

AN ABSTRACT OF THE THESIS OF

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al Occurrence of Weed Hosts At Key Sites of Aphid Buildup

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Green peach aphid and associated weed populations were monitored continuously from April, 1978 to March, 1979 at three orchards and a drainage ditch. Aphid populations at all sites peaked in spring and declined in summer. Although natural enemies were most active during the period of peak aphid abundance, they were not numerous enough to account for population declines at all locations. Green peach aphid population trends appeared to be related to the abundance and quality of preferred host plants. Two common weed species in the Yakima area, Descurania sophia and Solanum sarachoides, were found to be highly preferred and significant sources of aphid buildup in spring and early summer. In the absence of highly preferred types and during periods of high population density, less preferred species were colonized.

Laboratory studies of the green peach aphid's feeding preferences have shown an intrinsic preference for summer host plants as opposed to the winter host in all life

stages investigated. In choice chamber tests involving comparisons between 12 common crop and weed species, cruciferous plants were most highly preferred. Solanaceous plants were somewhat less preferred. Observations of settling behavior in these tests revealed no evidence of attraction to preferred hosts. Initial arrival appeared to be at random, and the buildup of aphids on preferred hosts resulted from a lower rate of departure than from non-preferred hosts.

Studies of the host selection behavior of green peach aphid have shown that aphids initiate probing more quickly, settle and feed more readily, and are less restless on preferred hosts. It was also found that the contents of the trichomes of Chenopodium album have no effect on the host selection behavior of this aphid, although the trichomes themselves may provide a physical barrier early in the life of the plant.

Host Preferences of Green Peach Aphid
and Seasonal Occurrence of Weed Hosts
At Key Sites of Aphid Buildup

by

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Typed by researcher for _____ Barry Alan Annis

To my wife and daughter.

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HOST PREFERENCES OF GREEN PEACH APHID
AND SEASONAL OCCURRENCE OF WEED HOSTS
AT KEY SITES OF APHID BUILDUP

I. INTRODUCTION

Weeds play a key role in the epidemiology of plant virus diseases. They serve in a dual capacity as both reservoirs of virus inoculum and hosts of insect vectors (Duffus 1971).

Most plant viruses are transmitted by aphids, which, because of their high reproductive rates, dispersal tendencies, and feeding behavior, are well suited as vectors (Kennedy 1960, Swenson 1968). In agricultural areas migrating aphids can cause serious crop losses by infecting fields with virus acquired from natural weed hosts. Weeds have been identified as important sources of cucumber mosaic virus (Faan and Johnson 1951, Tomlinson and Carter 1970), potato virus Y (Pontis and Feldman 1963), lettuce big vein virus (Campbell 1965), and beet western yellows virus (Wallis 1967a).

The green peach aphid (Myzus persicae Sulzer) is known to transmit over 100 plant viruses (van Emden et al. 1969), and in the Yakima Valley of central Washington is the major vector of yellows diseases of sugarbeet, which can result in a 15 to 30% reduction in yield (Duffus 1961). Thousands of acres of peach orchards produce large populations of green peach aphids, which begin migrating to other hosts in May (Tamaki 1973). Weeds growing on the floor of orchards provide a breeding site for the aphids, where large numbers of potentially viruliferous migrants are generated (Tamaki 1975).

Green peach aphids also overwinter anholocyclicly in drainage ditches fed by warm springs, which remain warmer than the surrounding environment. Alate migrants from infected weeds in these drains carry beet western yellows

to nearby fields in spring (Wallis 1967a).

Although many weed species have been identified as hosts of green peach aphid, little information is available on patterns of utilization of weeds by this aphid, host succession in weed communities, or the relative preferences of this aphid for the weed species involved.

In the spring of 1978, a field study was begun in the lower Yakima Valley to examine the seasonal occurrence of weed hosts in orchards and a drain ditch, and to evaluate the contribution of key weed species to the population dynamics of green peach aphid. Laboratory studies were also undertaken to observe this aphid's host preferences and selection behavior.

II. REVIEW OF LITERATURE

A. Life Cycle

The green peach aphid is a host alternating species with a complex life cycle. Depending on environmental conditions, it is capable of overwintering either holocyclicly or anholocyclicly (Blackman 1974). The holocycle consists of several parthenogenetic generations in spring and summer, and a single sexual generation in the fall (Figure 1). The primary factors which trigger the production of sexual morphs are photoperiod and temperature. Bonnemaison (1951) found the thresholds for development of sexuals to be about 13 hours of daylength and 22°C., although these thresholds are likely to vary depending on regional conditions (van Emden et al. 1969, Blackman 1974).

Green peach aphids overwinter as eggs on Prunus spp. Hill Ris Lambers (1946) listed ten species of Prunus where he found gynoparae (alate parthenogenetic female migrants whose progeny are sexual females). He reported that even though eggs were laid on several species of Prunus, nymphs reached maturity only on peach (P. persica). He concluded that fundatrices (the first generation following egg hatch, consisting of wingless parthenogenetic females) were specific to peach and could survive nowhere else. However, Shands et al. (1969) reported that Canada plum (P. nigra) was a primary host of green peach aphid in the absence of peach trees in Maine, and Tamaki et al. (1980) found that fundatrices survived and reproduced on secondary hosts when they migrated from prunings left on orchard floors. Previous research has not defined the exact role of the primary host in the population dynamics of this species.

In the Yakima Valley, large acreages of peach orchards provide the green peach aphid with abundant overwintering

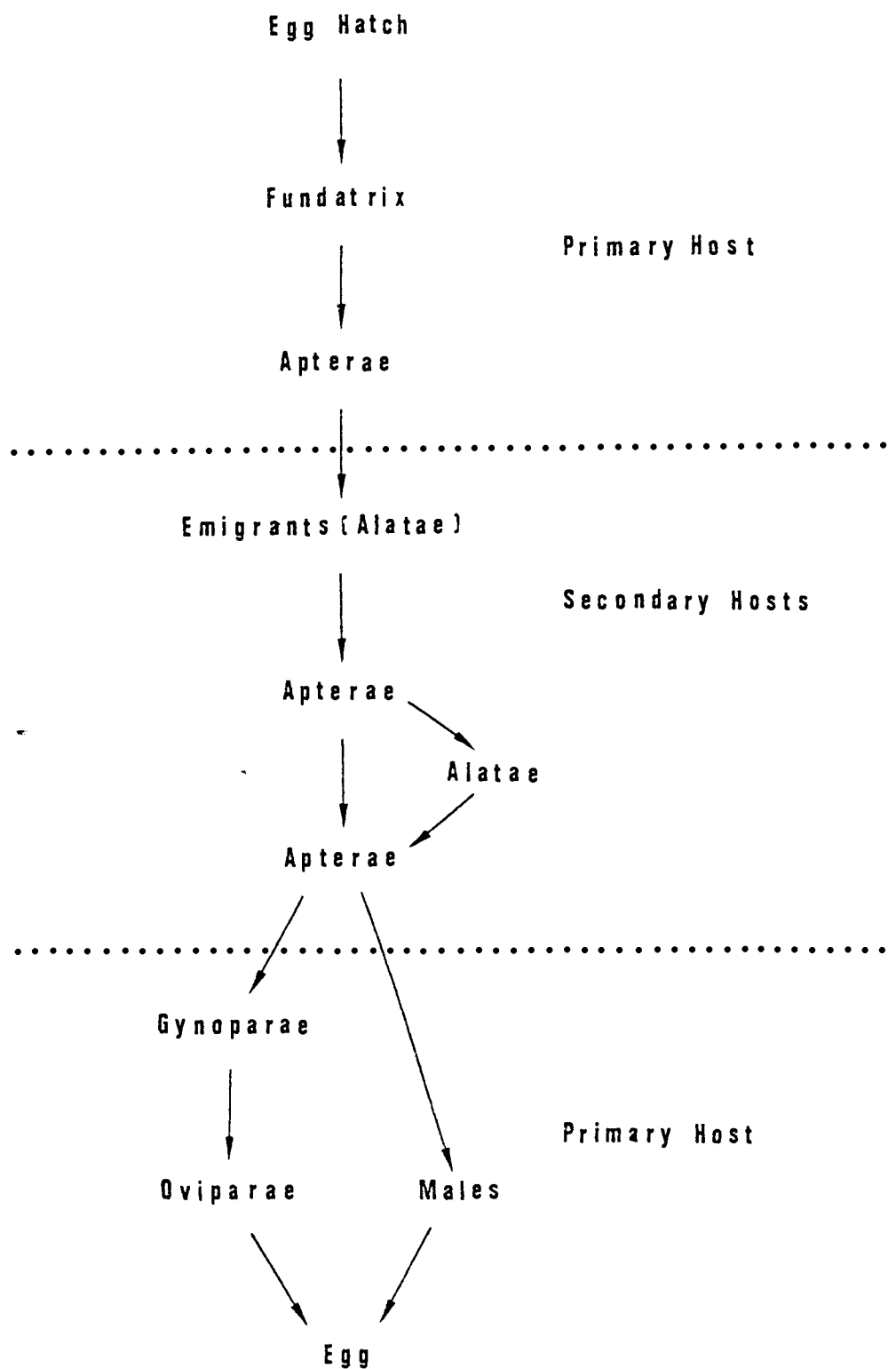


Figure 1. Holocycle of Myzus persicae.

sites. Gynoparae begin arriving on peach trees in mid-September (Tamaki et al. 1967) where they deposit wingless sexual females (oviparae). The arrival of males is synchronized with the maturation of oviparae. Mating and oviposition occur in mid-October.

Mature oviparae move from the leaves to branches where they deposit eggs in crevices and behind buds. Oviparae must migrate past the abscission zone to the stem before leaves fall or the number of eggs deposited will be reduced. According to Tamaki (1973b), early leaf fall is an important factor in suppressing aphid populations.

Eggs begin hatching in late February and continue to hatch through March (Davis and Landis 1951, Tamaki 1973a). The developmental period of the stem mother (fundatrix) is about 30 days, and the average reproductive period is about 20 days (Davis and Landis 1951). The stem mothers give rise to a series of agamic generations, and in the third generation some individuals develop into winged migrants.

The aphid population on peach trees reaches a maximum in late May, and then declines rapidly (Tamaki 1973a). Winged migrants populate a variety of herbaceous hosts, including weeds and vegetable crops. Their apterous offspring reproduce parthenogenetically throughout the summer until environmental conditions again trigger the initiation of the sexual cycle.

The Yakima Valley is influenced by a continental (cold temperate) climate, and successful overwintering by parthenogenetic forms of M. persicae is generally not possible under such conditions (Blackman 1974), although sheltered habitats do exist in which anholocyclic overwintering takes place. Drainage ditches which are fed by warm springs remain warmer than the surrounding environment and aphids in all stages of development have been found on secondary hosts in winter. Many of these hosts are also

reservoirs of beet western yellows virus, and aphids migrating from them in spring are highly infective (Wallis 1967a).

B. Host Plants

The green peach aphid has been found on at least 560 plant species representing 93 families (Leonard et al. 1970). Although the host range is extensive, there is considerable variation in the ability of this aphid to reproduce on different species (van Emden et al. 1969). The reproductive potential of the green peach aphid has been studied most extensively on cultivated crops. Heathcote (1962) examined reproduction on 11 cultivated varieties and found plants of the genus Brassica to be the best hosts. Other studies (Cook and Sylvester 1961, Chang 1968, Lowe 1973) have confirmed that cruciferous crops are highly suitable hosts for M. persicae.

Less attention has been given to the relationship of green peach aphid to its wild herbaceous hosts. Tamaki and Olsen (1979) evaluated the suitability of several weed species as hosts of M. persicae and found that reproduction on wild plants can be as high as or higher than on preferred cultivated crops. Crucifers (Cardaria draba (L.) Desv., Capsella bursa-pastoris (L.) Medic., and Lepidium perfoliatum L.) were good hosts, as were common mallow (Malva neglecta Wallr.) and field bindweed (Convolvulus arvensis L.).

Field observations have indicated that green peach aphid prefers members of the mustard family. Mustards are the most important overwintering hosts in the anholocyclic life cycle in Florida (Chamberlin 1950) and New Zealand (Lowe 1972). Wild mustards contribute to the spring buildup of green peach aphid populations in Maine (Simpson

et al. 1945), California (Duffus 1971), and the Pacific Northwest (Wallis 1967b).

Other plants on which populations of green peach aphids have been found include Chenopodium spp. (Simpson et al. 1945, Duffus 1971, Tamaki 1975, Tamaki and Olsen 1979), Malva spp. (Duffus 1971, Tamaki and Olsen 1979), Amaranthus spp. (Wallis 1967b, Tamaki 1975, Tamaki and Olsen 1979), and Rumex spp. (Duffus 1971).

There is little information on the seasonal occurrence of wild hosts of green peach aphid or host succession in weed communities. Mason (1922) traced the movement of green peach aphid populations throughout the year in Florida. Cruciferous crops such as cabbage, turnip, and rape were colonized in the fall and served as overwintering hosts. Lettuce and flower crops as well as beet and radish were the main hosts in early spring, followed by potatoes. Peppers and egg plant were colonized in June, and weeds served as summer hosts until Crucifers were again available in the fall. The aphids tended to colonize plants when new growth was young and succulent, but left the mature plants rather than remaining on the plants for their entire life.

C. Host Selection

The mechanism by which aphids select their host plants is not well understood, however they are probably unable to discriminate between species prior to arrival on the plant (Kennedy 1976). Host selection seems to depend on arrestant stimuli received from the plant after a period of probing. Aphids sample the vegetation in an area by repeatedly taking off and landing, and the buildup of aphids on preferred hosts has been related to a lower rate of departure than from non-hosts. This behavior has been

observed in M. persicae (Kennedy et al. 1959a), Brevicoryne brassicae (L.) (Kennedy et al. 1959b), and Aphis fabae Scop. (Muller 1958, Kennedy et al. 1959b). Evidence that stimuli received prior to probing are not decisive in host selection is provided by observations of aphids probing on plants they do not colonize and neutral surfaces such as plastic and glass (Kennedy and Booth 1950, McLean and Kinsey 1968, Klingauf 1970).

