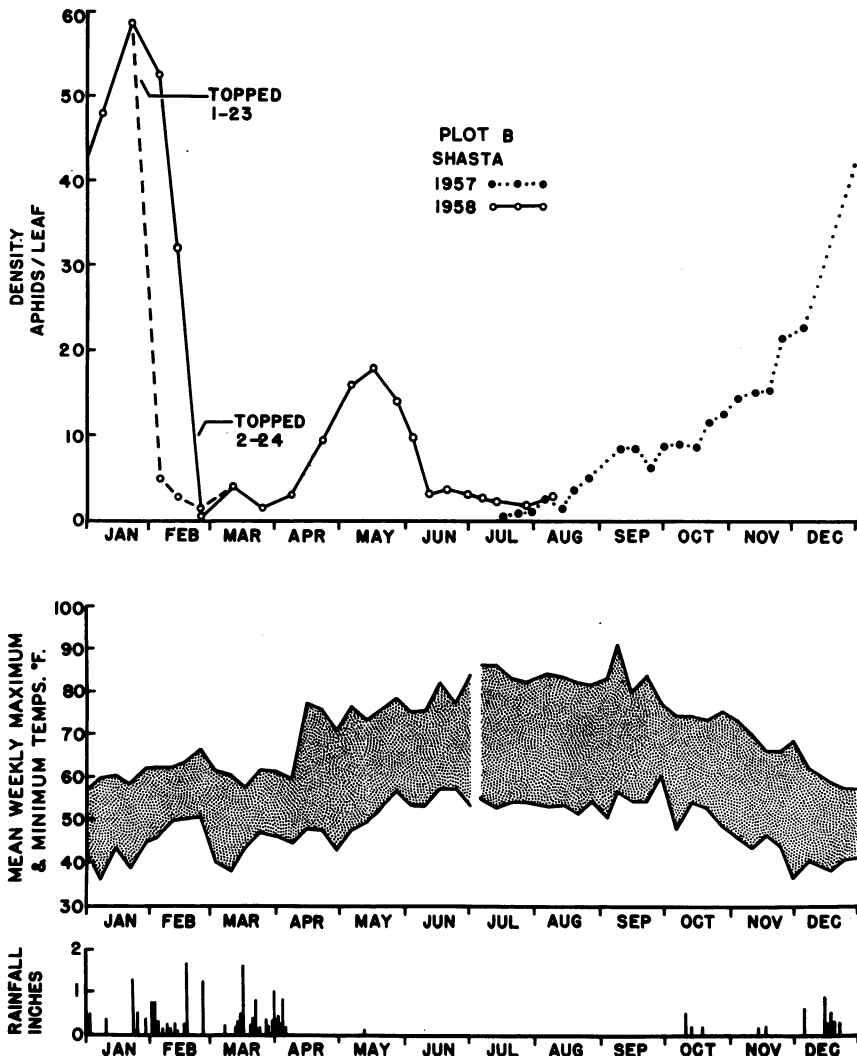


Fig. 8. (Plot B.) Seasonal population trends of *Pentatrichopus* species on cultivated strawberry at Santa Clara, California, during 1957 and 1958, with temperature and rainfall data for the corresponding periods.

in the preceding year, the population began to increase in late August and reached a peak of slightly over eleven aphids per leaf in late November of 1957.

The temperature records for this plot are shown in the middle graph in figure 7. The lines represent the mean weekly maximum temperatures and

the mean weekly minimum temperatures as they occurred in 1957. The highest temperatures occurred in late June, with several daily maximums exceeding 95° F. The lowest temperatures were observed in December, when daily minimum temperatures reached 30 and 31° F. on several occasions.

In the lower graph in figure 7 are shown the rainfall records in inches during 1957. The amount of rainfall observed was not unusual for this area. The rainy period extended from January through May, while no rain fell from late May until early October.

The seasonal population trends as they occurred on the Shasta variety in plot B are shown in figure 8. The dotted line indicates the aphid density in the fall of 1957 following planting. The aphid density increased in the middle of August in a manner similar to the trends observed in plot A, but at a somewhat more rapid rate. Instead of reaching a peak in late November and leveling off, however, the population in this plot continued to increase during the winter and reached a peak of 58.6 aphids per leaf on January 22, 1958. On January 23, two-thirds of the plot was topped by removing all but the youngest leaves. Topping is a more or less standard operation which is generally conducted late in dormancy to facilitate clean culture.

Population density in the topped part of the plot (broken line) dropped to 5 aphids per leaf by February 5. In the untopped portion of the plot, the density on February 5 was 52.5 aphids per leaf; on February 13, the density was 32 aphids per leaf in the same portion. This section was topped on February 24, and on February 25, the aphid density had dropped to 2 aphids per leaf. Following the rainy period, the population once again began to increase in April. After reaching a second peak of about 19 aphids per leaf on May 15, the population dropped to its summer low in the second week of June, about two weeks earlier than the drop occurring in 1957 in plot A.

The middle graph in figure 8 shows the temperature records for plot B. The records from July until December are for 1957, while the records from January until June are for 1958. Mean temperatures during January and February were approximately two to three degrees higher than those observed in 1957.

Rainfall records for the periods mentioned above are shown in the lower graph in figure 8. The winter and early spring of 1958 were characterized by exceptionally heavy rainfall.

