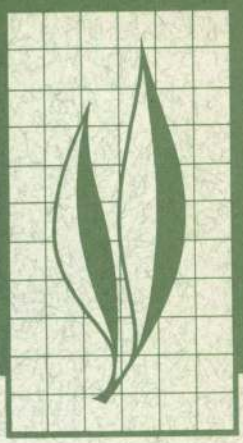
HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

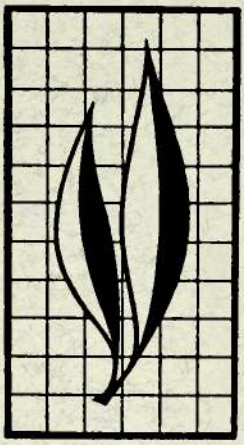


Volume 39, Number 17 · February, 1969

Competition and Other Factors Influencing the Population Dynamics of *Aphis gossypii* and *Macrosiphoniella sanborni* on Greenhouse Chrysanthemums

George Tamaki and William W. Allen

UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES



Although *Myzus persicae* is the major aphid pest of chrysanthemums grown in commercial greenhouses in this area, this study suggests that in the absence of insecticides *Macrosiphoniella sanborni* and *Aphis gossypii* are better adapted to chrysanthemums. Because *Myzus persicae* was so poorly adapted to chrysanthemums, the study emphasizes the effects of alate production, aphid size, distribution on the plant, and inter- and intraspecific competition on population regulation of *M. sanborni* and *A. gossypii.*

When *Macrosiphoniella sanborni* and *Aphis gossypii* were grown together, the stems and young leaves were preferred by *M. sanborni,* and young leaves and terminal buds were preferred by *A. gossypii.* Both species preferred the lower surfaces of the older leaves.

Single- and mixed-species populations of *Macrosiphoniella sanborni* and *Aphis gossypii,* after an accelerated growth period, reached a relatively stable equilibrium phase. The species that attained numerical superiority during the growth phase tended to maintain this advantage. Removal of alate forms, which simulated dispersal, reduced the high rate of population growth, but did not stabilize the populations. Because they were strongly influenced by aphid density, the main population regulating agents were (1) aphid size (related to birth rate) and (2) leaf mortality (related to death rate). Another indirect, regulating

continued on inside back cover

THE AUTHORS:

George Tamaki was a graduate student in Entomology and Parasitology, Berkeley, during this study and is now Entomologist, Entomology Research Division, Agricultural Research Service, U. S. Department of Agriculture, Yakima, Washington. William W. Allen is Lecturer in Entomology and Entomologist in the Experiment Station, Berkeley.

George Tamaki and
William W. Allen

Competition and Other Factors Influencing the Population Dynamics of *Aphis gossypii* and *Macrosiphoniella sanborni* on Greenhouse Chrysanthemums[1]

INTRODUCTION

IN THE SAN FRANCISCO BAY AREA, the cotton aphid, *Aphis gossypii* Glover, and the chrysanthemum aphid, *Macrosiphoniella sanborni* (Gillette), are rarely found on commercially-grown greenhouse chrysanthemums; but the green peach aphid, *Myzus persicae* (Sulzer), is a major pest. In contrast, chrysanthemums in the Insectary Greenhouse, University of California, Berkeley, were abundantly infected with *A. gossypii* and *M. sanborni,* while *M. persicae* was rarely found.

Insecticides for thrips and aphids are frequently applied to commercially grown chrysanthemums. In the Insectary Greenhouse, insecticidal treatments were kept to a minimum. Tests of different insecticides on these three aphid species showed that *Myzus persicae* was by far the most resistant to insecticides that are normally used in commercial greenhouses (Allen, unpublished data). When insecticides were removed from the environment, *Aphis gossypii* and *Macrosiphoniella sanborni* (apparently more highly adapted to chrysanthemums) established and increased rapidly, but *M. persicae* could be established only with difficulty.

In an integrated control program, chemical controls which are generally used in commercial greenhouses might be reduced. If this should occur, *Aphis gossypii* and *Macrosiphoniella sanborni* would replace *Myzus persicae* as the major aphid pest on commercially grown chrysanthemums. If biological or cultural controls for *M. persicae* are to be understood, so must aphid competition and competitive exclusion (Hardin, 1960), or competitive displacement (DeBach and Sundby, 1963). The authors of the present study sought to determine how alate production, aphid size, distribution and inter- and intraspecific competition affected the population dynamics of these different aphid species. A practical goal, moreover, was to determine which species are most likely to become pests of greenhouse chrysanthemums in the absence of insecticides.

The study was two-fold: The first part emphasized the factors that affected population during the logistic growth phase. Smith (1935) discussed how population growth under constant physical conditions usually fits the logistic curve which follows the Verhulst-Pearl law. The second part of the study emphasized the regulatory factors which maintain the population at the equilibrium position.

Many ecological terms used in this paper are defined in Stern *et al.* (1959).

[1] Submitted for publication January 17, 1968.