Following behavioral studies of the pea aphid, Acyrthosiphon pisum L., Klingauf (1978) concluded that host selection is influenced by waxy components of the leaf cuticle. He found that herbicide treatments which altered the waxy layer also affected selection behavior of this species.

Nault and Gyrisco (1966) found that short probes typical of aphids in the selection stage of behavior do not penetrate beyond the epidermis. Hennig (1963), studying A. fabae, found that such probes rarely involve the uptake of plant sap, lending support to the proposition that host discrimination takes place in surface waxes.

McLean and Kinsey (1968), however, found that 70% of pea aphids observed did ingest sap from epidermal or sub-epidermal cells during the first probe, regardless of the host status of the plant. They related continued penetration and ingestion of plant material to reception of proper nutrient stimuli.

Mittler and Dadd (1965) showed that the depth of penetration through parafilm membrane was influenced by the nutrient composition of the diet. This would indicate a definite role for nutrient stimuli at some stage of host selection. Similarly, sucrose (Mittler and Dadd 1963) and amino acids (Harrewijn and Noordink 1971) have been shown to have a stimulatory effect on green peach aphids in artificial diets. A sucrose-amino acid synergism has also

been demonstrated to greatly enhance the acceptability of chemical diets to this species (Mittler and Dadd 1964).

Kennedy has long espoused the importance of nutrient stimuli in host selection. He reviewed the importance of plant condition to infestation (1958), and attributed the preference of M. persicae and A. fabae for growing and senescing leaves to a higher concentration of soluble nitrogen compounds in these tissues.

Kennedy et al. (1950) also stated that the normal association of various aphid life stages with different hosts resulted from the nutrient status of the plant. He concluded, after studying the relations of A. fabae with its primary and secondary hosts, that plant condition was the dominant factor in host selection (Kennedy and Booth 1954).

The role of secondary plant substances in host selection by the green peach aphid is not clear. Eastop (1973) has suggested that host selection in polyphagous aphids is largely a response to positive stimuli. Nault and Styer (1972) found that non-host leaves treated with sinigrin, a mustard oil glucoside, became more acceptable to M. persicae. Yet this compound (Wearing 1968) and other secondary plant substances (Schoonhoven and Derksen-Koppers 1976) have generally been found to reduce the acceptability of chemical diets to the green peach aphid. Thus, it would seem that the location of the substance in the plant or the stage of selection behavior is an important factor in determining the insect's response to such compounds. Indeed, Montgomery and Arn (1973) found that, for Aphis pomi Degeer, phlorizin is neutral in the probing stage of behavior, but is an inhibitor in the ingestion stage.

III. SEASONAL OCCURRENCE OF WEED HOSTS OF GREEN PEACH APHID

A. Materials and Methods

Three peach orchards in the vicinity of Parker, Washington were selected for study. Studies were also conducted at a fourth site on the north bank of the Yost Drain approximately 18 miles south of Yakima, known to be an overwintering site of parthenogenetic green peach aphids in past years.

The size of the study areas varied between orchards depending on the spacing of the trees, however each area was 6 rows wide and 19 trees long. Each tree was numbered according to row and position in the row.

The weed complex at each site was sampled once a week using the following methods: One sample was taken adjacent to each of eight trees selected from a computer generated randomization of tree numbers. Samples were taken in four directions and at two distances from the trunks of selected trees. The first sample was taken east of the selected tree at a distance determined by the formula

$$d = 2/5(x - 2m) + 0.5m$$

where x is the distance to the adjacent tree. The second sample was taken in the same direction but closer to the trunk, at the distance

$$d = 1/5(x - 2m)$$

The third and fourth samples were taken west of selected trees, the third closest to the trunk and the fourth at the longer distance. The fifth through eighth samples were taken in the same manner, beginning on the north side of the selected trunks and moving south. Thus, there were four possible sampling sites between trees, spaced so that the distance between each was equal. This system assured

sampling throughout the range of environmental and cultural conditions in the orchard.

A steel frame 0.25m^2 , located at the appropriate distance from the trunk, delineated the sample plots. An acetate sheet divided into a grid was used to help estimate the percent of the plot covered by each species, and the number of plants of each species was recorded.

Six plants of each species were selected randomly and their heights measured. The number of alate, apterous, and parasitized green peach aphids on each plant was counted. The number of green peach aphids in each plot was estimated by multiplying the mean number of aphids on the six plants of each species by the number of plants of each species in the plot. A stepwise regression analysis (Neter and Wasserman 1974) was used to determine which species accounted for a significant proportion of the variation in the aphid population.

In most cases, whole plants were pulled, measured, and counted, however this procedure could not be used when sampling field bindweed (Convolvulus arvensis L.). This species' viney growth habit and tendency to intertwine with other plants made it impractical to follow all the runners from a single plant. Instead, the number of runners terminating in each plot was counted, and six runners were followed to their base and measured. Since green peach aphids tended to inhabit the succulent growth at the tip of each runner, the number of runners terminating in a plot was considered to be a more reliable measure of available host material than the number of runners originating there.

A modification of this design was used at the Yost Drain. A section of ditch bank 50m long was divided into eight rows each containing 100 0.25m^2 plots. Each of the 800 plots was assigned a number according to row and

position in the row. One plot from each row, selected from a computer generated randomization of plot numbers, was sampled each week. The same sampling procedure described above was used to estimate plant and aphid abundance.

B. Results

Orchard 1.-Flixweed (Descurania sophia (L.) Webb) was the dominant species at this site at the beginning of the study period (April, 1978). Flixweed covered 31.7% of the ground area in samples taken in April (Figure 2). Several other species were also present, but were much less abundant: field bindweed, 0.9% of the area; purple mustard (Chorispora tennella (Pall.)), 0.5%; hoary cress (Cardaria draba (L.) Desv.), 1.3%; lambsquarters (Chenopodium album L.), 0.1%; Canada thistle (Cirsium arvense Scop.), 0.1%, and grasses, 0.3%.

The mustards were the tallest plants in the orchard in April. Flixweed averaged 23.9 cm, purple mustard 26.4 cm, and hoary cress 21.2 cm. Lambsquarters and Canada thistle, by comparison, were only 5.2 and 4.5 cm high, respectively.

Cultivation of the orchard during the first week of May reduced the mean coverage of flixweed to 4%. Some of the less abundant species, including the other mustards, were eliminated from the study area. Flixweed was 47.4 cm high in May, which was near its maximum.

Few aphids were found in April, and the green peach aphid population was estimated to be only 0.4 aphids/m² at the end of the month (Figure 3). The green peach aphid population increased rapidly in May, and peaked at 3,680 aphids/m² in the last week of May, despite the fact that the abundance of the dominant host, flixweed, had been

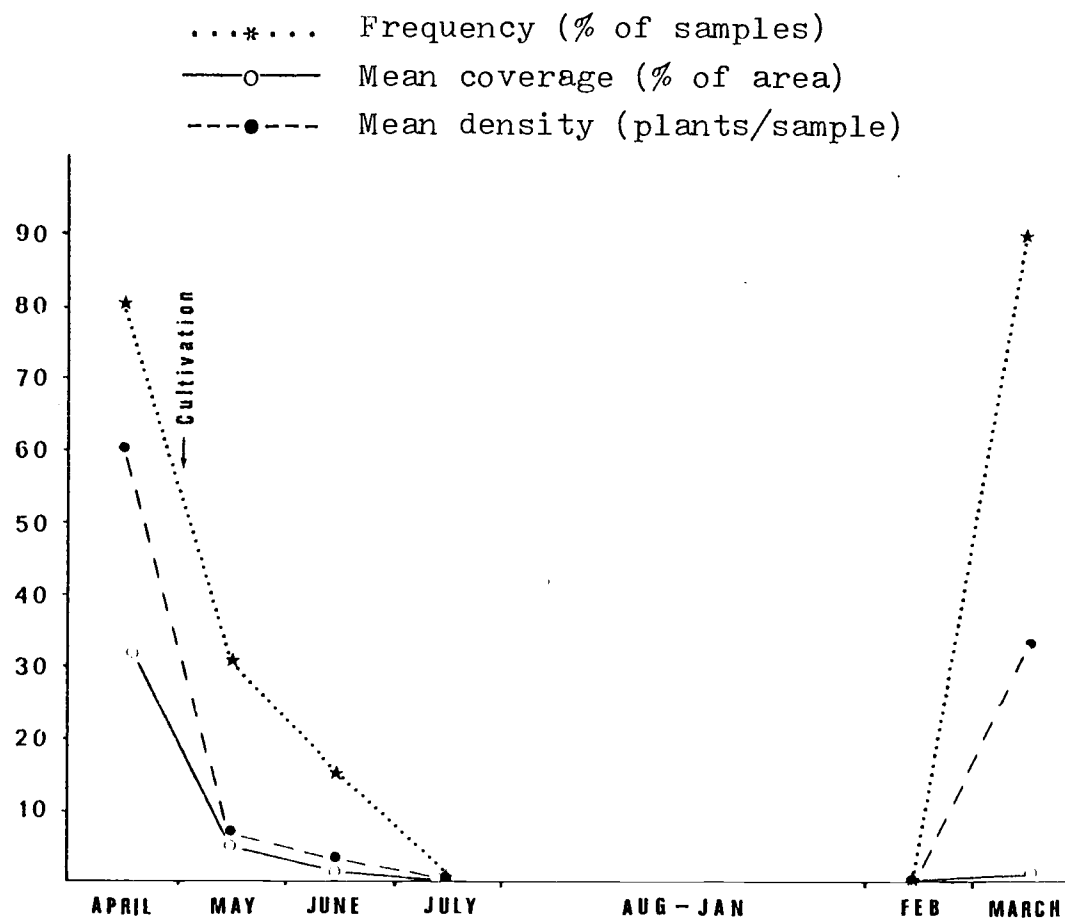


Figure 2. Occurrence of flixweed at Orchard 1.

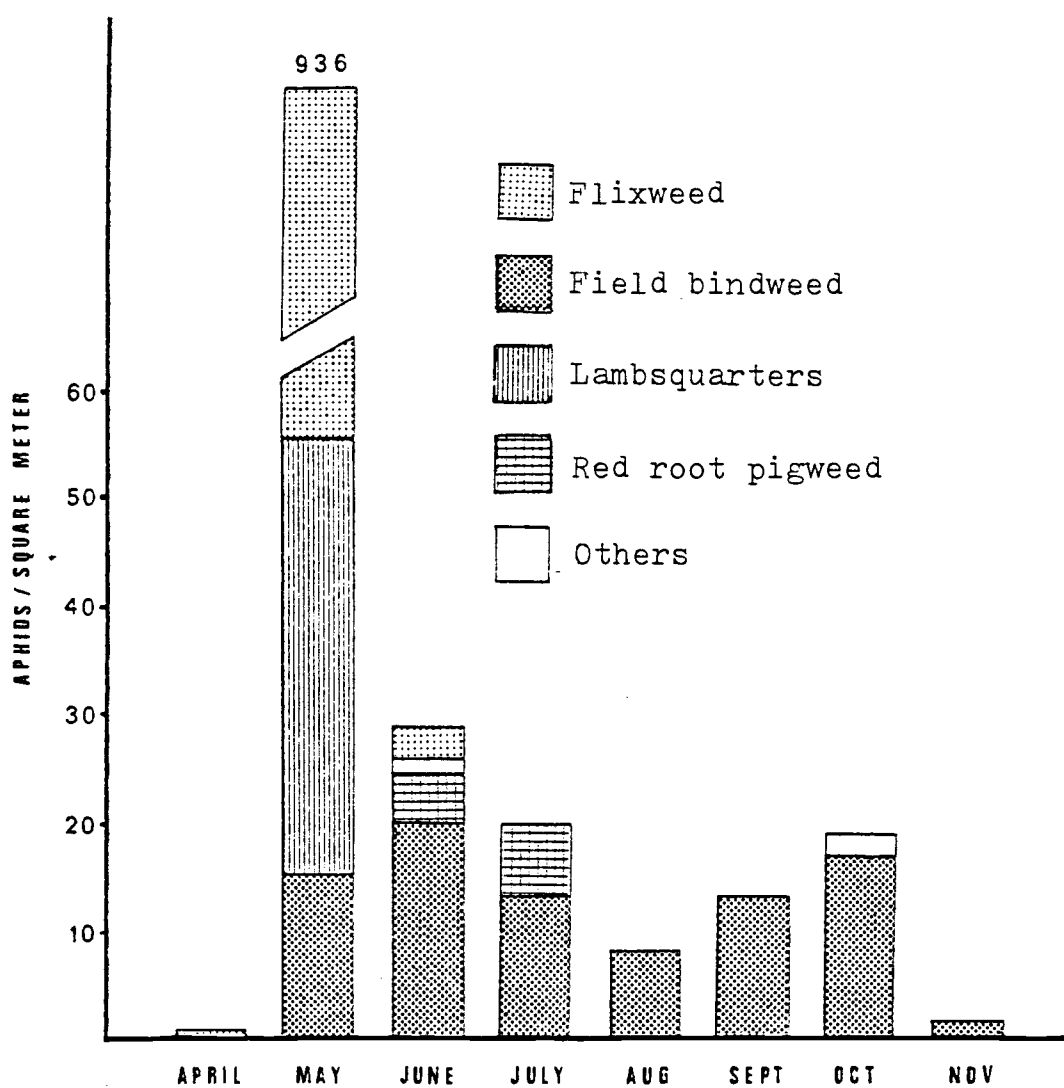


Figure 3. Green peach aphid populations at Orchard 1.

drastically reduced by cultivation.

Ninety-four percent of the green peach aphids were inhabiting flixweed, which averaged 132.7 aphids/plant. The remainder were distributed on field bindweed and lambsquarters. Sixty-nine percent of the variation in the green peach aphid population in samples taken in the last three weeks of May was associated with variation in the abundance of flixweed, a highly significant correlation ($p = 0.01$).