The population trends for plot C, as observed on the Lassen variety, are shown in figure 9. When sampling began in March, the spring increase was under way. On March 21, two weeks later than in plot A, a peak of 42.8 aphids per leaf was noted. The population dropped off during May in a manner similar to the drop in plot A, but to a much lower density. By late May, the infestation had all but disappeared, and only a few individuals were observed at any one sampling date for the remainder of the year. The population failed to increase in August, as took place for two years in plot A and one year in plot B.

The temperature and rainfall records for plot C, as shown in the middle and bottom graphs in figure 9, are not unusual for this area.

Upon observing the population trends in these three plots, it becomes ap-

parent that there is considerable variation from year to year and from field to field. Aside from the variations, however, there exist population density responses which are common to all plots. First of all are the high densities

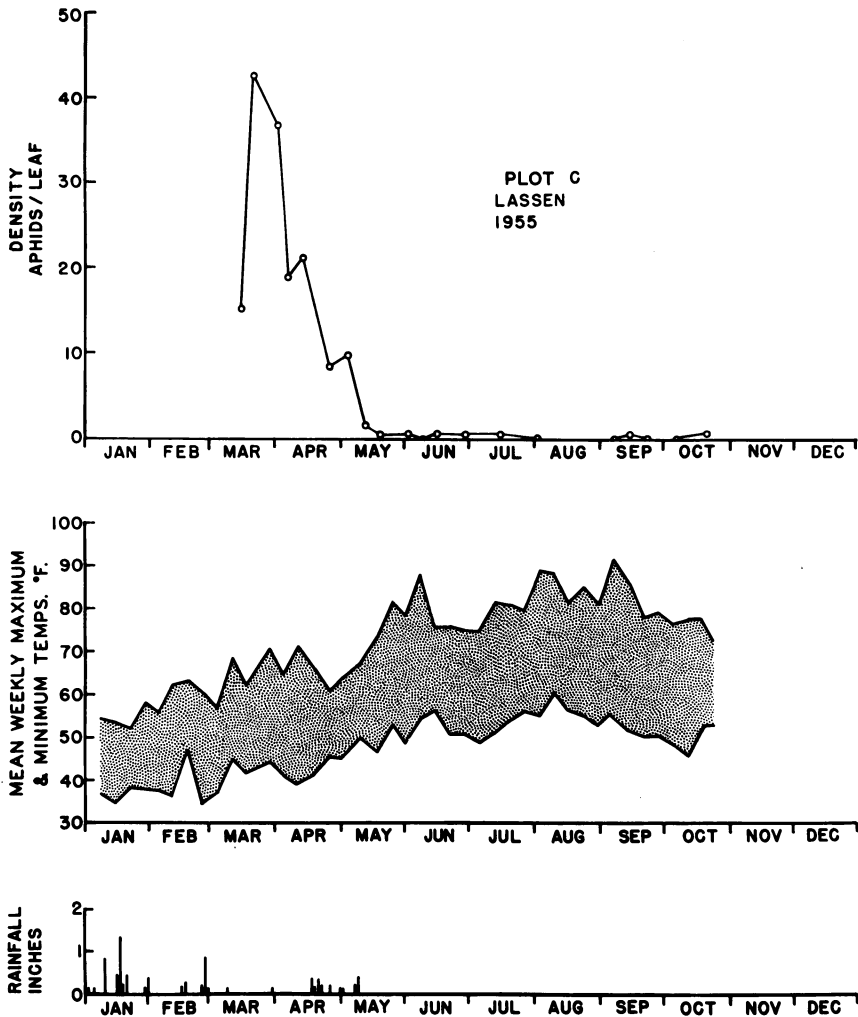


Fig. 9. (Plot C.) Seasonal population trends of *Pentatrichopus* species on cultivated strawberry at Santa Clara, California, during 1955, with temperature and rainfall data for the corresponding period.

observed in the late winter and early spring. In plots A and C, this peak occurred in March. In plot B, the peak occurred in late January, with a lower peak taking place in May. Following the spring peaks, the populations dropped rapidly and reached a summer low in density about June. During July and August in each case, the population continued at a very low level. Except for plot C, which was a very unthrifty field, populations

began to increase in August. A marked difference occurred in densities during the winter between plot A (Lassen variety) and plot B (Shasta variety). In the former, the density declined slightly during the winter, while in the latter, it continued to increase quite rapidly.

Occurrence of Alates

The seasonal occurrence of alatoid nymphs in plot A is shown in figure 10. The upper chart illustrates the numbers of alatoid nymphs per leaf on successive sampling dates from early August, 1956, until the end of November, 1957. First-year samples in this plot revealed a rare and sporadic occurrence of alatoid nymphs during August and September. In late September, the number began to increase gradually until a peak of 0.64 alatoids per leaf was observed on November 27. The number then declined until a low of 0.10 alatoid nymphs per leaf was noted at the end of December. Alatoid nymphs continued to be rare until the end of February, when a rapid increase marked the beginning of the spring dispersal period. By the third week in March, a spring peak of over 5 alatoid nymphs per leaf was observed. A rapid decline occurred from late March until the second week in April, at which time a gradual decrease continued until early May. During the period from May until August, only 10 alatoid nymphs were observed. Again, in late September, a gradual increase occurred until a peak of 0.76 alatoid nymphs per leaf was noted on October 29.

In the lower chart for plot A (fig. 10), the alatoid nymph count is expressed as a percentage of the total aphid sample. It is apparent, when alatoid nymphs are plotted in this manner, that there existed two rather distinct periods of alate production during the year, which in this case corresponded rather closely with the peaks of actual numbers. The spring dispersal period extended from the end of February until the end of May, while the fall dispersal period extended from September through late December. The spring peak occurred in late March, and the fall peak was seen to occur at the end of October in both 1956 and 1957. The sporadic increases in the percentage of alatoid nymphs during July and August reflected the occurrence of single alatoid nymphs in periods of very low densities and did not represent significant increases in alatoid populations.