LITERATURE REVIEW

A thorough literature review on alate production can be found in Bodenheimer and Swirski (1957), Bonnemaison (1951), and Paschke (1959). Lees (1961) suggested that many of the previous studies that related alate production to temperature, quality and quantity of food, water deficiency in plants, population density (crowding), and other environmental factors, should be reinvestigated in the light of Bonnemaison's (1951) analysis of the "group effect." Bonnemaison concluded that the presence of other aphids was the primary cause of alate formation rather than the environmental factors mentioned above. However, Mittler and Dadd (1966) recently showed that a change in a single amino acid in the synthetic diet of the green peach aphid resulted in different proportions of alatae. This suggests that the matter is perhaps not as simple as Bonnemaison would imply.

Recent review articles on competition are to be found in Andrewartha and Birch (1954), Birch (1957), Crombie (1947), DeBach and Sundby (1963), Klomp (1961, 1964), and Park (1962). Both Grant (1963) and Mayr (1963) give excellent discussions on competition and its evolutionary significance.

Ito (1952, 1954, 1960) conducted an ecological study on population increase and habitat segregation with three aphid species—*Rhopalosiphum maidis* (Fitch) (=*Aphis maidis* Fitch), *Macrosiphum granarium* (Kirby), and *Rhopalosiphum fitchii* (Sanderson) (=*Rhopalosiphum prunifoliae* Fitch). He found that each species had its own preferred micro-habitat. In their own niches, they increased in number. When crowded, they moved into unoccupied leaf areas and eventually expanded their ranges over the entire plant. When the population density approached the saturation point, the aphids emigrated from plant to plant. According to Ito, emigration was the primary mechanism in maintaining the equilibrium of the population density, rather than any increase in the death rate or decrease in the birth rate. Moreover, he reported (Ito, 1952, 1954) that intraspecific competition does not regulate a population; it is regulated instead by movement from saturated areas to virgin areas of the host plant.

Cook (1961) studied coexistence and competition in two legume-feeding aphid species, *Acyrthosiphon pisum* (Harris) and *Therioaphis maculata* (Monell). He found that both species had their own preferred habitats on different parts of the plant, and that at low and moderate densities the two species were well separated from each other. Cook reported that when suitable parts of the host plant were being fully exploited at higher densities, there was evidence of a depressing effect of the two species on one another. He concluded that populations coexist by virtue of differences in host habitat and need, and not because they are maintained by natural enemies at densities below a competitive threshold. He mentioned that when interspecific competition occurred under natural conditions, controlling mechanisms had failed to maintain population densities below the competitive threshold.

Although Ito (1960) emphasized emigration as the important regulating factor in maintenance of population equilibrium, his studies emphasized emigration by apterous rather than alate aphids. Cook (1961) did not investigate the relationship of alate aphids to emigration or to competition. In addition, both of the short-term studies dealt with the accelerated growth phase of the populations. The experimental designs and host plants were not suited for long-term experiments to study aphid populations at equilibrium positions.

MATERIALS AND METHODS

All of the experiments were conducted at the Insectary Greenhouse at the University of California in Berkeley. Originally, three aphid species were to be studied; but one, *Myzus persicae*, failed to become established. In the first experiment, after *M. persicae* died out, those treatments that were to have included mixed-species populations of *M. persicae* along with either *Macrosiphoniella sanborni* or *Aphis gossypii* were selected to compare the effects of alate removal and retention.

The host plants were *Chrysanthemum morifolium* (Compositae). Three varieties—Albatrose, Detroit News, and Pink Champagne—were use in the first short-term experiment. Special considerations were given in the second experimental design to establish *Myzus persicae*, and since this species had been observed in commercial greenhouses to infest the Albatrose variety more heavily than many other varieties, the Albatrose was used in this—and all subsequent—experiments.

To increase further the chances of *Myzus persicae* establishment, the times of inoculation by the different species were staggered. Alate forms of *M. persicae* were placed on their respective terminals on July 16. Six days later, when *M. persicae* averaged 13 aphids per terminal, *Aphis gossypii* was introduced. Because *Macrosiphoniella sanborni* was found to become established more rapidly, it was introduced on its specified terminals a week after *Aphis gossypii*. Approximately one month after the initial inoculation with *M. persicae*, the populations decreased in numbers, and these treatments had to be removed once again from the experiment.

We did not know why *Myzus persicae* failed to establish. It is known that different biotypes of *M. persicae* favor different types of plants, although the aphids used in these experiments originally had been collected on chrysanthemums. In commercial greenhouses, *M. persicae* is usually more abundant at the ends of the greenhouses where evaporative cooling pads are installed. High temperatures and low humidity may have contributed to the failure of establishment, but host physiology, photoperiods, and the like, may also have been involved. It can also be concluded that *Macrosiphoniella sanborni* and *Aphis gossypii* are better adapted to chrysanthemums, and in the absence of chemical control would be more serious aphid pests.

To study the effects of intra- and interspecific competition along with alate production, it was necessary to isolate the different aphid colonies from other aphids, predators, and parasites. A white cotton organdy cage was designed to enclose 2 to 3 inches of the growing terminal of the plant. The frame that fit tightly inside the cloth consisted of two ½-inch wide plastic rings, 5 inches in diameter. These two rings at each end of the cage were connected by three plastic strips, 4 inches long and ½ inch wide, placed equidistant around their circumferences. The 5-inch diameter of the cage allowed for sufficient lateral growth of the plant terminals. Although the plastic frame was only 4 inches high, the plant was still able to grow 6 to 8 inches before the terminal bud outgrew the cage. This extra space was provided by closing the overlapping ends of the cloth covering, so that there were a few inches of extra space on each end. New cages twice as long were provided when the terminals outgrew the cages in the long-term experiments.