Flixweed was present in samples until the third week of June, but was drying and generally in poor condition. It covered only 1.8% of the study area, and the mean density dropped to 13.6 plants/m² as compared to 25.6 in May. By the first week of June it was no longer a suitable host of green peach aphid, since the number of aphids/plant decreased to 0.3 from the peak of 132.7 the week before.

Field bindweed and grasses became codominant in June, covering 8.3 and 8.5% of the study area, respectively. Canada thistle reappeared in samples in June, and red root pigweed (Amaranthus retroflexus L.) appeared for the first time. Hoary cress was the only mustard eliminated by cultivation which reappeared in the samples.

Grasses and field bindweed reached maximum abundance in August, when field bindweed covered 22% of the study area (Figure 4) and grasses covered 27%. These species remained codominant until September, when the annual grasses dried. Many runners of field bindweed were also senescing at this time, although 12.4% of the area remained covered by this species. The area covered by field bindweed was reduced to one percent in November following the onset of sub-freezing night temperatures in late October. Field bindweed was the only species present in

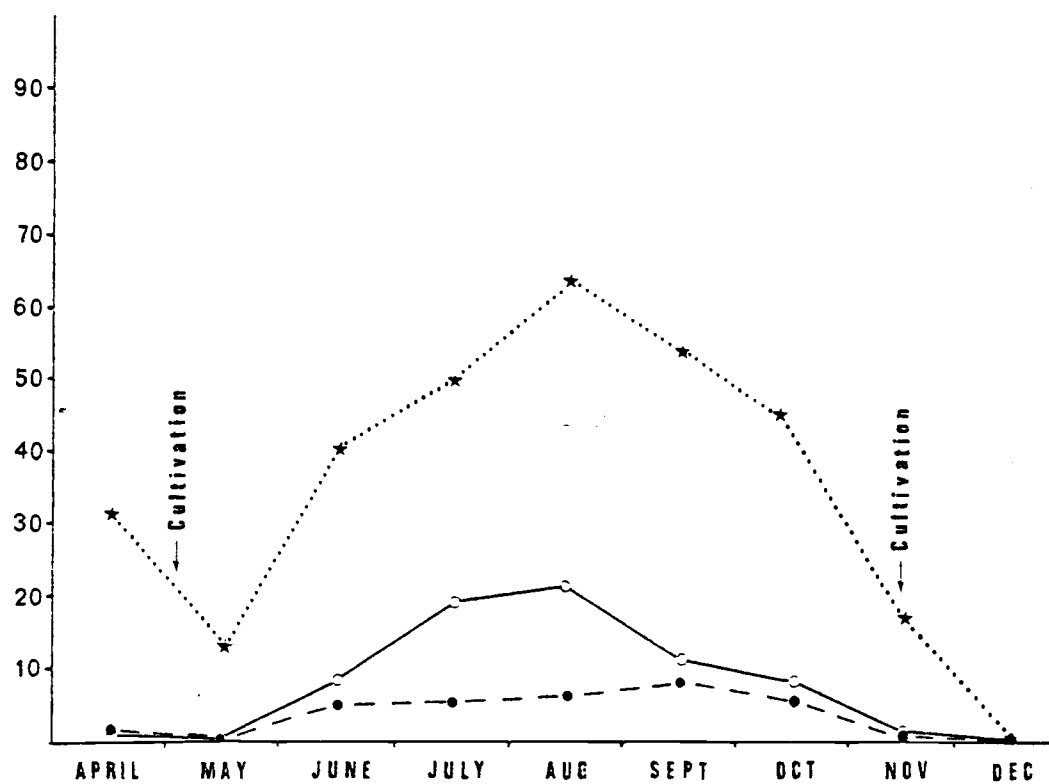


Figure 4. Occurrence of field bindweed at Orchard 1.

....*.... Frequency (% of samples)

—○— Mean coverage (% of area)

---●--- Mean density (plants/ sample)

the orchard in November, when cultivation destroyed all vegetation.

The green peach aphid population never reached the densities recorded in May, and remained low throughout the summer and fall. There was a slight increase in the number of green peach aphids on the orchard floor in the fall as oviparae from fallen leaves migrated to weeds.

Flixweed was the first species found in the orchard in samples taken the following March. Although continued germination increased the mean number of seedlings from 52.4/m² on March 1 to 212/m² on March 22, little increase in height took place during March. The mean height of flixweed seedlings was only one cm on March 22.

Lambsquarters, the only other species present in March, germinated later (appearing March 16) and was less abundant (5.2 seedlings/m²).

Orchard 2.-Sampling was begun at this site a month later than the other sites. The orchard had been clean cultivated in early May, but annual weeds were present by May 16, when sampling was begun. Lambsquarters, which was most abundant on this date, had a mean density of 30 plants/m², covered 1.7% of the study area, and was 4.1 cm high. Nightshade (Solanum sarachoides Sendt.), which apparently germinated later than lambsquarters, had a mean density of 5.2 plants/m², covered 0.2% of the study area, and was 1.7 cm high. By May 23 the mean density of nightshade had increased to 46.4 plants/m². Red root pigweed was found for the first time on this date.

Nightshade, lambsquarters, and red root pigweed formed a relatively stable complex and were present in roughly equal amounts throughout the summer (Figures 5, 6, and 7). Several other species were present in the orchard, but never occurred in more than 6% of the samples during the

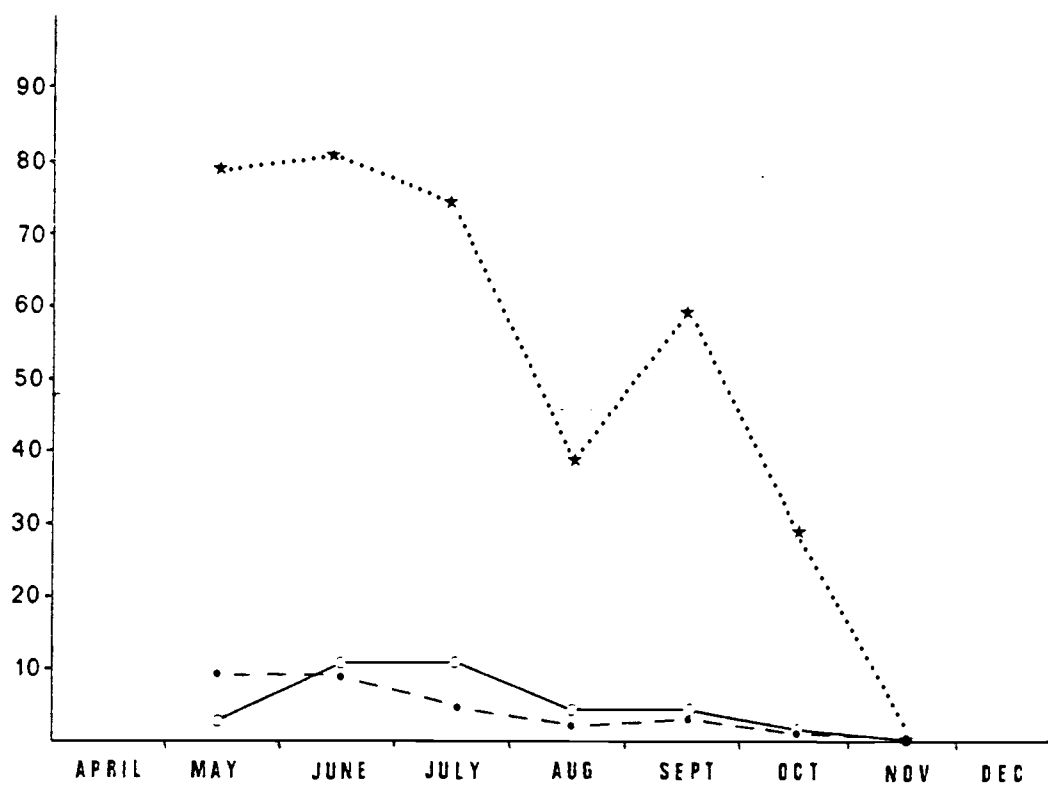


Figure 5. Occurrence of nightshade at Orchard 2.

....*.... Frequency (% of samples)
 —○— Mean coverage (% of area)
 ---●--- Mean density (plants/sample)

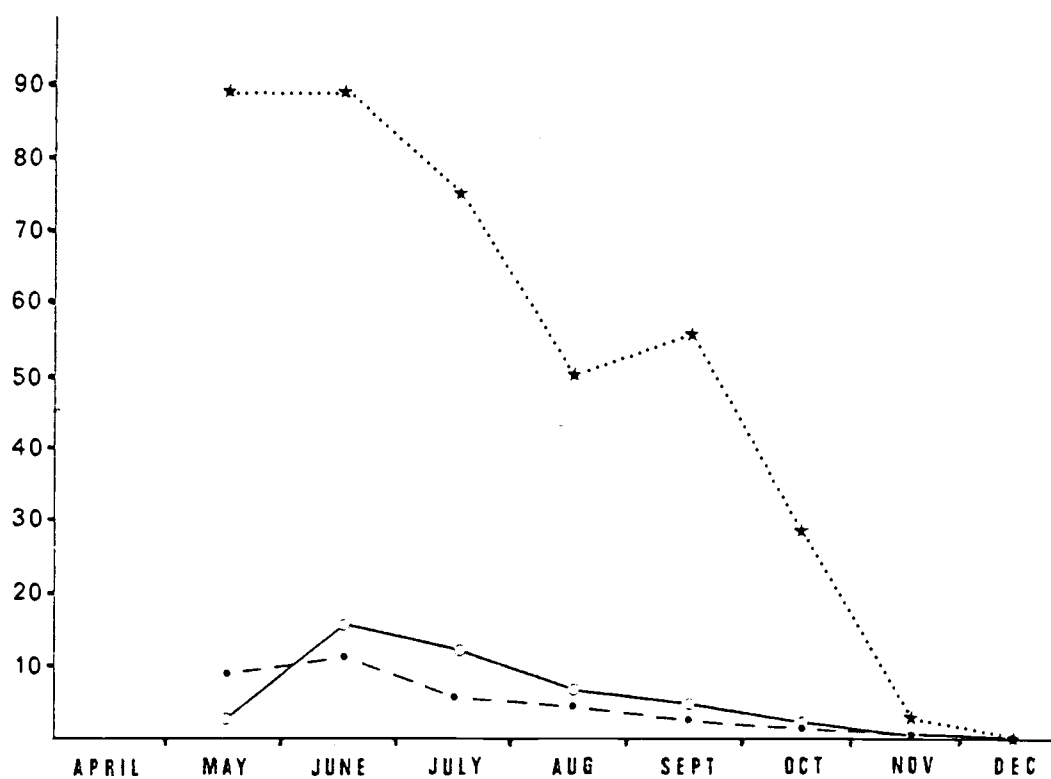


Figure 6. Occurrence of lambsquarters at Orchard 2.

....*.... Frequency (% of samples)

—○— Mean coverage (% of area)

---●--- Mean density (plants/sample)

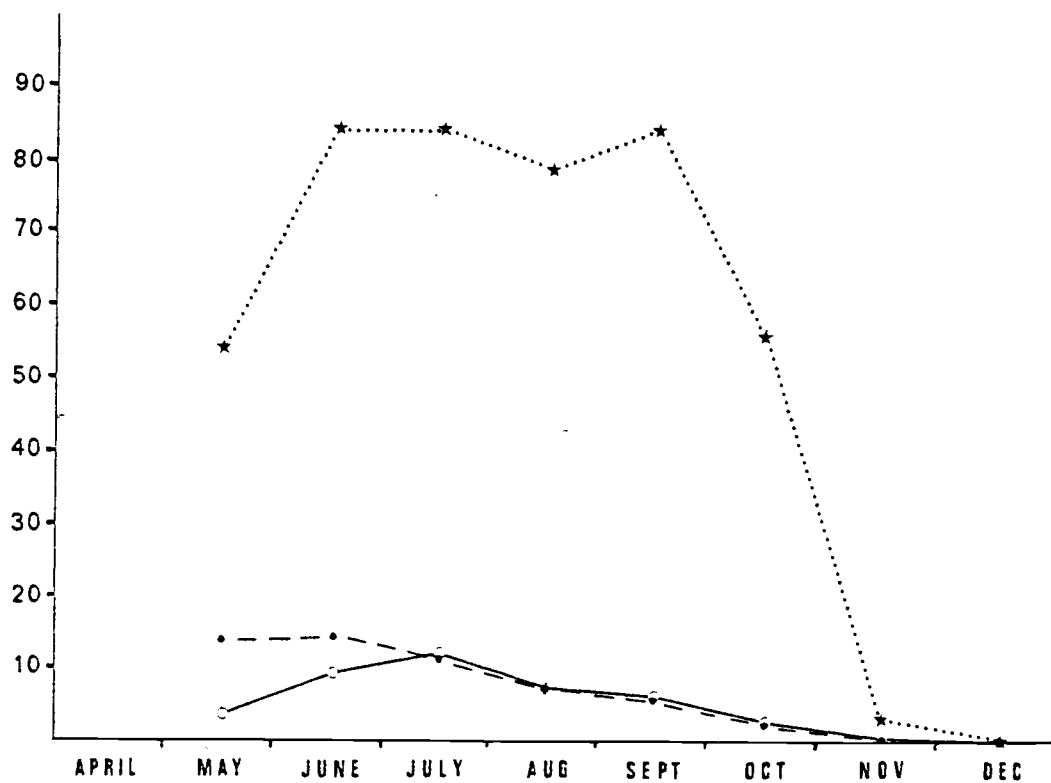


Figure 7. Occurrence of red root pigweed at Orchard 2.

....*.... Frequency (% of samples)

—○— Mean coverage (% of area)

---●--- Mean density (plants/sample)

year. Other species included flixweed, Canada thistle, field bindweed, prostrate knotweed (Polygonum aviculare L.), smartweed (Polygonum persicaria L.), dandelion (Taraxacum officinale Weber), common mallow (Malva neglecta Wallr.), tansy mustard (Descurania pinnata (Walt.) Britt.), and plantain (Plantago lanceolata L.).

There was considerable traffic through the orchard in late July due to harvesting activities, which decreased the abundance of all the dominant species, although red root pigweed was less severely affected than either lambsquarters or nightshade.