The seasonal distribution of alatoid nymphs in plot B on the Shasta variety strawberry is shown in the lower half of figure 10. As with the preceding plot, the upper chart illustrates the numbers of alatoids per leaf as observed on successive sampling dates from the middle of July, 1957, through early August, 1958. In a manner similar to plot A, the alatoid nymph count began to increase in September. Instead of declining during the winter, as occurred in plot A, the alatoid nymphs continued to increase, and during January and early February had reached a count of between 2 and 2.5 per leaf. This alatoid density is rather high in comparison to plot A at a similar time of year, but it is a reflection of the exceptionally high total aphid density present in plot B. When the plot was topped in February, the total aphid density declined, as did the number of alatoid nymphs. The slight increase in the counts in late April and May again reflects a total population increase.

In the lower chart for plot B (fig. 10), the alatoid nymph counts were

converted to a percentage of the total sample. The fall peak in this plot approximated quite closely the fall peaks observed in plot A. The spring peak preceded that observed in plot A by about three weeks. On February 5 and

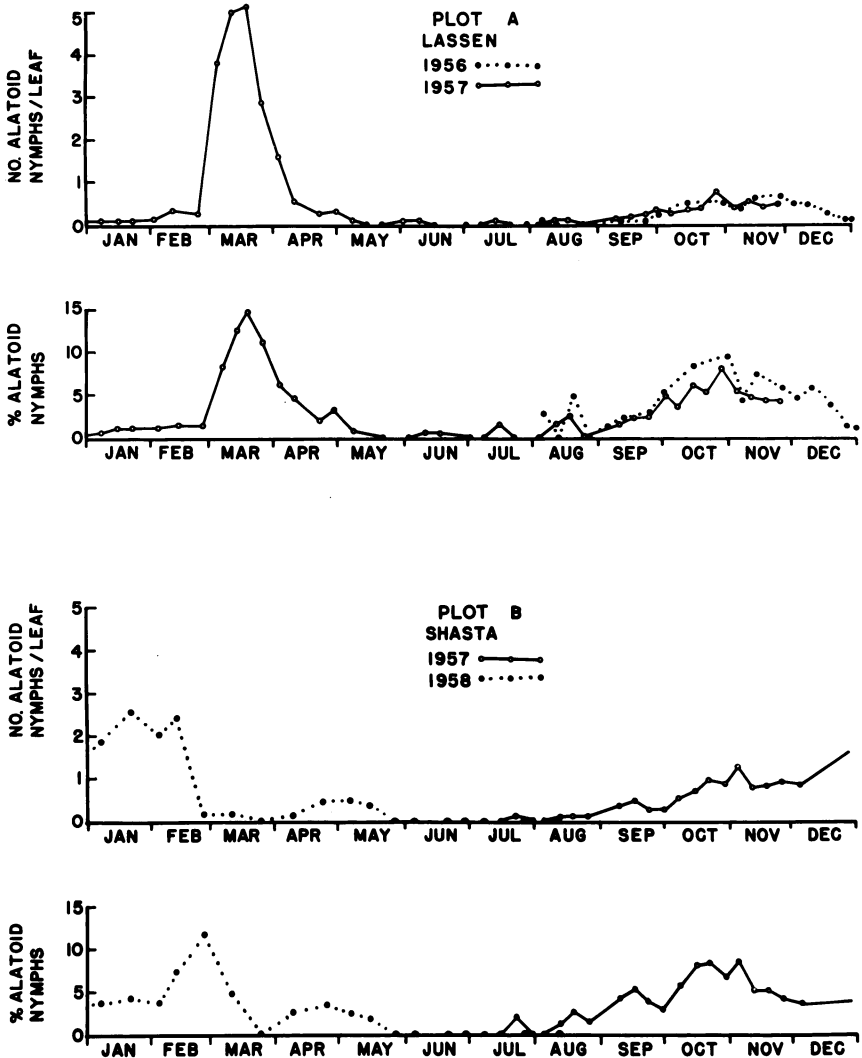


Fig. 10. Number of alatoid nymphs per leaf and percentage of alatoids, based on the total aphid sample for plots A and B at Santa Clara, California. (1956-1958.)

13, the alatoid nymph counts were taken only from the untopped portion of the plot, since the density in the topped portion was so low that an adequate sample could not be obtained. On February 26, when the entire plot had been topped, the sample size was increased to two fifty-leaf samples, one from each section of the plot. The counts in each case were very similar and were combined for calculating the percentage of alatoids. Due to a con-

tinued low density in March, the sample on March 11 consisted of four fifty-leaf subsamples. These also were rather similar with respect to numbers of alatooids in each subsample, and were combined in the final calculation. Because of the low densities, these results possessed wider confidence limits, but the data indicated that a peak alatooid population on the Shasta variety occurred at the end of February as contrasted to the late March peak observed on the Lassen variety in plot A. Following the peak, the percentage of alatooids decreased and continued at a level of less than 3 per cent through April and May. By May 26, the alatooid percentage had dropped to less than 0.5 per cent.

From these studies, it is apparent that alates are present in varying numbers throughout most of the year. When the alatooid nymphs are graphed as a percentage of the total population, however, two well-defined periods of alate production become evident. These generally occur in the early spring and late fall.