The cage was fastened to the plant terminal by tying the basal end of the cage around the stem with soft wire; leaves were removed that interfered with fastening. The top opening of the cage was likewise closed with wire. The

top of the cage was supported by a wire rod that extended horizontally from a stake inserted in the plant pot. Holes were drilled every few inches in this support stake so that the height of the horizontal rod could be adjusted as the plant grew.

An inverted cone, made from a 5 by 8-inch index card was attached with masking tape to the basal portion of the stem within the cage. This flange extending out from the stem acted as a barrier to aphids wandering down the stem and also helped catch aphids that fell from the terminal when counts were being made.

A band of sticky material, Stickem®, applied to masking tape wrapped around the stem below the cage was used to hinder contamination by natural enemies (Pritchard and Beer, 1950). However, this precaution did not always prevent contamination, for at times, chrysopid larvae had to be removed from the cages. Later, it was discovered that if the wire tying the base of the cage was looped twice around the stem tightly, it prevented most of the predators from entering the cage.

Stem cages similar to the ones used by Paschke (1959) were made from plastic tubes, 3.8 cm in diameter and 7.6 cm long. A hole, 1 cm in diameter was cut in the side of the tube, and fine mesh cloth was glued over the hole for ventilation. The tube was slipped over the apical end of the terminal and placed at the desired position on the stem. Foam rubber plugs, 1 cm thick, were fitted in both ends of the tube. These plugs, cut to the center, were used to form a tight seal around the stem. To facilitate alate removal, additional holes were made in the tube and plugged with corks. By removing the corks and using a piece of wire dipped in Stickem®, it was possible to remove the alates with ease.

The leaf cages were similar to the stem cages, except that one end of the plastic tube was covered with fine mesh cloth. The leaf was placed inside the cage and a foam rubber plug was used to seal the open end of the cage around the petiole. A piece of string suspended from a horizontal wire rod extending from the plant support stake was used to support the leaf cage in a horizontal position. The cage was slipped off when counts were made, and the alates were removed with an aspirator.

Stock colonies of the different aphid species were kept in separate rearing cages. These wooden frame cages, 17 by 17 by 28 inches, covered with cotton organdy, were large enough to hold four chrysanthemum plants in 6-inch pots. The original aphids used to start the colonies were found on chrysanthemums in the Insectary Greenhouse.

Before the experimental terminals were inoculated, the leaves just below each terminal were stripped, the cardboard flange was attached, and the basal portion of the cage was secured. Using a micro-aspirator, the stock colony aphids were first teased until the mouthparts were removed from the plants, the aphids were picked up by placing the tip of the aspirator on the dorsal surface of the thorax, and transferred to the terminals through the open top of the cage.

During the first three or four weeks, the lower leaves were removed from the stem until the aphids started to spread to the lower leaves. Until the aphid population reached its accelerated growth rate, it was necessary to maintain a short terminal area of 2 to 3 inches so that the plant would not outgrow the cage before the aphid population stunted the terminal.

In the first short-term experiment, all the aphids were counted with a finger-actuated counter. In subsequent experiments, after the aphids were evenly distributed on the leaves, the aphids were counted only on half of the

leaf area, on one side of the mid-vein. The count for each leaf was then obtained by multiplying by two. Except for the treatments with alates retained on the caged terminals, the alate aphids were removed with an aspirator after each count.

Throughout the experiments, two banks of fluorescent lights (190 foot-candles) were used for a 4-hour period during the night. This light intensity at cage height was necessary to prevent the chrysanthemum plants from forming flower buds (hence, different experimental conditions). However, even with this supplemental light, a few plants formed flower buds and had to be removed from the experiment.

The physical conditions were not constant. On hot days, two 12-inch fans were used to ventilate the room; and at night temperatures were kept above 55° F by thermostatically-controlled steam heat. Temperatures and relative humidities were recorded with a Bendix-Friez hygrothermograph placed centrally among the experimental plants at the approximate height of the caged terminals. Its aluminum shade minimized the effects of radiation. The mean daily temperature and relative humidity were calculated from readings taken at two-hour intervals.

A Brown recording potentiometer with copper-constantan thermocouples was used to compare the temperatures in the terminal cages with ambient air temperatures in the room. For a 24-hour period on April 27 and 28, temperature readings from the thermocouples placed inside the center of four cages were compared to the readings from four thermocouples placed about 5 inches outside of each cage. From sunrise to sunset, cage temperatures were materially higher than outside temperatures. The greatest difference occurred at midday when the cage temperatures were 2.5° C higher than the 29.5° C room temperature. After the daily maximum temperature, there was a gradual decrease in the temperature differential until about 7 p.m. when ambient and cage temperatures were the same.

Experiment 1: Alate production, population distribution, and competition

Chrysanthemum plants were given seven different treatments with various combinations of the three aphid species: three with single-species aphid colonies, three with two mixed-species colonies, and one with all three mixed-species colonies. However, since *Myzus persicae* did not become established, an investigation was undertaken to determine if alate removal and retention had an effect on the population growth curves. Treatments for alate retention were selected from colonies that were originally mixed with *M. persicae*. Each of these combinations was replicated eight times.