Nightshade was the first of the dominant species to die out in the fall, and did not appear in samples taken after October 18. Some red root pigweed and lambsquarters remained in the orchard until mid-November.

The aphid population on the orchard floor reached maximum density later than in Orchard 1, and remained at higher densities throughout the summer (Figure 8). The highest densities of green peach aphids were found on nightshade, but some aphids were also found on lambsquarters and red root pigweed. The number of green peach aphids in samples was significantly correlated ($p = 0.01$) with the abundance of nightshade as long as nightshade was present in the orchard (Table 1). Other species did not contribute significantly to the variation in the green peach aphid population.

Plantain was the last species to be frozen out, remaining in the orchard until December 8. Dandelion was the first of the perennials to begin regrowth in spring, appearing in samples March 1.

The order of appearance of annuals on Orchard 2 was the same as Orchard 1. Flixweed germinated first, appearing in samples March 9. Lambsquarters followed, appearing March 16. The germination of flixweed at this site was

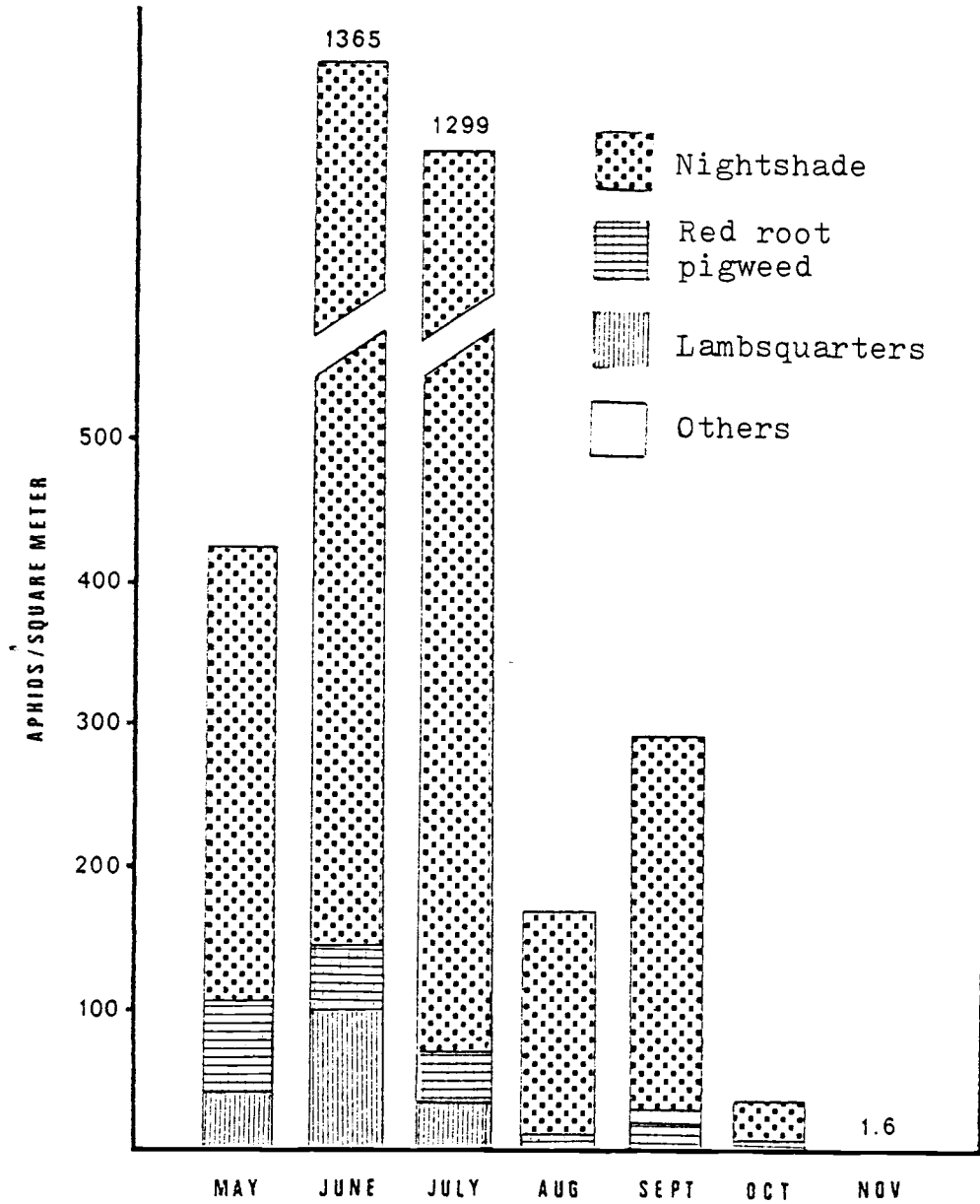


Figure 8. Green peach aphid populations at Orchard 2.

TABLE I. CORRELATION BETWEEN ABUNDANCE OF NIGHTSHADE AND ESTIMATED GREEN PEACH APHID POPULATIONS AT ORCHARD 2.

Month	r ²	df
May	.67**	21
June	.76**	28
July	.27**	28
Aug.	.63**	24
Sept.	.28**	28
Oct.	.56**	19

**Indicates statistical significance at the .01 confidence level.

later than at Orchard 1. Since Orchard 2 was not fall cultivated, as was Orchard 1, a thick carpet of peach leaves still covered the orchard floor in March. This no doubt had a suppressant effect on early germinating annuals, both by retarding the increase of soil temperatures and smothering small seedlings.

Orchard 3.-The weed complex at Orchard 3 consisted mainly of perennial weeds, the most abundant of which were field bindweed, dandelion, common mallow, and grasses (Figures 9, 10, and 11). Clovers (Trifolium spp.) were also present but were not abundant and occurred irregularly in samples.

Prostrate knotweed was the most abundant annual species in the orchard and occurred in more than 20% of samples during the summer (Figure 12). Lambsquarters and red root pigweed, in contrast, were found in less than 10% of the samples.

Field bindweed and knotweed predominated within rows, while dandelion and mallow were more common between rows.

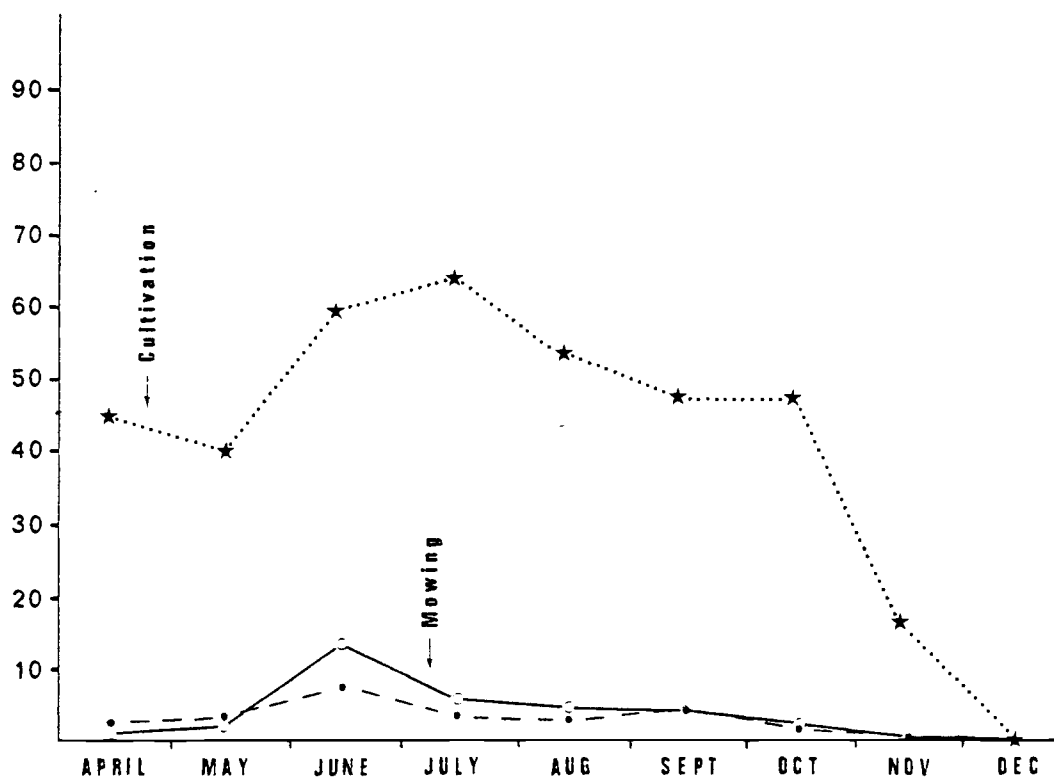


Figure 9. Occurrence of field bindweed at Orchard 3.

- ...*... Frequency (% of samples)
- o— Mean coverage (% of area)
- Mean density (plants/sample)

....*.... Frequency (% of samples)
 —○— Mean coverage (% of area)
 ---●--- Mean density (plants/sample)

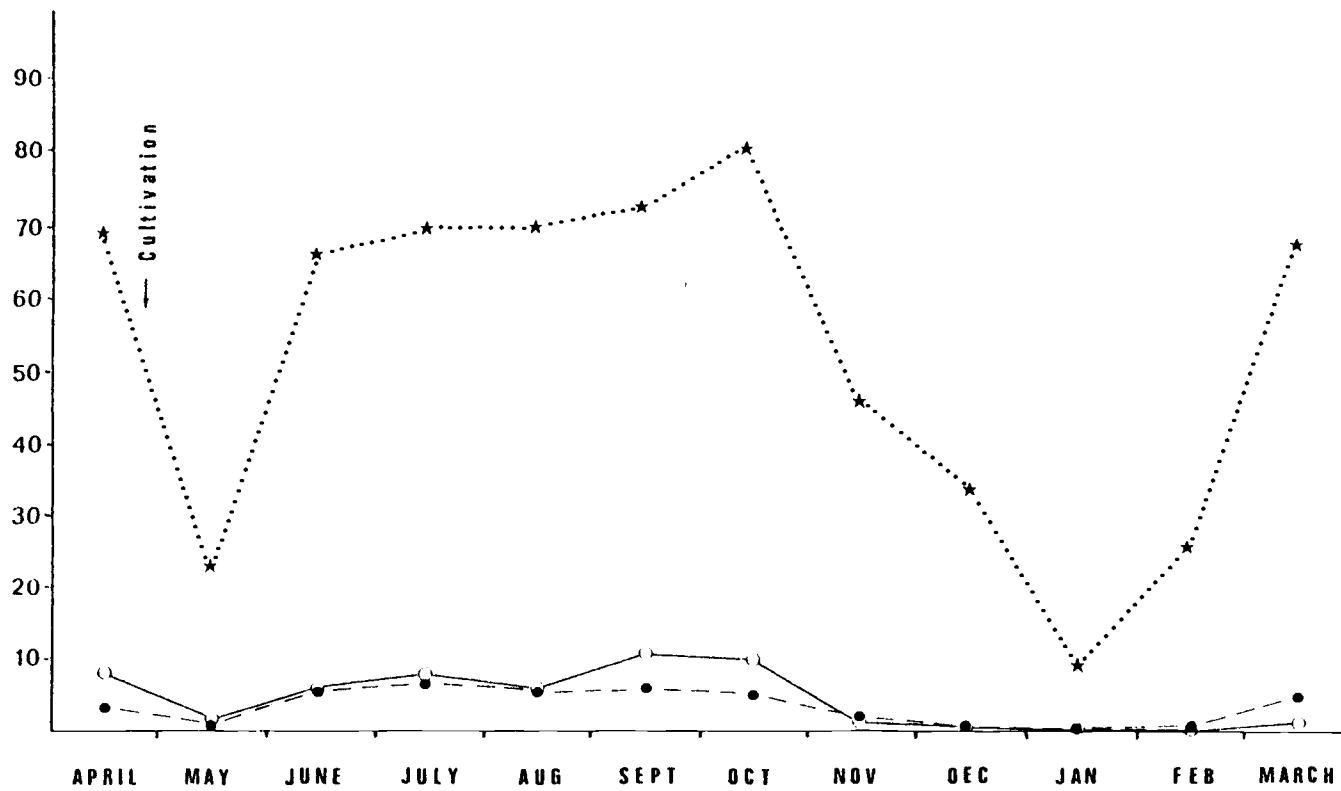


Figure 10. Occurrence of dandelion at Orchard 3.