In plot A (Lassen variety), the spring dispersal period extended from late February until early May, with a peak occurring in late March. In plot B (Shasta variety), the spring dispersal period extended from early February until the middle of March, with a peak occurring in late February. In other reports in the literature, the spring peaks occurred considerably later. Edwards and Zeller (1938), in Oregon, reported that alates occur in the Willamette Valley during April and May. Rosensteil and Vaughan (1952), also in Oregon, reported a peak flight of alates in mid-June. In England, Hodson (1937) reported that alates occur in the field from June onward, while Massee *et al.* (1938) and Dicker (1952*a*) observed their occurrence during May and June. All these areas have much later growing seasons than does the Santa Clara Valley.

The fall dispersal period in both plots was observed to extend from September through December, with peaks occurring in late October or early November. In England, Massee *et al.* (1938) observed an autumn flight of alates in September; Greenslade (1941) reported a second flight in August, although low in number; and Dicker (1952*a*) stated that a second flight commences in October and continues through early February.

Although these studies indicate the periodic occurrence of alates, it does not appear that vector control preceding these periods could, by itself, eliminate virus spread. The observations show that alates may occur at all times during the year, but sometimes in very low numbers. Although the highest *percentages* appear periodic in nature, higher *numbers* may occur during the winter or at other times if aphid populations become exceedingly high.

Occurrence of Sexual Forms

The seasonal occurrence of sexual forms of strawberry aphids in plot A is illustrated in figure 6. Although the females differed somewhat from more typical *Pentatrichopus thomasi* oviparae collected at Grass Valley, California (Schaefers, 1960), they still conformed more closely to this species than to *P. fragaefolii*. Two of the males lacked additional setae in the second marginal row, thus corresponding to *P. fragaefolii*, and two corresponded to *P. thomasi*. In each case the males were apterous, as were the females. Other

collections of sexual forms at the Deciduous Fruit Station included a single oviparous female on January 8, 1958, and a male on January 17, 1956.

Sexual forms of the strawberry aphid have also been observed in other plantings throughout the central coast regions of California. Oviparae and apterous males of both species have been collected on rare occasions from November until January at Felton, Soquel, and Watsonville, California.

Greater numbers of sexual forms have been observed at Grass Valley. This area is approximately 150 miles north of Santa Clara, and is located in the Sierra Nevada at an altitude of 2,500 feet. Winter temperatures in this region are considerably lower than in the Santa Clara region, and it receives a moderate snow cover in late winter. A collection made in February, 1957, revealed the presence of approximately 40 oviparae on about 125 leaves, but no males were observed. Numerous black, shiny eggs were found on the leaves and petioles. These were placed in a temperature box at 60° F., and only two of the eggs hatched. These aphids died during the second stadium. In November, 1957, a second collection at Grass Valley revealed a similar number of *P. thomasi* oviparae and about twenty apterous males.

In the greenhouse at Berkeley, *P. fragaefolii* oviparae were found each year from November through February. During December, when they occur most commonly, one oviparous female may be found on each group of fifteen to twenty heavily infested plants. No males have been observed in the greenhouse over a period of three years of extensive searching. Only a single egg has been seen, and this failed to turn to the characteristic black of a fertilized egg.

Because sexual forms occur in such low numbers in the central coast region of California, mating probably takes place infrequently if at all, and no eggs have been observed. The inutility of sexual forms in this area is further evinced by the presence of large numbers of viviparae throughout the winter months. Only near Grass Valley were sexuals observed in numbers sufficient for mating to take place, but even there, large numbers of viviparae provided an overwintering population.

Collections of sexuals in North America have been reported in the literature on only a few occasions. Davidson (1914) observed alate males, oviparous females, and eggs during January and February near Walnut Creek, California. He attributed these forms to *P. fragaefolii*, but actually, they may have been *P. thomasi*. Hottes and Frison (1931) reported that they observed mating forms (apparently *P. fragaefolii*) on November 11 in Illinois. Thomas and Jacob (1941) observed material collected on *Potentilla* which they believed could represent the sexual forms of the species now known as *P. thomasi*. Recent observations by the senior author indicate that overwintering in the egg stage is the more common phenomenon in the northeastern United States.

The occurrence of sexual forms in the field in Europe seems to be even more rare than in North America. Hodson (1937) failed to find sexuals in the field, despite intensive searching. Massee *et al.* (1938) reported that sexual forms are found each year during late December and January. Thomas and Jacob (1940) observed only a single oviparous female out of doors. Greenslade (1941) observed sexuals in January and February. Dicker

(1952a) reported that sexuals occur very rarely in the field in England, and he observed only a single oviparous female and an alate male. Hille Ris Lambers (1953) stated that the strawberry aphid in Europe lives throughout the year on its hosts without normally forming sexuals. According to Dicker (1952a), the egg stage has never been recognized with certainty in the field.

In Europe, as in North America, sexuals are found commonly under greenhouse and laboratory conditions (Hodson, 1937; Thomas and Jacob, 1940; Dicker, 1952a; and Hille Ris Lambers, 1953). Eggs have been found in greenhouses in Europe, but only Hodson has observed them to hatch. In the university greenhouse at Berkeley, only sexual females of *P. fragaefolii* were found.

The conditions necessary for the production of sexuals are unclear, but it appears that factors other than low temperatures are necessary. Uichanco (1921) concluded that amphigonous reproduction in aphids is an adaptation for survival under adverse conditions, but it is retained at cyclical intervals even when the adverse conditions are removed. This hypothesis provides a possible answer to the occurrence of sexuals in the greenhouse and during mild winters at the same time conditions are highly favorable to normal parthenogenetic reproduction.