The plants were arranged in four rows with five potted chrysanthemum plants in each row. Each potted plant had two to four terminals. The treatments were replicated twice and placed at random in each row. Only one apterous adult of each species was used to inoculate the individual terminals.

Aphids were counted two to three times a week, except for the last two counts which were taken three weeks apart. During this three-week period, however, the alates were still removed every four days.

Occasional censuses were taken to determine the distribution patterns of the aphids on the different parts of the enclosed terminals. Each leaf was measured, and the number of aphids on the top and bottom surfaces were recorded along with the number of aphids on the stems and terminal buds. The terminal bud included the leaf bud and leaves less than 1 cm long. The area of the leaves was estimated by using the formula: ½ length × width. Although not

precise, it was sufficiently accurate to compare the areas of different-sized leaves.

Since all terminals did not have the same number of leaves in each treatment, it was not possible to make a leaf-to-leaf aphid density comparison from top to bottom. Therefore, the caged area of the plant was arbitrarily divided horizontally into four sections with the leaves on each terminal divided into four equal parts. For each section, the average aphid density per square centimeter of leaf surface was determined for all terminals in a treatment.

The results of Experiment 1 are graphically presented in figures 1 to 9.[2]

Experiment 2: Removal and retention of alate forms

The effects of removal and retention of alates from mixed-species populations were investigated; in Experiment 1 these effects were studied for only the single-species populations.

In nature, alatae would be expected to leave the plants. Such a condition was simulated in this experiment by the removal of alate forms. On the other hand, when alate forms were confined to the plant they contributed to the population much like the apterous forms, thus making it possible to determine what effects alate production had on the populations.

One major difference, however, must be recognized in the progeny of adult apterous and alate forms. Apterous adults are known to produce both alatoid and apterous nymphs depending on the environmental conditions. It is known that winged adults produce a much lower proportion of alate progeny than do the apterous adults (Lees, 1961). White (1946) reported that *M. sanborni* wingless parents tend to produce more winged progeny than the winged adults. Reinhard (1927) also found instances when alate parents under similar conditions produced less alate progeny than apterous parents.

Unfortunately, in Experiment 1, numerous winged adults died in the treatment in which the alates were retained. Mortality was due to heavy honeydew deposits on the upper surfaces of the leaves which entrapped the wings of the aphids. On the other hand, only a few apterous aphids were observed trapped in the sticky honeydew. Thus, under these conditions the retained alate forms suffered higher mortality than did the apterous forms they were supposed to simulate. Understandably, under natural conditions alate forms would not suffer this high mortality, for they would soon leave the honeydew-contaminated environment.

An experiment was designed, therefore, to reduce the accumulation of honeydew and increase the chance of alate survival. The experiment was also designed to limit the area of plant growth, so that competition would occur more quickly, and information could be obtained in a shorter period of time.

To restrict the area of the plant in the cage, the terminal growing point was cut off, and only two leaves on opposite sides of the stem were retained. Although the physiology of the plant was undoubtedly changed by the removal of the terminal growing point, the experimental area of the plant was limited to the two leaves. The same organdy cages were used as in Experiment 1. The cage enclosed 2 inches of the stem and two young leaves. Since the leaves were on opposite sides of the stem, the honeydew from the aphids feeding on the under surfaces of the leaves fell onto the paper. Filter paper to absorb the honeydew was used to line the flange and was changed after heavy accumulation.

Each of six treatments were replicated four times. The treatments included two single-species populations of both *A. gossypii* and *M. sanborni* and another two of the mixed species. One

[2] See center-fold pages for all figures.

treatment of each pair was designated for alate removal and the other for alate retention. A total of nine plants were used, averaging three terminals per plant. The treatments were placed on the plant terminals at random. Each replication was initially infested with three adult aphids (one alate and two apterae from each species).

The results of Experiment 2 are graphically presented in figures 10 to 14.

Experiment 3: Density fluctuations in long-sustained aphid populations

This experiment was initiated to substantiate the findings in the short-term experiment and to continue it until the aphid populations eventually crashed. One purpose was to investigate factors which regulate the populations; however, before such factors could be studied, it was necessary to show that the populations were actually being regulated. To do this, an experiment was needed over a long enough period so that one or both of the species populations would reach or fluctuate numerically about an equilibrium level.

The original experimental treatments consisted of the seven possible aphid combinations. These included each aphid alone, each aphid in combination with one of the others, and one treatment with all three of the aphid species. However, since *Myzus persicae* did not become established, the number of treatments was actually reduced to three.

Each treatment was replicated four times, but one replicate from each of the single-species treatment had to be omitted, because two of the terminals flowered; and in the other terminal, a syrphid consumed half of the aphid population. Every plant had three terminals; therefore, only ten plants were needed to provide the necessary 28 terminals. The plot was designed with three rows of three to four plants per row. All treatments were assigned to the terminals at random. In contrast to the first experiment when only one adult for each species was used to inoculate the terminals, three adult aphids, (two apterous and one alate) were used to infest the terminal and hasten the buildup of the populations.

The results of Experiment 3 are shown in tables 1, 4, and 5 and graphically presented in figures 15 to 18 and 21 to 25.

Experiment 4: Size variation

In contrast to the extensive literature on size variation in *A. gossypii,* workers have not reported on size or other variations in *M. sanborni* populations that might affect alate production and population growth. Before discussing *M. sanborni* in the long-term experiment, some of the size differences that were found in these aphids are essential to know.