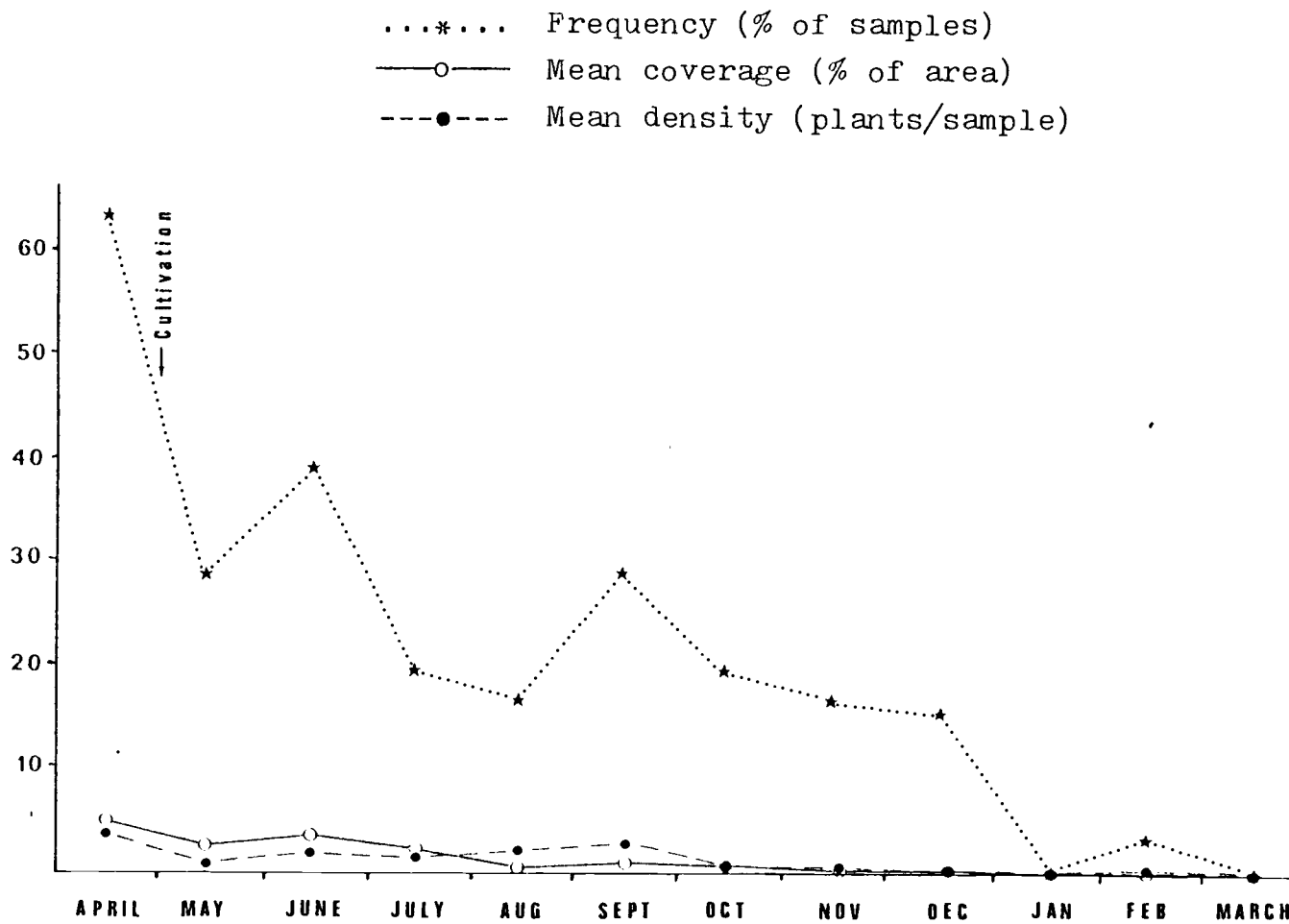


Figure 11. Occurrence of mallow at Orchard 3.

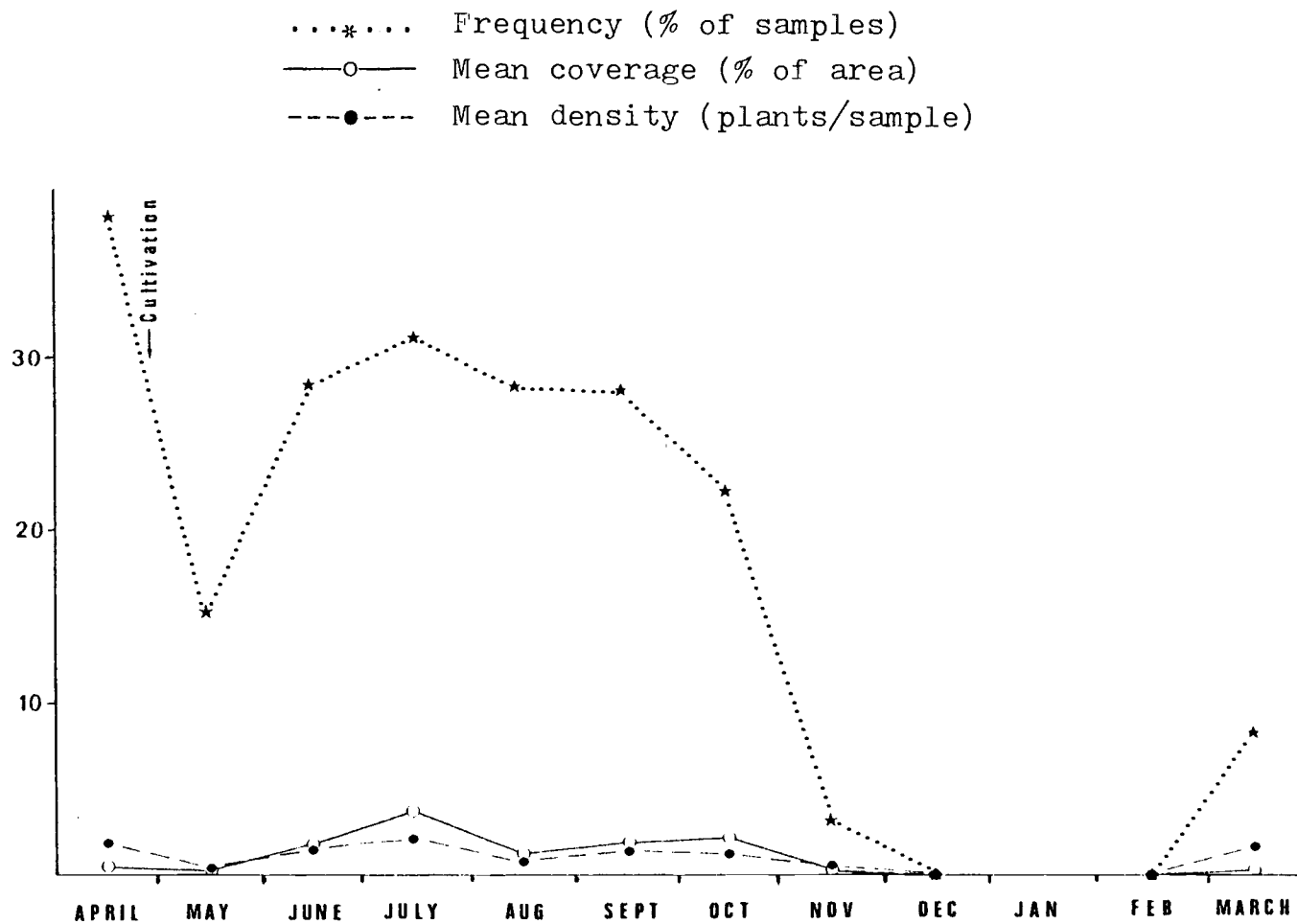


Figure 12. Occurrence of prostrate knotweed at Orchard 3.

Knotweed appeared to be the least competitive of the dominant species, and in late summer and fall became restricted to shady areas within rows not colonized by field bindweed or grasses.

Mallow and dandelion are both low-growing species, However dandelion appeared to be more tolerant of shading than mallow. The area covered by mallow began to decline in July as taller growing plants such as grasses and climbing runners of field bindweed shaded much of the area. Mowing also had less effect on dandelion, as dandelion leaves tend to remain low, out of the reach of mower blades.

Some dandelion and mallow remained in the orchard throughout the winter, however plants were small and restricted to areas where a thick cover of fallen peach leaves provided insulation.

The green peach aphid population remained at much lower densities at this site than at Orchards 1 and 2 (Figure 13). This may be due to the species composition of the area. Tamaki and Olsen (1979) found that reproduction of green peach aphid in the field is significantly lower on bindweed and mallow than on either mustards or nightshade. Bindweed did not support large numbers of green peach aphids at any time in Orchard 1, and only during the spring buildup in Orchard 3 were populations on bindweed moderately high. Although bindweed supported most of the green peach aphids in the area, variation in the population at this site was not consistently correlated with the abundance of any particular species. This may have been due to a lack of population pressure which did not stimulate dispersal, resulting in a patchy distribution of the population and less than full utilization of available hosts.

Yost Drain.-Hoary cress was the dominant species on

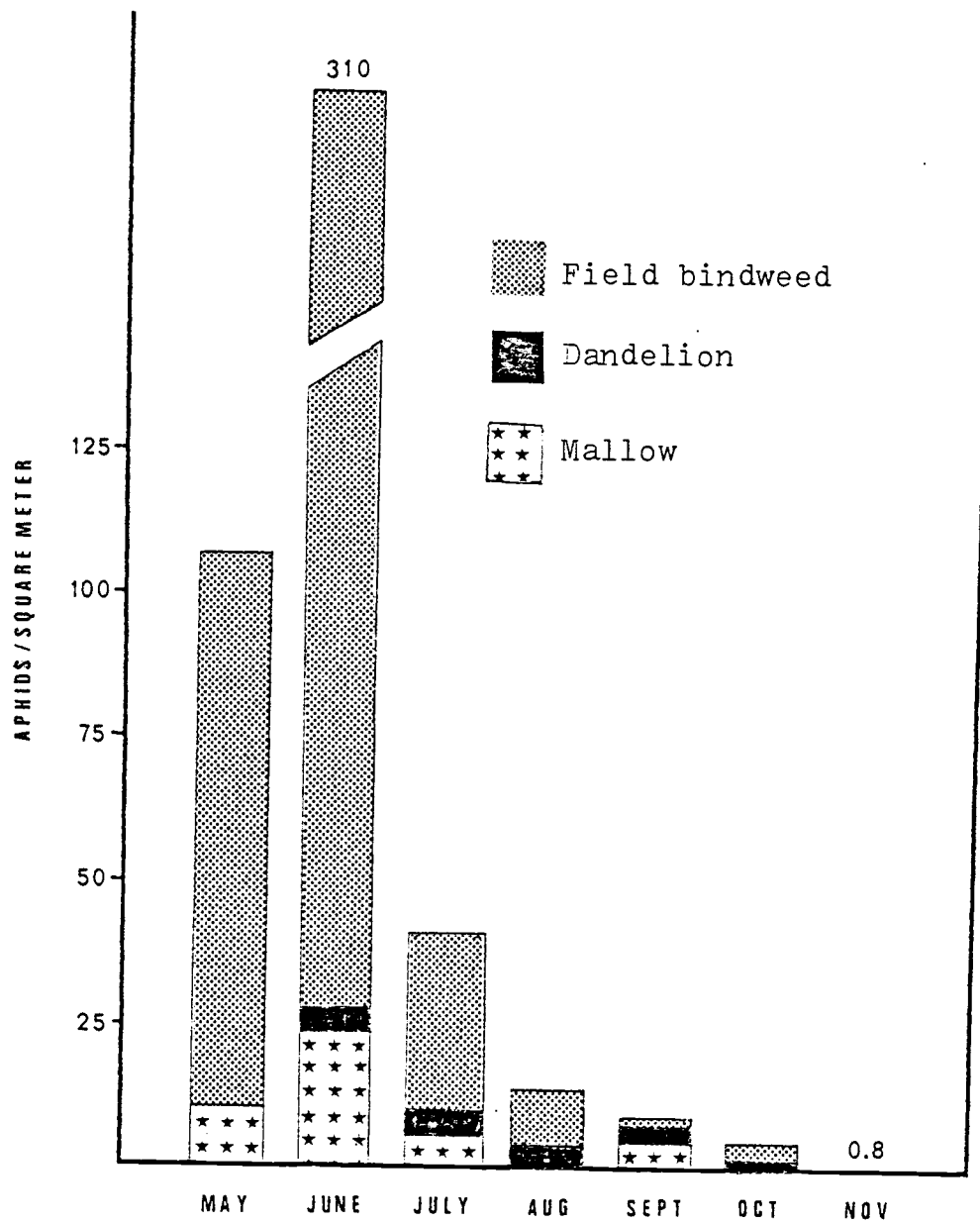


Figure 13. Green peach aphid populations at Orchard 3.

the drain bank. It occurred in 100% of samples taken in April and covered 58.4% of the bank (Figure 14). Hoary cress was taller on the drain bank than in Orchard 1, averaging 41.3 cm high in April as compared to 21.2 cm. In May the mean coverage reached 64.9% and the mean height was 49.2 cm.

The decline of hoary cress began in June, when the tall flowering stalks dried and went to seed. Regrowth from the base of the plant began in July, and the abundance of hoary cress increased through late summer and early fall. Plants remained small, however, as growth was limited to basal leaves and height never exceeded ten cm for the remainder of the year.

A 12.4 cm snow fall in mid-Novemeber caused a decline in the abundance of hoary cress which continued until the first week of February. Although night temperatures were often below -6.7°C. in November and December, hoary cress did not become dormant and showed consistent regrowth during warmer periods. The north bank of the ditch receives direct solar radiation in winter as the sun remains low on the southern horizon. Thus the north bank is suitable for the growth of hoary cress during much of the winter while the south bank remains frozen and lifeless.

Another 25.4 cm of snow fell in mid-January and the north bank remained covered with snow until the second week of February. Most hoary cress plants were frozen, although a few plants which were sheltered under the debris of the previous summers' growth remained green.