Factors Responsible for Seasonal Fluctuations in Density

Because of interactions, it is extremely difficult to evaluate any single factor in relation to its effects on strawberry aphid populations. It is apparent from this study, however, that certain factors become less limiting at certain times of the year, and it is possible in some instances to determine their relative effects on population density. For convenience, the factors of greatest importance are discussed here under the subheadings Temperature, Rainfall and Humidity, Host Plant Condition, Dispersal, and Natural Enemies.

Temperature. It was shown in the section on temperature relations that with short periods of exposure, such as occur in the field, temperatures of 100° F. are necessary before appreciable mortality can be expected. Since temperatures in this range occur rarely in the Santa Clara Valley, mortality can only on a few occasions be attributed to high temperatures.

In plot A (fig. 7), in 1957, temperatures of 99, 101, 99, and 103° F. were recorded for June 17, 22, 23, and 24. These weather shelter temperatures were between 1.5 and 2 degrees higher than the crown temperatures of plants, but it is likely that the density decline observed during this period was at least in part due to the lethal effects of these exceptionally high temperatures. Maximum temperatures of 80 to 95° F. usually occur from June until September in the Santa Clara Valley, and although not producing immediate lethal effects, may result in a suppressing action on aphid populations. If the aphids wander or drop from the plant, which may occur between temperatures of 80 and 95° F., then the aphids are certainly exposed to a variety of other mortality factors.

Temperatures in the sublethal range still have an important influence on the capacity for increase of populations. Developmental time, deposition period, deposition rate, and predeposition period all affect population in-

crease, and are all influenced by temperature. Under constant temperatures, development of immature individuals is most rapid at about 77° F. Since weekly means at Santa Clara never reach this temperature, the maximum rate of development is attained from June until September, when weekly mean temperatures approximate 70° F. Both the maximum deposition period and the highest deposition rate occur at temperatures between 65 and 70° F. Weekly mean temperatures are close to this range from the middle of May until the middle of October. Although maximum temperatures of 90 and 95° F. cause a marked decrease in the deposition of young, it has been shown earlier in this paper that an increased deposition rate occurs during the cooler part of the day, which tends to offset the temporary reduction.

Although the developmental rate is at its seasonal maximum and fecundity is at its optimum during the summer, it can be noted that the expected high populations do not occur (fig. 7). It is possible that the high daily maximums during the summer can, in view of their repeated occurrence, result in a reduction in the capacity for increase. However, other factors which will be discussed later must also contribute to the low aphid density during the summer.

At temperatures below 65° F., the developmental and fecundity rates decrease, while the longevity increases. On the basis of temperature alone, it might be expected that population densities would be somewhat lower during the cooler parts of the year. On observing the population trends in plot A (fig. 7), it can be noted that the highest seasonal density occurred in early March when the weekly mean temperatures were between 50 and 55° F. Similarly, when the temperatures dropped below the optimum in the fall, the population density increased slightly. During December and January, when weekly mean temperatures were between 45 and 50° F., the population density in plot A (fig. 7) decreased. At similar temperatures in plot B (fig. 8), however, the population density increased rapidly. It is apparent from these observations that although minimum temperatures are of importance in England (Dicker, 1952*a*), they are not usually responsible for pronounced population reductions in the coastal areas of California.

Rainfall and Humidity. Under certain conditions, the mechanical action of rainfall can result in a marked reduction in aphid densities. Hodson (1937) reported that up to 70 per cent mortality may occur during periods of heavy rainfall. Observations made at Santa Clara indicate that there is little direct mortality due to splashing if the plants have not had the canopy of leaves removed by topping. During the winter of 1957 in plot A (fig. 7), heavy rains during January and February failed to cause any marked population decreases on the untopped plants. In plot B (fig. 8), during the winter of 1958, a count of 58.6 aphids per leaf was made on January 22. On January 23, two-thirds of the field was topped, so that only a few of the young leaves remained. During the ensuing two-week period, over two inches of rain fell on the plot. Counts made on February 5 revealed a density of 52.5 aphids per leaf in the untopped section of the field, while the density in the section which was topped had declined to 5 aphids per leaf. Although some mortality undoubtedly occurred due to the topping procedure, this was probably offset by a concentration of the surviving aphids on the remaining

growth. Since temperatures at this time of year are not in the lethal range, the greatest portion of the 90 per cent decrease on the topped plants was in all likelihood due to the driving rains on the exposed aphids. Further evidence of the effect of rainfall on aphid populations may be noted in plot B during late February and early March. During this period, only a single day of heavy rainfall occurred. The aphid density increased during this interval, but when heavy rains commenced in March, the population again declined. The subsequent increase in aphid density during the period of continued rainfall may be partially explained by the fact that plant growth once again provided a protective canopy.

Although investigations were not conducted to determine the effects of relative humidity on development, fecundity, and mortality, observations indicate that *Pentatrichopus fragaefolii* and other members of the complex are favored by moderately high humidities. Observations made during greenhouse rearing experiments indicated that colonization by the aphid was much more successful when the humidity was increased by covering the bench tops with wet sand. Hodson (1937) reported that the reproductive rate diminished in hot, dry weather. Staniland (1928) noted that the aphids seemed to prefer hot, moist conditions rather than hot, dry conditions. Edwards and Zeller (1938) observed that in certain localities where the humidity is kept high by irrigation, the aphids may be more numerous. Although strawberry fields are irrigated throughout the summer months in the Santa Clara Valley, populations remain quite low. This may be due to the fact that the two- to three-foot-wide rows are irrigated by means of furrows, which leaves the tops of the beds comparatively dry. In Oregon, where Edwards and Zeller made their observations, cultural practices differ, and sprinkler irrigation is frequently used. It is possible that the humidity is raised much higher by the sprinkler type of irrigation, thus making conditions more favorable for the aphids. During the period from June to September in the Santa Clara Valley, the weather is generally free of rainfall. The hot, dry conditions during this period may have serious consequences with respect to aphid densities; however, further investigations will be necessary before this factor may be fully evaluated.