Macrosiphoniella sanborni individuals observed on young and vigorously growing plants during the early growth phase were very large compared with individuals that were present during the period of equilibrium. A gap also seemed to occur between the size of the large and small aphid individuals.

An experiment was designed to determine if alate production and population growth patterns were different for large and small forms of *M. sanborni.* Two stock colonies were selected as sources for the large and small adult aphids. Three aphids selected at random from either small- or large-aphid colonies were placed in their respective cages around the stem about 2 cm below the terminal growing point; leaves were removed that interfered. Periodic counts were taken of the number of aphids, and alates were removed after each count. Each treatment was replicated four times.

The small and large apterous and alate adults measured before the experi-

ment were adults selected at random from the same two colonies as were the adults used in this experiment. To establish that quantitative differences existed between the two colonies, the length of the aphids was measured from the vertex of the head (excluding the protruding antennal ridges) to the tip of the abdomen (excluding the caudal and cornicle protrusions). Width was considered the widest part of the abdomen. Measurements of the original colonies and the size of the individuals at the end of the experiment are compared in table 2, and the results of Experiment 4 are graphically presented in figure 19.

Experiment 5: Influence of feeding site

Bonnemaison (1951) found, as many others had, that on unhealthy and stunted type of branches, aphids were not numerous, and that their fecundity was reduced. On the other hand, vigorous plant growth attracted aphids and increased their fecundity, which led rapidly to high aphid populations.

Aphids were caged on young stems, old stems, and on young leaves. Since adults of different sizes would affect the outcome, each cage was infested with five large, apterous adults. Isolated cages on the three different sectors of the plant were replicated four times on different plants. The aphids caged on the young stem growth were placed a few centimeters below the terminal growing point, and the aphids caged on the older stem growth were placed on the basal portion of the shoot. Only the young and recently unfolded leaves were used because of the limited cage size and anticipated leaf growth. The results of Experiment 5 are graphically presented in figure 20.

RESULTS

Distribution on the plant

Lack (1945) showed that two closely related species of birds, *Phalacrocorax carbo* and *P. aristotelis*, with different food requirements can exist without competition in the same habitat. Gause and Witt (1935) reported that two *Paramecium* species had identical food requirements, but they existed in different habitats. He found that these species could feed on bacteria at different parts of the culture without competing. Mayr (1963, p. 73) reported on Wagner's (1944) work with two closely related species of Drosophila:

> The larvae of these two closely related species occur simultaneously in the ripe fruit of the cactus *Opuntia lindheimeri*, feeding on the microflora of the fermenting pulp. Competition between the larvae of the two species appears to be complete. Yet analysis of the intestinal contents showed that the two species of *Drosophila* tended to feed on different species of yeast and bacteria with a certain amount of nonoverlap in the requirements. . . . The difference in food utilization of the two species of *Drosophila* in *Opuntia* proves that their niche is not the same.

Aphids, however, do not obtain their food in the same manner as does *Drosophila*. With few possible exceptions, most aphid species derive their nutrition by tapping the phloem vessels (Kennedy and Stroyan, 1959). Different aphid species feeding on the same part of the plant may have different nutritional needs; however, the selection of these needs takes place inside the aphid and not at the point where the stylet is inserted into the phloem sieve tube. Kennedy and Mittler (1953) amputated the stylets of *Tuberolachnus salignus* (Gmelin) and demonstrated that phloem sap moved under turgor pressure through the stylets. Under this condition, aphids are not likely to be able to segregate the necessary nutrients at the point of insertion. Two aphid

species feeding on different parts of the plant, however, could be obtaining phloem sap with different concentrations of nutrients.

Mittler (1954) found that actively growing plants had a higher amino-nitrogen concentration than mature plants. Mittler also found that aphids on an actively growing plant assimilated more amino-nitrogen and excreted less honeydew than aphids on a mature plant. However, his study was conducted on two different plants and not on different-aged portions of the same plant.

Biddulph and Biddulph (1959) suggested that sugars are formed in mature leaves, vitamins are formed in immature leaves, and proteins are synthesized at the growing tips of the stem and roots. However, all of these products are transported throughout the plant. Nevertheless, one would expect to find a higher concentration of the materials at the site of synthesis or storage.

Kennedy (1958) said that there is no direct evidence of nutritional difference of phloem sap composition in different-aged leaves and other plant organs on the same plant at the same time. However, from Mittler's (1954, 1957, 1958) studies, and other evidence, Kennedy proposed the following:

> Our hypothesis to account for the leaf-age effects was that the aphids' food (phloem sieve-tube sap) would be especially rich in soluble organic nitrogen compounds of high nutritive value—amino acids and amides—at or near places where growth and hence protein synthesis was going on in the plant, and again where senescence with protein breakdown was going on; but poor in those compounds where neither growth nor senescence was in progress, as in mature green leaves.

Therefore, the investigation for this paper included the study of distribution of aphid species in relation to leaf age. Kennedy *et al.* (1950) studied the distribution of *Myzus persicae* and *Aphis fabae* Scop. on spindle trees and sugar beet plants. Although variation occurred, a general distribution pattern was evident for all the aphids recorded on the two host plants. They found that on plants with leaves of all ages (young, mature, senescent, and dying), aphid density was highest on young and senescent leaves and the lowest on maturing or dying leaves.