Vigorous regrowth began in mid-February, although it was limited to basal leaves and there was little increase in height (from 3.2 cm on February 16 to 8.8 cm on March 22). Hoary cress seedlings began to appear the first week

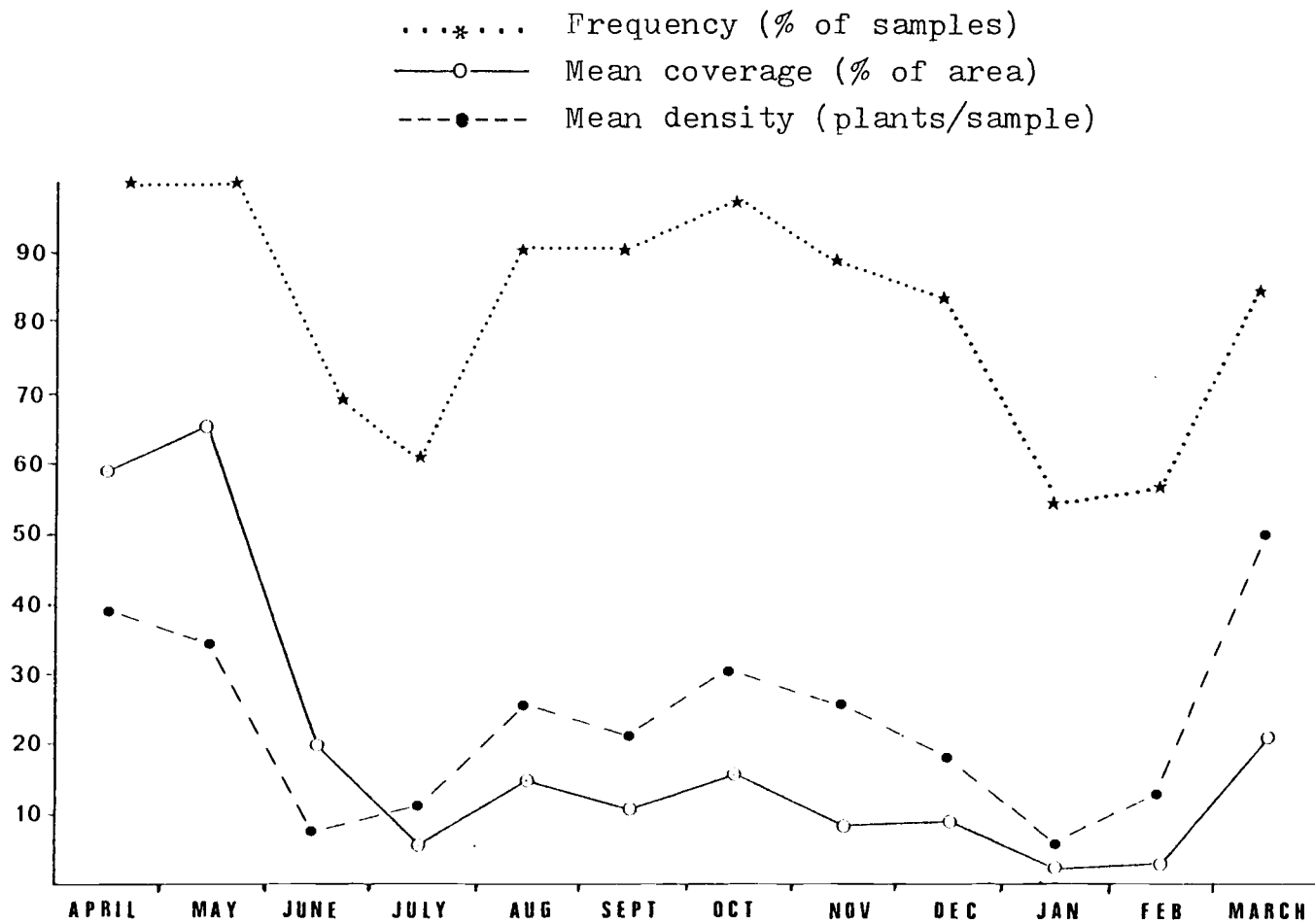


Figure 14. Occurrence of hoary cress at Yost Drain.

of March, but were never as abundant as plants growing from perennial roots.

Flixweed and yellow-flowered pepperweed (Lepidium perfoliatum L.) were also present on the ditch bank, but did not exceed one percent coverage at any time during the study. Flixweed seedlings on the ditch bank were also taller than their counterparts in the orchard, averaging 6.5 cm as compared to one cm on March 22.

Canada thistle and curly dock (Rumex crispus L.) were common near the water, and Canada thistle reached maximum abundance in September, covering 6.4% of the area.

Atriplex patula var. hastata (L.) Gray and Russian knapweed (Centaurea repens L.) were interspersed with hoary cress on the bank. Russian knapweed reached maximum abundance in May (2.5% of the area) and Atriplex reached maximum abundance in July (3.7% of the area).

Other species which were found occasionally at this site were prostrate knotweed, bassia (Bassia hyssopifolia (Pall.) Kuntze), Russian thistle (Salsola kali L.), milkweed (Asclepias speciosa Torr.), prickly lettuce (Lactuca serriola L.), and annual sow thistle (Sonchus oleraceus L.).

Few green peach aphids were found at any time in the ditch. The maximum estimated green peach aphid population occurred in April, with a density of 13.6 aphids/m². This dropped to 3.6 in May, and none were found in June. No green peach aphids were found again until September, when the population was estimated to be four aphids/m². The population decreased to 0.8/m² in October, and none were found after October 27.

C. Discussion

Green peach aphid populations on the floor of all three orchards peaked in spring and declined in summer.

In this study, the reason for the decline of the aphid populations could not be clearly established. Predators were most abundant during mid-summer at all sites, as was evidence of parasite activity (Table 2), yet predators and parasites were not abundant enough to cause the rapid declines observed in the green peach aphid populations.

Mid-season declines in aphid populations have been reported in several species. Perrin (1976) found that self-induced regulation was more important than predation in the population decline of Microlophium carnosum (Buckt.) even though the host plant, nettle, supported a rich aphidophagous fauna. Effects of aphid feeding on the host plant and reduced vigor of the population were cited as factors causing decline.

Dixon (1977) concluded that predators and parasites were not important in regulating populations of Eucallipterus tilae L. Mid-season population decline occurred even in the absence of predators, and was attributed to reduced vigor among the aphid population.

High temperature, reduced food quality, and predation were cited as factors in the decline of populations of Chromaphis juglandicola (Kalt.) in California during June and July (Sluss 1967). Declines did occur, however, in areas where predators were not active.

On the floor of Orchard 1, there was a sharp increase in the population to a high level, followed by a sharp decline with no resurgence of the population. Predators did not play a key role, and the decline of the aphid population paralleled a decline in host quality, in this case the death of flixweed.

The behavior of the green peach aphid population at Orchard 2 was characterized by a slower increase to high levels, followed by a sharp decline, with predation and parasitism contributing to the decline. In September

TABLE II. TOTAL NUMBER OF PREDATORS AND PARASITIZED GREEN PEACH APHIDS FOUND IN SAMPLES IN THREE ORCHARDS.

Orchard 1				
Month	Syrphid larvae	Coccinellids (all stages)	Parasitized green peach aphids	# of samples
April	0	0	0	16
May	0	0	6	32
June	0	2	3	40
July	0	0	2	32
Aug.	0	0	0	24
Sept.	0	0	0	40
Oct.	1	0	1	32
Nov.	0	0	0	32
Orchard 2				
Month	Syrphid larvae	Coccinellids (all stages)	Parasitized green peach aphids	# of samples
April	-	-	-	-
May	0	0	4	24
June	5	19	48	32
July	3	13	82	32
Aug.	5	0	55	32
Sept.	5	0	3	32
Oct.	0	0	4	32
Nov.	0	0	0	32
Orchard 3				
Month	Syrphid larvae	Coccinellids (all stages)	Parasitized green peach aphids	# of samples
April	0	0	0	16
May	0	0	5	40
June	3	1	8	32
July	0	1	9	32
Aug.	0	0	4	32
Sept.	0	0	0	32
Oct.	0	0	0	32
Nov.	0	0	0	32

there was a moderate resurgence of the population.

Host plant quality may be the dominant factor affecting the aphid population at this site, as there was a visible decline in the quality of nightshade plants in late July. Heavy traffic through the orchard during harvest had a severe effect on nightshade, and resurgence of the green peach aphid population could be associated with the recovery of nightshade plants following harvest.

The situation is less clear at Orchard 3. The low green peach aphid population can not be attributed to the activity of natural enemies. Species and condition of host plant and their effects on multiplication rate may be the most important factors influencing populations of M. persicae (van Emden and Way 1973, Dixon 1977). Tamaki and Olsen (1979) have shown that the multiplication rate of green peach aphid in the field is significantly lower on bindweed and mallow than on mustards and nightshade. Species composition of the host complex is the only apparent explanation for the low population levels at this site.

Aphid populations in the Yost Drain were low throughout the year. Wet spring conditions in 1978 resulted in a higher than normal incidence of fungus which reduced the aphid population (Tamaki, personal communication). The drying of host plants precluded any recovery by the population. Aphids did not reappear until fall, when migrants reinfested the ditch, however they were again eliminated by colder than normal temperatures during the winter.

Wallis (1967a) attributed winter survival of parthenogenetic forms of green peach aphid to the moderating effect of warm springs which feed the drainages. He stated that water in the ditches did not freeze even when

temperatures dropped to -27.2°C . The winter of 1978-79 was unusually cold, however (maximum temperatures did not exceed freezing at any time during January), and the water in the ditch did freeze adjacent to the sampling site. The soil of the north bank remained unfrozen during clear periods and hoary cress plants showed active regrowth following freezing, undoubtedly due to differential warming of the north bank by the low winter sun. In milder winters, the warming effect of direct solar radiation no doubt contributes to the suitability of this site for anholocyclic overwintering by M. persicae.

IV. FEEDING PREFERENCES

A. Settling Behavior In a Laboratory Choice Chamber

Kennedy (1950) investigated the feeding preferences of A. fabae using two-leaf choice cages on growing plants in the field or greenhouse. Weather was a major factor influencing the results of these tests, particularly the amount of solar radiation and its effect on aphid activity. Changes in activity levels affected the degree to which preferences were expressed, therefore preferences could be determined but no conclusions could be made regarding the strength of preferences.

Dixon (1971) used a similar method to examine the feeding preferences of Rhopalosiphum padi L. Aphids were offered a choice between two leaves in a clip cage attached to the leaves of potted plants. No attempt was made to standardize the amount of leaf area offered in these tests.

Since the green peach aphid colonizes a wide range of secondary hosts, it was desirable to determine not only the nature of its preferences, but also the relative strength of those preferences. A method was needed in which aphids could be offered choices under uniform conditions with an equal opportunity to sample both types of host tissue. The following technique was used.

Materials and Methods.-Four discs two cm in diameter were cut from mature leaves of corn and radish plants. The discs were placed alternately around the perimeter of a plastic petri dish on moist filter paper.

Ten adult apterous green peach aphids were removed from their feeding sites on radish leaves with a camel's hair brush and placed in the center of the dish. Another petri dish bottom was inverted over the top and the chamber

TABLE III. SETTLING BEHAVIOR OF GREEN PEACH APHID IN A LABORATORY CHOICE CHAMBER

Elapsed Time (Min.)	Arrivals on radish	Departures from radish	Arrivals on corn	Departures from corn
5	17	0	17	0
10	12	3	7	6
15	8	5	3	7
20	4	5	1	6
25	6	2	3	4
30	7	1	4	4
35	2	4	2	4
40	7	1	3	4
45	2	1	3	4
50	3	2	1	3
55	1	0	1	0
60	4	1	1	1
65	6	1	2	2
70	5	0	1	1
75	2	1	0	1
80	2	1	0	2
85	0	0	1	0
90	3	2	1	1
Sum	91	30	51	49

was sealed with masking tape to prevent escape of the aphids.

Aphid behavior was observed, and counts of the number of aphids which had settled on each disc were taken at five minute intervals for 90 minutes. Positive changes in the number of aphids on a leaf disc were recorded as arrivals; negative changes were recorded as departures. The test was replicated eight times.

Results.-Aphids were unable to discriminate between hosts prior to arrival on the leaf discs. After five minutes there there was an equal number of aphids on each host (Table 3).

As is the case with A. fabae (Kennedy and Booth 1950),

M. persicae expresses its preferences through "kinesis" rather than "taxes." Aphid buildup on radish resulted from a lower rate of departure from radish than from corn, on which the number of departures nearly equaled the number of arrivals. As a result of the fact that radish is a stronger arrestor of movement than corn, 78% more arrivals were recorded on radish. Nearly all aphids which arrived on corn left within 90 minutes and wandered in the chamber until arriving on a radish leaf disc. Only 32% of green peach aphids arriving on radish departed, however, and the majority arriving on radish first remained there and did not sample other discs. The number of aphids settled on radish was positively correlated with elapsed time (Figure 15).

Discussion.-This method proved satisfactory for examining feeding preferences of the green peach aphid in the laboratory. Because of its simplicity and the ease with which aphids can be observed, the technique was adopted for the remaining experiments described below. The short duration of such tests makes the leaf disc method practical, allowing an examination of feeding preferences in a standardized manner under a uniform laboratory environment.

B. Comparison of Life Stages

Little is known about the factors which influence the green peach aphid to return to its primary host. Kennedy and Booth (1951) have suggested that aphids respond to nutritional changes in plants, and leave the primary host as its leaves mature, becoming less suitable for growth and reproduction. The senescence of its leaves in the fall allows colonization by returning migrants.

Their research indicates that for A. fabae, condition

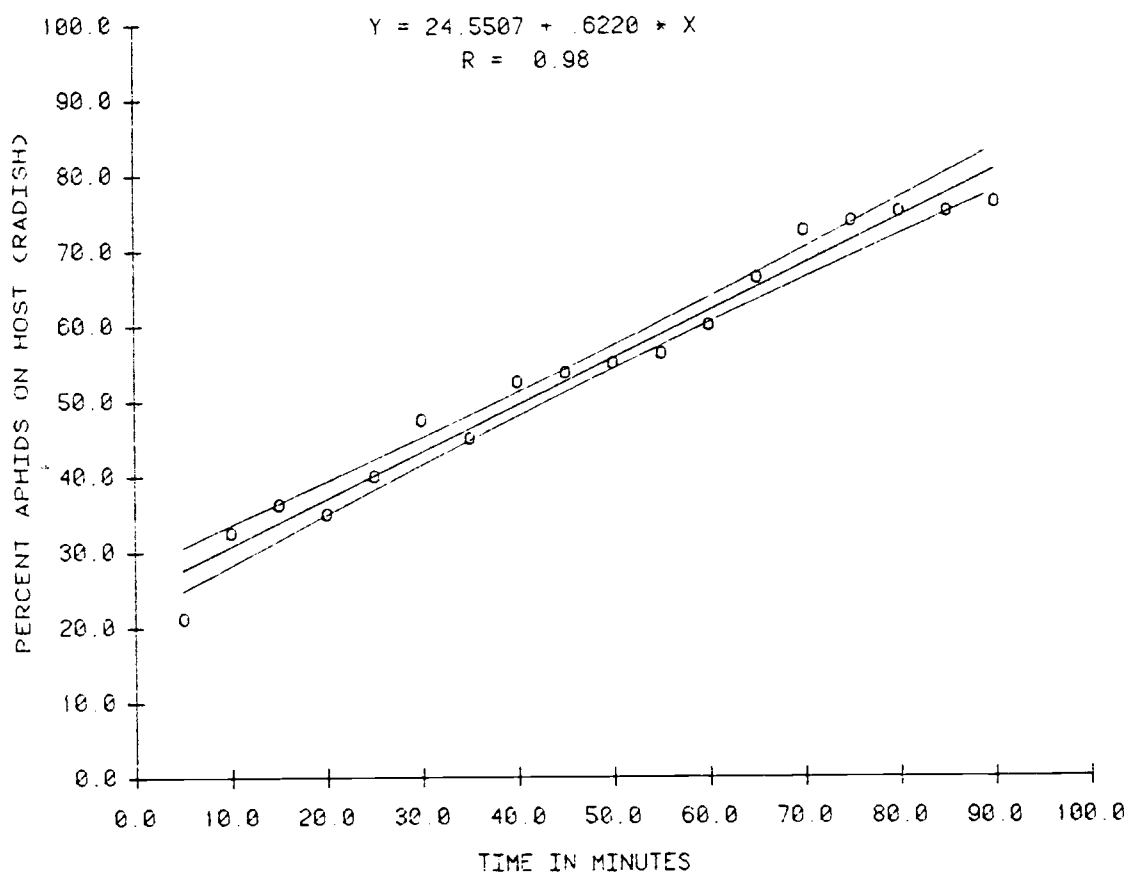


Figure 15. Rate of settlement by Myzus persicae in a laboratory choice chamber.

of the host plant is the dominant factor in host selection. All life stages tested showed an intrinsic preference for the winter host, Euyonemus spp. (Kennedy and Booth 1951, 1954).