Host Plant Condition. After several years of field studies on *Pentatrichopus fragaefolii* in England, Dicker (1952a) concluded that two distinct seasonal cycles in aphid density occurred, depending on the age of the host plants. On first-year plants, where vegetative growth was rather uniform, aphid densities increased slowly and reached a peak later in summer than was the case with older plants. After this increase, population density gradually declined as winter approached. He attributed these changes to normal seasonal climatic cycles and to changes in the nutritional condition of the host plant as it was influenced by day length. In second-year plantings, he observed that the populations increased rapidly in late May or June. The density then decreased rapidly and remained at a relatively low level until further reductions occurred during the winter. He concluded that the summer decline (comparable to the early-spring decline in plots A and C) occurred as a result of reduced leaf quantity and quality when blossoms and fruit developed. The migrating apterae, on finding no suitable

young leaves, become restless and disperse, causing a general drop in reproduction. Dicker pointed out that this hypothesis was not the complete explanation, and questioned the rapidity of the summer decline as well as the absence of a build-up in density following the fruiting period. He noted that in England, the rapid increase in population density on the older plants occurred toward the end of the spring flush of growth, and in general the peak populations coincided with the ripening of the earlier fruit.

With most species of plants, it is generally recognized that reproductive growth occurs at the expense of vegetative growth. Meyer and Anderson (1952) pointed out that such a large proportion of available foods is diverted to developing flowers or fruits that other organs suffer a deficiency and hence are checked in growth. These workers stated further that developing flowers and fruits are organs of high assimilatory and respiratory activity, hence their maturation may result in a considerable drain on the available food supply. Dicker (1952*a*) observed that by removing the blossoms from strawberry plants, he could obtain up to 60 per cent more leaves during May and June. In addition, he reported that the quality of the leaves on the deblossomed plants improved, and the plant did not wilt during the hottest part of the day as did the plants carrying the normal crop of fruit.

In the central coast area of California, strawberry varieties have very different growth characteristics from those observed by Dicker in England. Fruit production by the Lassen and Shasta varieties has been discussed by Thomas and Goldsmith (1945). The Shasta variety commences fruit production about the last week of April. Production is almost continuous until October or November, but there are periods of increased production in May, in late August or early September, and sometimes in October. The Lassen variety generally commences fruit production a few days after Shasta. It likewise produces fruit until November, with three peaks during the fruiting season. These peaks are separated by periods of low production, which usually extend from June 15 to July 15 and from September 15 to October 15.

In plot A (fig. 7), which consisted of the Lassen variety, the plants broke dormancy in early February as the mean temperatures reached about 50° F. At this time, vegetative growth was quite vigorous, but blossoming commenced almost simultaneously. This situation is in contrast to that in England, where Dicker (1952*a*) reported that older plants pass through a phase of vegetative growth in the spring which reaches a maximum in late April or early May, at which time blossom trusses appear. It may be noted in figure 7 that the aphid density reached its peak in early March, while the fruit did not begin ripening until the end of April. In England, aphid densities seem to reach their peak about the same time the earlier fruits begin to ripen. On the Lassen variety in plot A, the density peak preceded the production of early fruit by six to eight weeks. In plot C (fig. 9), which also consisted of the Lassen variety, the aphid density reached its peak about four to five weeks before the production of early-ripening fruits. Although not significant because of contrasting topping procedures and unusually heavy rains, the peak density in plot B (fig. 8) on the Shasta variety followed fruit production by about three weeks. It appears that

the factors associated with the marked population declines under California conditions are not so intimately associated with fruit production as Dicker hypothesized under the conditions in England.

If heavy fruit production materially affects aphid populations in the Santa Clara area, such an action will take place on the Lassen variety during May and again from early July until early September, at which times the greatest amounts of fruit reach maturity. It may be noted in figure 7 that there existed no marked response by the population during May. In the late summer of 1957, the aphid density increased about the middle of August, when ripe fruit was in full production. The effects of fruiting on vegetative growth seem to be less pronounced under California conditions, and there appears to be little correlation with aphid densities. It seems more likely that the favorableness of the plants does vary, but the changes are not tied so closely to fruit production. During the late winter and early spring, after the plants break from dormancy, they are very vigorous and in an apparently favorable physiological condition. Throughout the late spring and summer, physiological changes probably occur in the plants, making them less suitable for the aphids. During the fall, the plants once again seem to become suitable for the aphids. Whether the more gradual increase in the fall than in the spring is caused by the favorableness of the strawberry plants or some other extrinsic factor cannot be determined.

Dispersal. Although alates occur through most of the year, the peak dispersal periods occur from late February until early May and again from the middle of September until the end of December. The greatest effect on population fluctuations from dispersing alates occurs during these periods.