Short-term experiments. Since nutrient content or concentration may vary in different parts of the plant, feeding sites of the two aphid species was an important part of a study on aphid competition.

Aphids on different parts of the plants were counted periodically in an attempt to locate preferred feeding sites and to find areas of overlap where competition might take place at different densities. Also, feeding sites of single- and mixed-species populations were compared to study their effects on intra- and interspecific competition.

Leaves, stems, and buds. Counts were taken on four different occasions in Experiment 1 to illustrate aphid distribution on leaves, stems, and buds. These counts were represented as percentages of the total number of aphids on all terminals in a treatment on the various parts of the plant. Distribution patterns changed as the aphid populations increased or as the plants grew and aged (fig. 1).

Macrosiphoniella sanborni showed similar distribution patterns in single- and mixed-species populations. In both cases, *M. sanborni* populations were not abundant on the terminal leaf buds of the plants. Early in this experiment *M. sanborni* were more abundant on the stems, but by the end of the experiment, approximately 80 per cent of the population was found on the leaves. This was due primarily to an increase of aphids on the leaves rather than to a decline in aphid numbers on the stems.

Early in the experiment, *A. gossypii* populations in the single-species experi-

ments were concentrated on both the leaves and buds. By the last count, however, over 90 per cent of the population was on the leaves. Mixed-species population appeared to have no substantial influence on the general distribution pattern of *A. gossypii*. Moreover, under single- and mixed-species populations, *A. gossypii* did not favor the stems to any great extent.

During the early phase of the experiment when population numbers were low, the aphid densities per occupied area were higher than might be expected because of the gregarious behavior of both aphid species. Since both species had different micro-habitats on the plant at low aphid densities, interspecific competition was less severe early in the experiment.

In the latter part of the experiment, the most likely site for competition was on the leaves where populations of both aphid species increased the most.

Leaf surface. A study was undertaken in the first experiment to determine the preferred habitats of both species in relation to the lower and upper surfaces of different-aged leaves. Distribution counts were made on June 5 and July 8, by which time the majority of both aphid populations were on the leaves, and all plants had lost their vigorous growth because of high aphid densities.

Distribution patterns on the leaves are represented as the mean densities per square centimeter for all the replications for each treatment (figs. 2 and 3). Throughout the experiment, *M. sanborni* was more concentrated on the lower leaf surfaces than on the upper leaf surfaces in all sections of the plant. On June 5 (fig. 2) single-species populations of *M. sanborni* on the lower leaf surfaces displayed an increasing density from the top to the lower sections of the plant. In the following month, densities were fairly evenly distributed on the lower leaf surfaces, but *M. sanborni* had the highest mean density on the upper leaf surfaces of the young leaves.

In the mixed-species treatment, *M. sanborni* again was more abundant on the lower leaf surfaces. There were no apparent meaningful differences in the preference for the lower leaf surfaces in the mixed- and single-species populations. However, as the leaves became older, the aphid densities were lowest on the basal portions of the plants with the mixed-species populations.

Unmixed populations of *A. gossypii* in both sampling periods, were about equally distributed on the upper and lower leaf surfaces of the younger leaves as shown in figure 3, but in all other sectors of the plant, the aphids favored the lower surfaces.

The distribution patterns of *A. gossypii* were generally similar in the single- and mixed-species populations. Except for some minor differences on June 5, unmixed populations of *A. gossypii* occurred in greater density on the upper surfaces of the younger leaves and on the lower surfaces of the older leaves than they did in the mixed-species populations.

Both species were more abundant on the lower surfaces of the leaves. As for the upper leaf surfaces of different-aged leaves, *A. gossypii* occurred in greatest numbers on the young leaves. Both species in single- and mixed-species populations displayed different general distribution patterns on the upper and lower surfaces of the leaves in the four sectors of the plant, except for *A. gossypii* on July 8, which was the same in single- and mixed-species populations. The significance of this difference will be discussed in the next section where it deals with the mean total density on the different-aged leaves.

Age of leaf. In the above categories, there were no meaningful differences in aphid leaf distribution patterns between single- and mixed-species population. However, important differences

were evident when aphid densities on the upper- and lower-leaf surfaces were combined under the same arbitrarily established, four vertical divisions of the plant terminal.

On June 6, the unmixed *A. gossypii* populations showed a distribution pattern described by Kennedy *et al.* (1950) as having two peaks, one peak on young leaves and the other on senescent leaves (fig. 4, upper half). At the beginning of our experiment, the terminal shoot was stripped of all its leaves around the area of cage attachment, and only a few young leaves were left near the terminal leaf bud. After the first few weeks, no leaves were removed, and the aphid population increased and infested all the leaves. By June 6, several months after the start of the experiment, leaves were young, maturing, senescent, and dying.

The unmixed *M. sanborni* colony did not follow the generalized aphid distribution pattern on different-aged leaves. Instead, it was more abundant on maturing and older leaves, as indicated by the increase in aphid densities from the upper to the lower portion of the caged plant (fig. 4). A probable explanation for the lower density on the upper one-fourth of the plant was that on June 6, 25 per cent of the *M. sanborni* population was still on the stem (fig. 1). If these aphids on the stem were considered in the distribution pattern of the entire plant, *M. sanborni* would then follow the generalized aphid distribution pattern reported by Kennedy *et al.* (1950).