Dixon (1971) however found life stages of the bird cherry-oat aphid, R. padi, to have differing preferences. Apterous summer forms preferred oats in behavioral trials, while gynoparae showed a strong preference for bird cherry, the winter host. He concluded that a basic change in the aphid's feeding preferences resulted in host alternation.

The following tests were conducted to determine the feeding preferences of various forms of the green peach aphid and to examine the role of such preferences in host alternation.

Materials and Methods.-Gynoparous and oviparous green peach aphids were collected from naturally infested peach trees in early September. Apterous summer forms were obtained from continuous glasshouse culture where they were reared on hoary cress with a 16 hour photoperiod and a minimum temperature of 24°C.

Leaf discs two cm in diameter were cut from field collected peach and maple leaves, and from the mature leaves of radish plants grown in field plots. Two discs of each species to be compared were placed alternately on moist filter paper in a plastic petri dish ten cm in diameter. Ten green peach aphids were placed in the center of the dish and the chamber was sealed as described previously. The dishes were observed in the laboratory under uniform illumination.

The number of aphids which had settled on each type of host was counted two and four hours after beginning the test. Each test was replicated ten times and each replicate was rotated 90° relative to the preceeding replicate to compensate for positional effects. A "T"

test was used to determine if the settling behavior of the aphids differed significantly from a random distribution.

Results.-When given a choice between radish and peach, gynoparae and oviparae as well as apterous exules of green peach aphid preferred radish a summer host. The preference was strongest in the apterae and weakest in the oviparae, although in all cases the degree of preference was statistically significant (Table 4).

Gynoparae which were offered leaf discs of peach and silver maple (Acer saccharinum L.) preferred peach, although only 21% of the aphids tested had settled on either species within four hours (Table 5).

Discussion.-These results indicate that feeding preferences alone cannot account for the phenomenon of host alternation by green peach aphid. All life stages tested preferred radish to peach even though the peach leaves were senescent and therefore nutritionally superior to the mature radish leaves (Kennedy and Booth 1951). This would suggest that "flavor" discrimination is more important than "nutritional" discrimination in M. persicae, but still does not explain the return of aphids to peach.

Field observations have shown that gynoparous green peach aphids attempt to colonize a number of tree species and are not particularly selective in alighting (Hill Ris Lambers 1946, Kennedy et al. 1959a). Kennedy has reported that only a small fraction of alighting green peach aphids stay on peach although the rate of departure may be lower than from other species (Kennedy et al. 1959a).

Although all forms of the green peach aphid which were tested preferred radish, a summer host, to peach, gynoparae did discriminate between peach and silver maple, a non-host. Still, only 21% of the aphids had settled in four hours. While feeding preferences may to a limited extent allow this species to discriminate between arboreal

TABLE IV. SETTLING BEHAVIOR OF LIFE STAGES OF M. PERSICAE IN CHOICE CHAMBER (% OF TOTAL ON INDICATED SPECIES).

Time (Hrs.)	Species	Life Stage		
		Apterae	Gynoparae	Oviparae
2	Radish	96	52	52
	Peach	1	16	30
	"T" value	39.15**	3.77**	2.66**
4	Radish	99	61	58
	Peach	0	18	28
	"T" value	99.0**	3.72**	3.58**

**Indicates statistical significance at the 0.01 confidence level.

TABLE V. SETTLING BEHAVIOR OF GYNOPARAE OF M. PERSICAE ON WINTER AND NON-HOST IN CHOICE CHAMBER (% OF TOTAL ON INDICATED SPECIES).

Species	Type of Host	Time	
		2 Hrs.	4 Hrs.
Peach	Winter	20	16
Silver maple	Non-host	4	5
	"T" value	2.85**	1.82*

*Indicates statistical significance at the 0.05 confidence level.

**Indicates statistical significance at the 0.01 confidence level.

species, it is clear from these tests and the field observations of Kennedy et al. (1959a) that peach does not strongly arrest green peach aphid. Therefore it would appear that the aphid relies partly on a "shotgun" approach to host alternation.

The problem of studying host alternation is further complicated when working in agro-ecosystems. Irrigated agriculture provides the green peach aphid with numerous alternate hosts throughout the season. Weeds in all stages of development can be found in irrigated fields and orchards much of the time. In an undisturbed ecosystem the senescent leaves of woody plants may provide the only desirable food source late in the season.

On the other hand, field observations provide evidence that host alternation is not entirely a response to host availability. Kennedy et al. (1959a) found that gynoparous migrants of the green peach aphid avoided potted Brussels sprout plants placed next to peach trees. In the fall of 1978, gynoparae were scarce in radish plants grown in field plots at the Yakima Agricultural Research Laboratory, while peach trees in an adjacent orchard accumulated large numbers.

Another complication of the agro-ecosystem is the tendency to view the return to the primary host as a retreat. Each fall large numbers of migrants accumulate in orchards and their offspring cause serious damage to adjacent fields the following spring. In an undisturbed system the gynoparous population disperse in all directions through a diverse flora in search of the relatively rare primary host. The gynopara is as much an agent of dispersal as its alate viviparous counterpart. A primary host which strongly arrested movement would be a hindrance to dispersal, while a slight preference over other tree species would allow a gradual accumulation on the proper

host over a wide area.

The data also suggest that habituation to the primary host could occur among the members of a migrating population. The preference for radish was strongest among the apterae, which had never been exposed to peach. It was weakest in the oviparae, which had spent their entire life on peach. The gynoparae, which had spent some time on both types of host, were intermediate.

Gregariousness also aids the buildup of aphids on the primary host. Tamaki et al. (1970) found that the settlement rate of male M. persicae was six times higher on apple twigs to which females were glued than on control twigs with no females. Likewise, females were shown to have an aggregating response on peach trees (Tamaki et al. 1973). While feeding preferences contribute to the settling of green peach aphids on peach, it is clear that a number of factors must influence the behavior of the population in its annual migration.

C. Rating of Host Acceptability

Alate aphids are thought to be highly selective and primarily responsible for dispersal and host selection (van Emden et al. 1969). Kennedy and Booth (1954), studying A. fabae, found behavioral preferences were weakly expressed in the apterae. Their conclusion was, that as a specialized food exploiter, rather than selector, the aptera is not particularly demanding of plant flavor.

The green peach aphid, however, is known to be more prone to wander between plants than other aphids (Simpson et al. 1945). An examination of the feeding preferences of the apterous green peach aphid was undertaken to determine if apterae could discriminate between various

plant species.

Materials and Methods.-Adult apterous green peach aphids were obtained from continuous glasshouse culture.

Leaves of Brassica nigra, Brassica oleracea, Solanum tuberosum, Malva neglecta, Amaranthus retroflexus, Chenopodium album, Zea mays, and Taraxacum officinale were taken from field plots. Foliage of Raphanus sativus, Cardaria draba, Solanum sarachoides, and Beta vulgaris was obtained from greenhouse grown plants. In all cases mature leaves of vigorous plants were used.

The same procedure described in the preceeding section was used, except that early tests were counted 1, 2, and 24 hours after beginning the tests. Later tests were terminated after two hours and aphids were counted at that time.

Results.-Apterous green peach aphids had definite preferences for certain host species and expressed preferences rather rapidly. An analysis of variance showed no difference between 1, 2, and 24 hour counts in each test where leaf discs remained turgid for 24 hours (Table 6).

Marked differences in preference occurred even between species considered to be good hosts (Table 7). R. sativus was preferred in all tests, while T. officinale was preferred in none.

Plant species can be grouped according to the degree of preference. The mean number of aphids settling on a species in tests in which it was preferred or no preference was expressed gives an indication of its relative desirability. The groupings thus obtained roughly follow taxonomic lines (Table 8). In general, Cruciferae were most highly preferred, followed by the Solanaceae and Malvaceae.

Discussion.-The apterous green peach aphid discrim-

TABLE VI. NUMBER OF APHIDS SETTLED ON PREFERRED SPECIES
IN CHOICE CHAMBER (MEAN OF TEN REPS.).

Species		Time (Hours) ^{1/}			
Preferred	Non-preferred	1	2	24	F
<u>R. sativus</u>	<u>C. album</u>	7.6a	8.2a	8.1a	0.357
"	<u>A. retroflexus</u>	7.3a	7.3a	7.6a	0.150
"	<u>B. nigra</u>	5.3a	5.5a	4.7a	0.566
"	<u>B. oleracea</u>	8.6a	9.1a	8.5a	0.825
<u>A. retroflexus</u>	<u>C. album</u>	5.9a	6.4a	4.8a	1.267
<u>C. album</u>	<u>B. vulgaris</u>	5.4a	5.5a	6.1a	0.539

^{1/}Means in the same row followed by the same letter are not significantly different ($p = 0.05$).

TABLE VII. FEEDING PREFERENCES OF THE GREEN PEACH APHID AS EXPRESSED BY SETTLING BEHAVIOR IN A LABORATORY CHOICE CHAMBER (TWO HOUR COUNTS).

Species in left column corresponds to numerator.	<u>B.</u> <u>nigra</u>	<u>C.</u> <u>draba</u>	<u>S.</u> <u>sara-</u> <u>choides</u>	<u>S.</u> <u>tuber-</u> <u>osum</u>	<u>M.</u> <u>neg-</u> <u>lecta</u>	<u>A.</u> <u>retro-</u> <u>flexus</u>	<u>C.</u> <u>album</u>	<u>B.</u> <u>oler-</u> <u>acea</u>	<u>B.</u> <u>vul-</u> <u>garis</u>	<u>Z.</u> <u>mays</u>	<u>L.</u> <u>officinale</u>
1. <u>B. sativus</u>	55/38*	68/28**	72/23**	81/19**	84/15**	73/17**	82/14**	91/4**	92/1**	81/13**	83/5**
2. <u>B. nigra</u>	---	60/30**	70/26**	55/44	90/7**	94/1**	83/5**	83/10**	91/5**	88/5**	82/9**
3. <u>C. draba</u>		---	69/30**	62/36*	63/21**	87/7**	86/5**	68/12**	85/7**	85/11**	93/5**
4. <u>S. sarachoides</u>			---	63/31**	36/41	66/20**	49/27**	71/15**	70/16**	66/23**	52/17**
5. <u>S. tuberosum</u>				---	46/48	69/17**	59/23**	50/31**	76/17**	56/19**	77/16**
6. <u>M. neglecta</u>					---	70/13**	70/14**	63/30**	23/48**	34/22	81/10**
7. <u>A. retroflexus</u>						---	64/11**	62/20**	35/25	21/27	42/20*
8. <u>C. album</u>							---	59/21**	57/22**	39/22**	35/15**
9. <u>B. oleracea</u>								---	39/42	37/39	46/16**
10. <u>B. vulgaris</u>									---	30/27	46/14**
11. <u>Z. mays</u>										---	31/17*
12. <u>L. officinale</u>											---

*Indicates statistical significance at the 0.05 confidence level.

**Indicates statistical significance at the 0.01 confidence level.

TABLE VIII. A CLASSIFICATION OF PLANT SPECIES BASED ON PREFERENCES OF THE GREEN PEACH APHID.

Species	Sum ^{1/}	n	\bar{x}	Family	Dif. ^{2/}
<u>R. sativus</u>	862	11	78.4	Cruciferae	
<u>B. nigra</u>	796	10	79.6	Cruciferae	1.8
<u>C. draba</u>	700	9	77.8	Cruciferae	16.2
<u>S. sarachoides</u>	473	8	59.1	Solanaceae	
<u>S. tuberosum</u>	431	7	61.6	Solanaceae	3.5
<u>M. neglecta</u>	407	7	58.1	Malvaceae	10.6
<u>A. retroflexus</u>	222	5	44.4	Amaranthaceae	
<u>C. album</u>	190	4	47.5	Chenopodiaceae	
<u>B. oleracea</u>	122	3	40.6	Cruciferae	9.3
<u>B. vulgaris</u>	191	5	38.2	Chenopodiaceae	9.0
<u>Z. mays</u>	146	5	29.2	Gramineae	29.2
<u>T. officinale</u>	0	0	0	Compositae	

^{1/} Total aphids on indicated species in tests in which it was preferred or no preference was expressed.

^{2/} Spread from highest to lowest in a group; lowest of one group to highest of next.

inated between host species within one hour. Previous results (Part B) indicated that host preferences of the various life stages of M. persicae were rather uniform and were representative of the species as a whole.