In table 8 are listed the percentages of alates maturing at approximately fourteen-day intervals during the periods mentioned. Between February 14 and May 7, 16.7 per cent of the individuals reaching maturity were lost as dispersing alates. The greatest loss during this period occurred from March 14 until April 11, when 26.1 per cent of the maturing aphids were alates. When this time interval is observed in figure 7, it may be seen that it correlates with the period of rapid decline in density.

In the lower half of table 8 are listed the estimated losses of alates during the fall dispersal period in plot A for 1956. In this case, the period of greatest loss occurred between October 16 and November 29, when 19.6 per cent of the maturing aphids were alates. It may be observed in figure 7 that the population density during this period was increasing.

Whether the periods of greatest dispersal in the spring and fall have any effect on the population growth form is dependent on the relative stability of the population. Thus, if natality and mortality possess a ratio of 1:1, then a loss of reproductive individuals as dispersing alates can bring about a population decline. On the basis of temperature, natality during these periods may be expected to more than offset the low percentage lost as alates. In the present investigation, dispersal probably added to the decline which was precipitated by other factors. No decline occurred in the fall, and it is apparent that the loss of reproductives to this extent probably produced only a retarding effect on the rate of population increase.

Natural Enemies. The following list contains the natural enemies observed to occur commonly in the fields studied at Santa Clara.

PARASITES

Eulophidae	<i>Aphelinus semiflavus</i> Howard
Braconidae	<i>Aphidius rosaphidis</i> C. F. Smith

PREDATORS

Lygaeidae	<i>Geocoris pallens</i> Stål
Anthocoridae	<i>Orius tristicolor</i> White
Miridae	<i>Deraeocoris</i> (<i>Camptobrachis</i>) <i>brevis piceatus</i> Knight
Nabidae	<i>Nabis ferus</i> (Linnaeus)
Chrysopidae	<i>Chrysopus</i> sp.
Hemerobiidae	<i>Hemerobius</i> sp.
Syrphidae	Numerous species
Coccinellidae	<i>Hippodamia convergens</i> Guérin and other species

DISEASES

Entomophthoraceae	<i>Entomophthora</i> spp.
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Among the natural enemies listed above, the parasite *Aphidius rosaphidis* and lacewing larvae probably have the greatest effect on aphid densities in the field. Various syrphid flies become of importance in the greenhouse and cause marked reductions in aphid colonies. In no case in the field was it possible to correlate population declines with the occurrence of any single species of parasite or predator; however, more critical counts will have to be made before their true value may be accurately ascertained. Dicker (1952b) concluded that the majority of predators are found in such low numbers that their combined action on the aphid populations can only be slight. He provided a list of predators which, at the familial level, corresponds quite closely with those discussed here. He stated that only members of the genera *Anthocoris* (Anthocoridae) and *Tachyporus* (Staphylinidae) occurred with sufficient regularity to warrant consideration with respect to the summer declines in aphid populations. Thomas and Jacob (1940) observed that syrphid flies were responsible for some reduction of strawberry aphid densities in England.

Thomas and Jacob (1940) reported that a parasitic fungus (probably *Empusa* sp.) was primarily responsible for the summer decline in aphid density in the field observed. Dicker (1952b) noted that *Empusa planchoni-ana* (Cornu) was frequently observed to attack strawberry aphid populations in May and July in England, and also during October and December. He concluded, however, that the irregularity in time and intensity of outbreaks makes it very unlikely that the fungus is a factor of primary importance in causing the marked seasonal variations in population observed annually in the field.

In the main strawberry-growing areas of California, fungus diseases have been observed to cause marked reductions in aphid densities on numerous occasions. In 1957, in plot A (fig. 7), two undetermined species of *Entomophthora* (= *Empusa*) attacked the aphids from the middle of March until the last week in April. Counts made on March 21 and April 4 revealed that 10 per cent of the aphids which were shaken from the young, unfolding

leaves were in the advanced stages of fungus attack. The actual percentage was somewhat higher than this, since aphids in the early stages of attack did not show obvious symptoms and were not included in the counts. In addition, some of the mummies remained stuck to the leaves and were not included. During February, in plot B (fig. 8), another severe attack was noted. In that section of the field which was not topped until February 24,

TABLE 8
LOSS OF REPRODUCTIVE UNITS IN THE FORM OF MATURING ALATE STRAWBERRY APHIDS AT SANTA CLARA, CALIFORNIA, IN THE SPRING OF 1957 AND THE FALL OF 1956

Sample date	Estimated date of aphids maturing	Total third- and fourth-instar nymphs*	Third- and fourth-instar alatoïds*	Estimated alates (per cent)
Spring 1957				
February 14.....	February 28.....	375	16	4.3
February 26.....	March 14.....	379	13	3.4
March 14.....	March 28.....	940	252	26.8
March 28.....	April 11.....	567	142	25.1
April 11.....	April 25.....	277	28	10.1
April 23.....	May 7.....	226	11	4.8
		2,764	462	16.7 (mean)
Fall 1956				
September 13.....	September 19.....	69	4	5.8
September 25.....	October 2.....	71	5	7.0
October 2.....	October 10.....	109	14	12.8
October 16.....	October 24.....	125	25	20.0
November 1.....	November 11.....	133	29	21.8
November 15.....	November 29.....	176	31	17.6
November 27.....	December 11.....	252	32	12.7
December 11.....	December 27.....	182	22	12.1
December 28.....	January 14.....	180	5	2.8
		1,297	167	12.9 (mean)

* Number per fifty leaves.

the fungus *Entomophthora aphidis* Hoffman caused a marked reduction in the aphid population. On February 5, 5.3 per cent of all the aphids observed, both those shaken from the leaves and those still stuck on, were in the advanced stages of fungus attack. By February 13, 39.5 per cent of all the aphids observed were in the advanced stages of fungus attack. After the field was topped, the aphid density dropped to a low level, and mummies were observed only rarely for the next two weeks. Fungus attacks were also observed to cause high mortality in other fields in the study area.