In the mixed-species populations (fig. 4, upper half) both species showed a marked decrease in leaf density on the leaves on the basal one-fourth of the terminal. Competition was taking place on the older leaves. There was little difference apparent between the number of aphids per square centimeter on the top and bottom sectors, but the actual number of aphids was much greater on the lower leaves, due to the greater leaf area.

The lower half of figure 4 represents the last count taken a month later when densities were higher, with presumably more competition. The distribution pattern of *A. gossypii* by itself was similar to the previous month's pattern, except that density decreased on the lower one-fourth of the plant relative to the other plant levels.

Macrosiphoniella sanborni by itself reversed its distribution pattern after a month; densities decreased as the leaves became older. The difference, however, between the upper one-fourth and the lower one-fourth of the plants was not great.

On July 8, *A. gossypii* in the mixed-species populations displayed a distribution pattern similar to that of the single-species population. This indicated that interspecific competition had little effect on *A. gossypii* at this time. On the other hand, *M. sanborni* in mixed-species populations decreased in density on the lower half of the caged shoot. Thus, interspecific competition did have an effect on the density of *M. sanborni* on the older leaves.

It is evident that early in the experiment *M. sanborni* was abundant on the young leaves and stems, and *A. gossypii* was abundant on the young leaves and terminal bud; however, towards the end of the experiment both species were found mainly on the lower surfaces of the older leaves. Aphids were more abundant on the upper leaf surfaces of the young leaves than on older leaves, and *A. gossypii* was more abundant on the upper leaf surfaces than were *M. sanborni.*

In the short-term experiment, the distribution patterns of the different aphid species were studied and compared during the accelerated aphid growth phase. In Experiment 3, the population trends were followed again in the accelerated growth phase and continued through

the period of population equilibrium. Distribution counts on different parts of the plant were taken during each of these two phases. Doutt and DeBach (1964, p. 119) discussed the phenonenon of population equilibrium as follows:

> ...a single species population tends to fluctuate both positively and negatively with varying intensity and that an "average" density can be derived from the observed numerical fluctuations. Although occasional fluctuations may be rather extreme, the population thus moves about an average level for its particular environment.

Long-term experiments. In the long-term part of Experiment 3, a distribution count was taken late in the period of accelerated growth of the aphid population on August 27 (fig. 16). At this time, about 90 per cent of the *A. gossypii* population was on the leaves; whereas only 60 per cent of *M. sanborni* population was on the leaves, and most of the remaining aphids were on the stems. Therefore, the part of the graph depicting *M. sanborni* density per square centimeter of leaf surface on different sections of the plant represented only about two-thirds of the total aphid population.

Nevertheless, the distribution patterns of each species in the mixed-species treatment can be compared to its own distribution pattern in the single-species treatment. For instance, *M. sanborni* under interspecific competition had a lower density on the leaves than when it was alone on all parts of the plant. The difference can be more clearly seen from the mean number of aphids. The *M. sanborni* alone averaged 1,340 aphids per terminal, but in the mixed-species population the *M. sanborni* count was 658 per terminal. This clearly indicated that interspecific competition with *A. gossypii* definitely depressed the growth rate of *M. sanborni*. The distribution of *M. sanborni* under single- and mixed-species treatments also indicated that interspecific competition affected the total distribution of this aphid on all parts of the plant. Figure 16 shows that 9 per cent more of the *M. sanborni* were found on the leaves in the single-species experiments than in the mixed-species experiments. Since *A. gossypii* was shown earlier to favor the leaves, it was not surprising that competition effects on *M. sanborni* took place in this area.

A comparison of total aphid counts between single- and mixed-species populations indicates that *A. gossypii* was affected by interspecific competition, although this was not clear early in the experiment. In the single-species experiment, population density was only slightly greater on the lower one-fourth of the plants; this proved to be significant, however, in terms of the total aphid counts (see figure 15). Since density is expressed in number of aphids per square centimeters, the total leaf surface area is essential to determine total populations. This difference was especially evident on the lower one-fourth of the plant where the leaves were much larger than on the upper one-fourth of the plant. The mean number of aphids per terminal in the single-species population was 1,126; whereas, only 941 aphids were present under the mixed-species conditions. These data indicate that *A. gossypii* in mixed-species populations was affected by interspecific competition, and that the site of competition was most probably on the basal leaves of the caged terminals.

The distribution counts during the period of population equilibrium were made on November 9. At this time, most of the aphids were found on leaves. Except for *M. sanborni* in the mixed-species populations, where only 85 per cent of its population was on the leaves, all other populations had over 90 per cent of their populations on the leaves (fig. 16).

Macrosiphoniella sanborni under sin-

gle- and mixed-species conditions showed the same general patterns, with the highest density on the younger leaves and steadily decreasing densities on the lower parts of the shoots. However, *M. sanborni* in the mixed-species populations had a lower density in all sectors of the plant. The average density per terminal was 3,050 aphids in the single-species population compared with 1,411 aphids in the mixed-species population. The lower populations of *M. sanborni* under the mixed-species conditions were largely due to differences on the lower half of the plant. Leaf distribution patterns of *M. sanborni* on August 27 and November 9 cannot be compared, because the distribution pattern of the earlier count represented less than two-thirds of the total population. Nevertheless, the shift from stem to leaves which was found in the first experiment occurred again in this experiment.