The behavioral preference expressed for the Cruciferae is consistent with the reports of several workers regarding the suitability of members of this family as hosts of green peach aphid. Surprisingly, however, in the selection stage of behavior, broccoli (B. oleracea), was not preferred over less suitable hosts such as A. retroflexus and C. album. This discrepancy may be due to physical factors of the broccoli leaf, which is thick, waxy, and glaucous. Evidence suggests that one or a combination of these factors may be repellent to the green peach aphid. The basal leaves of the commercial mustard plant (B. nigra) are similar to radish leaves, while leaves arising from the flower stalk are waxy and glaucous, similar in texture to broccoli leaves. When given a choice between the two, 86% of green peach aphids settled on the basal leaves, while only 10% settled on the upper leaves. Similarly, non-waxy varieties of Brussels sprouts are more susceptible to M. persicae than waxy varieties (van Emden et al. 1969), and treatment with wetting agents has been found to increase the susceptibility of some Brassica species to green peach aphid (Heathcote and Ward 1958).

The restlessness of M. persicae on less favored hosts was readily apparent in these tests. If one or both species of a choice-test pair were highly preferred, a large proportion of the aphids settled during the tests. An average of 91% of all aphids settled in tests involving Crucifers. When offered a choice between two non-preferred hosts, the settlement rate was much lower. In tests involving only Amaranthaceae, Chenopodiaceae,

Gramineae, and Compositae, an average of only 59% of the aphids settled.

Results of this study indicate that the less preferred a species is, the greater the aphid's restlessness and tendency to wander from plant to plant. Thus, restlessness of the apterae may contribute to the buildup of aphids on preferred hosts in the field. It may also be a significant factor in the spread of virus diseases, especially on less preferred hosts such as sugarbeet.

The role of apterous aphids in the spread of virus diseases has been a matter of considerable controversy. Alatae have been implicated in the secondary spread of virus diseases in potato crops, while apterae have appeared to be less important (Broadbent 1950, Schepers et al. 1955, Hollings 1955, Fisker 1959). Good correlations have been found, however, between numbers of apterous green peach aphids and the spread of yellows diseases in sugarbeets (Schepers et al. 1955, Ribbands 1963, 1965). Ribbands (1963) cited the frequency with which apterae moved between sugarbeet plants. While Watson and Healy (1953) did not find any correlation between numbers of apterae and virus spread in sugarbeet, Ribbands (1965) attributed their results to inadequate sampling of the apterous population.

The differing views on the role of apterae in the spread of virus diseases in potato and sugarbeet may result from a fundamental difference in aphid behavior on the two crops. Potato, being a preferred host, is a stronger arrestor of aphid movement than sugarbeet. Apteræ would be more likely to remain settled on potato, while alatae would assume the dominant role in dispersal and virus spread. On sugarbeet the apterae would have a greater tendency to wander and would therefore contribute to the spread of virus diseases.

V. HOST SELECTION BEHAVIOR

A. Behavior On Resistant and Susceptible Plants

Tjallingii (1976) studied host selection behavior of the cabbage aphid (B. brassicae). Aphids were placed on resistant and susceptible plants and their behavior was observed for 30 minutes. Frequency of proboscis contact (p.c.), mean duration of p.c., and the percent of time spent in p.c. were found to be reliable parameters of host acceptance. The occurrence of p.c. was not affected by plant species. Probes were less frequent and of longer duration on susceptible plants, and the total time in p.c. was greater.

Klingauf (1978) used the duration of the first walk and first p.c. as criteria of host acceptance in studying the behavior of A. pisum, however Tjallingii found these characteristics to be more variable than those mentioned above.

The host selection behavior of M. persicae was studied to determine which aspects of behavior were associated with host acceptance.

Materials and Methods.-Leaf discs two cm in diameter were cut from the leaves of susceptible (radish) and resistant (corn and sage, Artemesia sp.) plants. Third and fourth instar nymphs of green peach aphid were obtained from glasshouse culture. One aphid was placed in the center of the disc on the stage of a dissecting microscope and observed for five minutes or until the aphid left the disc.

Four behavioral components were recorded; number of probes, length of each probe, total time spent probing, and the length of time aphids remained on the disc.

Ten aphids were observed on each host in each of five

replicates.

Results.-The number of probes per aphid and the duration of probes was highly variable on resistant and susceptible plants (Table 9). The number of aphids probing within five minutes, total time on leaf disc, and percent time in p.c. were good indicators of host acceptance (Table 10). Aphids stayed longer on discs from susceptible plants and spent a greater percentage of time in p.c.

Discussion.-Although probes were slightly less frequent on susceptible plants and the mean length of the first probe considerably longer, these characteristics were highly variable on both types of plants. Other workers (Esau et al. 1961, Sylvester 1954) have noted the great amount of variability in feeding activities of M. persicae.

Fewer aphids probed on resistant species than on radish, although this is no doubt a reflection of the restricted area of the leaf disc. Klingauf (1978) found that the length of the first walk is longer on non-preferred plants, and aphids probably left the leaf disc before reaching the end of the first walk.

Although no conclusions can be drawn about the nature of the stimuli to which aphids respond in early stages of host selection, it is clear that they are influenced by some aspect of the plant prior to probing. Aphids probe more readily and wander less before probing on preferred species. Thus olfactory or tactile stimuli must influence the rate at which probes are initiated.

B. Effect of Trichomes of *Chenopodium album*

The leaves, stems, and buds of common lambsquarters (C. album) are covered by hair-like appendages known as

TABLE IX. PROBING ACTIVITY OF M. PERSICAE ON SUSCEPTIBLE AND RESISTANT PLANTS.

Species	Probes/aphid ^{1/}		Mean length 1st p.c. (seconds)	
	\bar{x}	range	\bar{x}	range
Radish	1.96a	0 - 4	40.3a	3 - 190
Corn	2.34a	0 - 6	13.9b	4 - 61
Sage	2.80a	0 - 6	16.0b	3 - 46
F	1.921		13.083**	

^{1/}Means followed by the same letters are not significantly different by Duncan's multiple range test ($p = 0.05$).

**Indicates statistical significance at the 0.01 confidence level.

TABLE X. ACCEPTANCE BEHAVIOR OF M. PERSICAE ON LEAF DISCS OF SUSCEPTIBLE AND RESISTANT SPECIES.

Species	# GPA probing ^{1/}	Total time on leaf disc (sec.)	% time in p.c.
Radish	7.6a	242.2a	42.9a
Corn	4.0b	118.3b	8.4b
Sage	4.8b	149.3b	9.7b
F	5.89*	10.18**	59.08**

^{1/}Means followed by the same letter are not significantly different by Duncan's multiple range test ($p = 0.05$).

*Indicates statistical significance at the 0.05 confidence level.

**Indicates statistical significance at the 0.01 confidence level.

trichomes. Observations of these plant hairs revealed that, in early stages of growth, they are spherical in shape and filled with apparently volatile compounds (Figure 16). As the tissue ages, these compounds are lost and the trichomes collapse, so that after about one month of age, depending on environmental conditions, they are devoid of contents (Figure 17).

Levin (1973) hypothesized that volatile compounds in plant trichomes serve as a "pre-contact advertisement" to phytophagous insects, informing them before the commencement of feeding that the plant is not a suitable host. In such a way, the plant would avoid even the damage resulting from sampling and rejection.

Since previous experiments have shown C. album to be resistant to the green peach aphid, the following experiment was conducted to determine if the volatile contents of its trichomes acted as feeding deterrents in the manner described by Levin.

Materials and Methods.-Discs two cm in diameter were cut from the leaves of greenhouse grown radish and lambsquarters plants. Discs were cut from the second and third whorls of young plants (one to two weeks of age) and from fully expanded mature leaves of older plants (one to two months of age).

Observations were made as described in the preceding section. Ten observations per treatment were made in each of seven replicates.

Results.-Aphids probed more readily on radish than on either young or old lambsquarters. There was no difference between either the number of aphids probing or the amount of time spent in p.c. on young leaves with full trichomes and mature leaves with collapsed trichomes (Table 11).

Aphids remained on radish discs longer than on

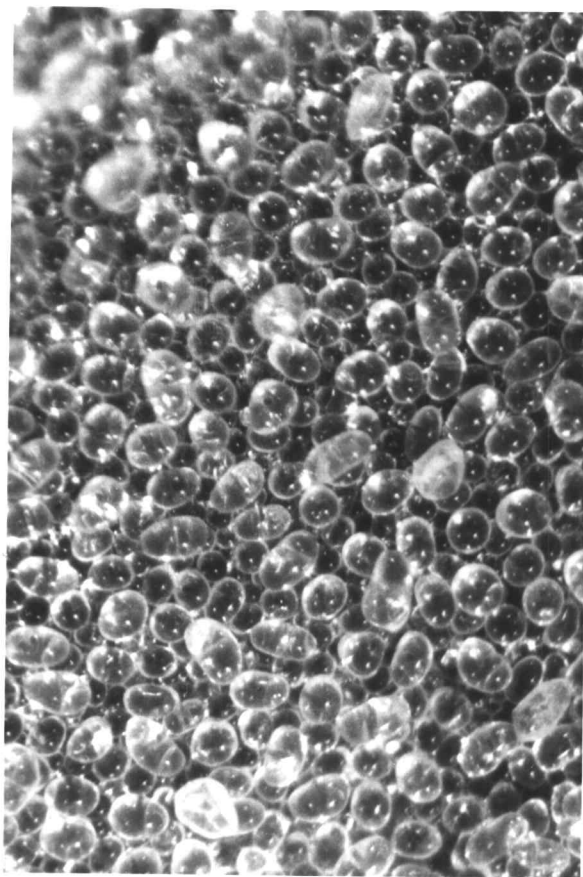


Figure 16. Trichomes on young leaves of Chenopodium album (31x).

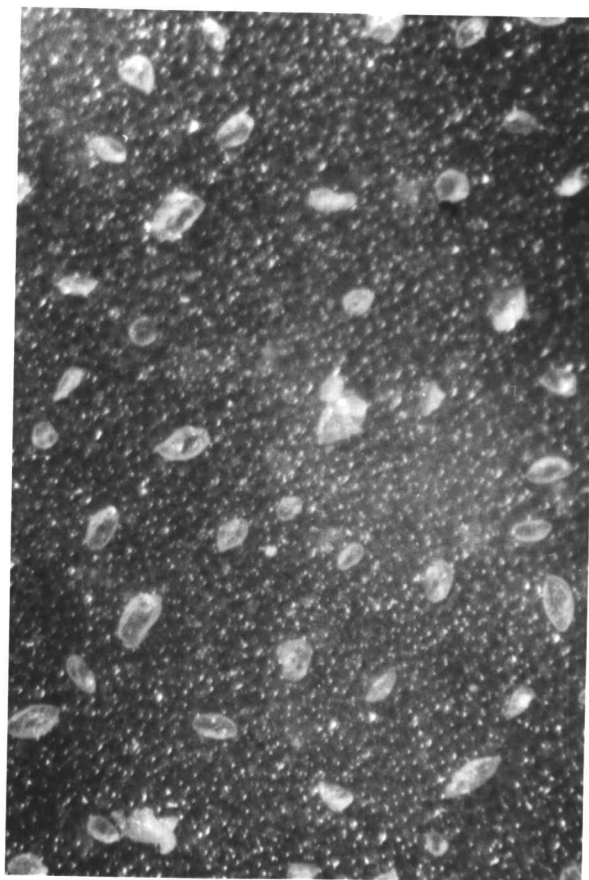


Figure 17. Trichomes on mature leaves of Chenopodium album (31x).

TABLE XI. ACCEPTANCE BEHAVIOR OF *M. PERSICAE*
ON RADISH AND CHENOPODIUM ALBUM.

Treatment	# of aphids probing ¹	Total time on leaf disc (seconds)	% time in p.c.
Radish	8.6a	263.2a	43.3a
Lambsquarters- full trichomes	4.7b	141.8b	11.2b
Lambsquarters- empty trichomes	4.8b	150.7b	13.2b
F	8.661**	18.208**	17.529**

¹Means followed by the same letter are not significantly different ($p = 0.05$).

**Indicates statistical significance at the 0.01 confidence level.

lambsquarters, staying an average of 87% of the five-minute observation period. In contrast, they remained on young and old lambsquarters leaf discs only 47% and 50% of the observation period, respectively. A mean of 6.1 aphids per replicate remained on radish and were feeding at the end of five minutes, while only 1.0 and 1.4 did so on young and old lambsquarters.

Discussion.-The volatile contents of trichomes of C. Album apparently do not act as a feeding deterrent to the green peach aphid. There was no difference in the amount of probing on leaf discs with full trichomes and those with collapsed trichomes.

There was a small difference, although not statistically significant, in the average time aphids stayed on young and old lambsquarters leaves. This may reflect the increased difficulty in getting a satisfactory foothold on the plant on younger leaves, as the full, spherical trichomes are slippery and densely packed.

VI. SUMMARY AND CONCLUSIONS

Variation in populations of Myzus persicae appeared to be related to seasonal and local differences in the abundance and quality of host plants. Predators, while active at periods of highest aphid density, were not numerous enough to account for population declines at all locations. Descurania sophia and Solanum sarachoides, two of the most common weed species in the Yakima area, were highly preferred by the green peach aphid and were significant sources of aphid buildup in spring and early summer. In the absence of highly preferred hosts or during periods of peak population density, less preferred species were colonized.

The effect of enhanced solar radiation on the sloping north bank of the Yost Drain was evident in the growth of hoary cress during the winter and in the faster growth of weeds in the spring. During winters mild enough for the survival of parthenogenetic forms of M. persicae, it no doubt contributes to the suitability of the drain bank as an overwintering site.

In the laboratory, green peach aphids have shown a definite preference for Cruciferae, on which they probe more quickly, settle and feed more readily, and are less restless than on non-preferred hosts. Feeding preferences of the various life stages of M. persicae appear to be rather uniform and favor summer hosts, therefore it does not seem likely that feeding preferences play a dominant role in host alternation.

The restlessness of green peach aphid on poor hosts may be a contributing factor in the spread of virus diseases. The use of deterrent compounds in management of green peach aphid has been suggested (Greenway et al. 1978), however in light of these findings it appears that

such a strategy may only worsen the problem of virus transmission. An alternative approach in situations where virus spread is the major concern would be the use of arrestant compounds which would inhibit interplant movement by apterous M. persicae.

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