On the basis of these observations, it appears that an attack by fungi is dependent on very high humidities and high aphid densities. Dicker (1952b) noted that fungus attacks in England usually coincided with warm, humid

conditions, but that temperature did not appear to be the most important controlling factor. On one occasion, a severe fungus attack was observed at Grass Valley, California, as the snow was melting in late winter. Although a different species of fungus may have been involved, this observation tends to support Dicker's conclusion that temperature is not such a critical factor for the fungus disease. In both plot A and plot B, the fungus outbreaks occurred during periods of rainfall when aphid densities were very high.

DISCUSSION

Although this study does not precisely determine which factors are regulating population densities, it does make it possible to offer some suggestions as to their relative influences on the seasonal trends of the strawberry aphid.

It is apparent that high temperatures are not the reason for the population declines that occur in the spring and early summer. Not only are temperatures very near optimum for development and reproduction when this decline takes place, but in the spring, when populations increase rapidly, temperatures are far below those that would seem to be optimum. In addition, mean temperatures during the spring decline are always lower than those encountered in the fall, when populations once again commence to increase.

This spring decline corresponds to the sharp May or June decline observed in England. Dicker (1952*a*) discounted natural enemies, dispersal, and climatic factors as being primarily responsible for the decline in density, and attributed it to a reduction in leaf quantity and quality during fruiting. It has not been possible under California conditions to correlate the decline in the spring with growth characteristics.

Although the physiology of the strawberry plant, as correlated with fruiting, does not seem to be the actual cause of the spring decline, it does seem very likely that the physiology of the strawberry plant is one of the underlying causes of continued low density during the summer. Following dormancy, in the late winter and early spring, the host plant is very vigorous and favorable for the aphids. During the late spring and summer, new leaves and fruit are still being produced, but it appears that a physiological change takes place which makes the plant less suitable for them. This does not cause marked mortality and hence the rapid decline, but does prevent the populations from building up once they have been reduced to low levels. The continued action of natural enemies and unfavorable low humidities may also contribute to the suppression of populations during the summer.

The actual cause and time of the spring decline in California seem to vary from time to time and from place to place. During the winter and spring, rainfall may be responsible for severe reductions in aphid densities. This is particularly true when the plants have little foliage or have been topped recently. In the presence of high humidity and high aphid densities, various fungi can likewise produce marked depressions in aphid densities. In late March and early April, some losses occur due to alate dispersal, but it does not appear that this factor alone can cause the sudden decline. Exceptionally high daily temperatures, although infrequent, also cause marked reductions

during the summer. It is possible that the parasites and predators have been underestimated in their effectiveness, and that these natural enemies, in combination with dispersal and gradual changes in host physiology, are acting together to cause the sharp spring decline.

SUMMARY

Three members of the strawberry aphid complex occur in California. Two of the species, *Pentatrichopus fragaefolii* and *P. thomasi*, are abundant in commercial strawberry plantings and are important vectors of strawberry viruses. The third form, *P. jacobii*, has not been found in commercial plantings and appears to be restricted to the thin-leaved wild strawberries. Although *P. fragaefolii* and *P. thomasi* occur on other hosts such as the sand strawberry (*Fragaria chiloensis*), five-finger (*Potentilla*), and rose, populations are so low that they would seem to have little effect on virus spread to commercial strawberries.

Laboratory studies on *P. fragaefolii* indicated that development takes place at constant temperatures ranging from 45 to 85° F. The minimum developmental period was 7.1 days at 76.5°. The earlier instars appear to have somewhat higher optimum temperatures for development than do the later instars. At 85°, development required twelve days, but there was considerable mortality, and the adults survived for only a few days. At 50°, development took twenty-nine days, and the adults lived for fifty-two days.

The optimum reproductive rate for this species seems to occur at temperatures between 65 and 70° F. Within this range, the predeposition period was 1.7 days, the mean deposition per aphid was 56.1 nymphs, and the rate of deposition was 2.1 nymphs per female per day. Temperatures of 100° and over caused mortality of the adults in four hours or less. Temperatures of 95° produced a temporary inhibitory effect on deposition, which, under normal diurnal cycles, would be offset by an increased rate during the cooler part of the day.

Seasonal history studies were conducted on a mixed population of *P. fragaefolii* and *P. thomasi* at Santa Clara, California. The aphids showed a marked preference for the young, unfolding leaves; as the leaves matured, they migrated down the petiole to the next developing leaf. The investigations indicate that maximum populations occur during the cooler parts of the year, with the peak usually occurring as the plants break dormancy. The lowest densities occur from June until August. Alates are present throughout the year, but their relative abundance is much greater in the early spring and late fall. The actual number of alates, an important consideration in virus control, is a function of total aphid densities, in addition to the season of the year.

Sexual forms are rarely found in the main strawberry-growing areas of California. Overwintering is accomplished almost entirely by the apterous viviparae.

It was impossible to correlate seasonal population trends with any single environmental factor. Interactions of temperature, humidity, rainfall, natural enemies, dispersal, and host plant physiology all contribute to popula-

tion fluctuations. Changes in host plant physiology seem to be important governing factors, but they cannot be tied directly to flower-bud formation and fruit maturation.

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