Aphis gossypii displayed different distribution patterns on the leaves under single- and mixed-species conditions. The average density per terminal was 2,629 aphids in the single-species populations compared to 1,142 *A. gossypii* in the mixed-species populations. In the mixed-species populations *A. gossypii* densities were suppressed in all sectors of the plant, but this was especially true on the upper one-fourth. However, again, it must be emphasized that the differences in the total counts were due to the differences in density on the lower half of the plant.

In the mixed-species populations, interspecific competition affected both species in all sectors of the plant, but the intensity of competition appeared to be greatest for *A. gossypii* near the upper one-half.

The general distribution patterns for the two species alone were similar in both the short- and long-term experiments (figs. 4 and 16). Under mixed-species conditions, only *M. sanborni* appeared to be affected by interspecific competition in the short-term experiment; however, in the long-term experiment both species were affected.

Alate removal and population growth

Alate production clearly suppressed the growth curve of *M. sanborni* (fig. 6). At the end of the experiment to study the effects of alate removal and retention, *M. sanborni* populations with alates retained reached an average of 2,521 aphids per terminal compared with 1,594 aphids when the alates were removed. Although the alate retention resulted in twice the number of aphids, this did not indicate the reproductive potential of the alate segment of the population with certainty. During the last count, over 50 per cent of the alate aphids, or approximately 900 aphids, were trapped on honeydew deposits on the upper surfaces of the leaves before they were able to reproduce.

A similar comparison, when alates were removed in one treatment and not in the other, was made with *A. gossypii* and can be seen in figure 8. From May 29, the first date of alate retention, to June 18, there was no large difference in the growth curves for the two populations, since alate production up to June 18 was relatively low. After this date, however, the aphids increased rapidly in the treatment with alate retention. In the final count there were 5,367 aphids when the alates were allowed to remain and only 3,297 aphids when the alates were removed. This big difference must have been due to increased alate production from June 18 to July 8.

In Experiment 2, the effects of alate removal and retention on mixed-species populations were studied, but single-species populations were also observed. Although the effect of alate removal in single-species populations had already been studied in the first experiment, these treatments were repeated here in

order to compare results to those of the mixed-species treatments. Aphid growth curves were also studied in terms of physiological changes in the plant that resulted from the removal of the terminal growing point.

The two *A. gossypii* single-species treatments in this experiment indicated that there was little difference between the growth curves with alate removal and retention (fig. 10) since alate production was low.

The population growth curves in the *M. sanborni* single-species treatments clearly reflected the effects of alate removal (fig. 11). In the treatment in which the alates were retained, the population steadily increased until the middle of September when the plants collapsed. The alate-removal treatment suggested that an equilibrium level had been established; however, this equilibrium level, maintained for over a month, could have been due to plant decline as well as to the intensity of alate production. Alate adult removal was probably responsible for the first half of the plateau, and decline of the plant was probably responsible for the last half.

In the mixed-species treatments when alates were removed, *A. gossypii* reached higher densities in two replications, and *M. sanborni* became higher in the other two replications. Apparently the two most important factors determining which species became more abundant were: first, the early establishment of numerical superiority and, second, the interspecific competition that followed. The experiment was not designed to determine how aphid populations with different initial densities would affect the numerical superiority of each species. However, variations in initial densities did occur, even though the terminals were originally infested with the same number of individuals.

Figure 12 shows the effects of early numerical superiority in the alate-removal treatment. Colonies of *M. sanborni* on plant numbers 2 and 4 were numerically superior to *A. gossypii* colonies in the early accelerated growth phase. This numerical superiority was maintained in both colonies up to the time that the plants declined. In plants 1 and 3, both species were equally abundant until about August 14. Subsequently, *A. gossypii* increased more rapidly and reached higher peaks than *M. sanborni.*

It seems that when *M. sanborni* had an early numerical advantage it reached a higher level than *A. gossypii,* but when the aphid densities of both species remained the same for some time, *A. gossypii* became numerically superior before the populations declined. In the other mixed-species treatment with alates retained, the species that had an early numerical advantage also reached a higher aphid density than the other species (fig. 13). In three out of four colonies (plant numbers 5, 6, and 8), *M. sanborni* maintained its numerical superiority until the plants declined. In all of these mixed-species colonies, the species with the numerical disadvantage was considerably more depressed than in the alate removal treatments. This greater differential between populations with alates retained seemed to take place because more potentially reproductive adults made possible a faster growth rate, thus greater interspecific competition with the other species.

In most cases, the colonies in which the alates were retained displayed a steeper accelerated growth curve than the colonies from which the alates were removed. Moreover, it was not only a matter of alate formation affecting the aphid growth rate, but the growth rate also affected alate production. By comparing the different replications as shown in figure 12, it can be seen that the aphid species having the earliest and highest initial growth and having the steepest growth curves produced the most alates. Even though these colonies produced the most alates they were able to maintain their numerical superi-

ority, because their high numbers hindered the other aphid species through interspecific competition. Under these experimental conditions, the intensity of alate production probably was not a primary factor in the determination of the numerically superior species, but the intensity of alate production was dependent on the type of population growth.

Moreover, early initial numerical superiority of each species was not determined by interspecific competition, because the difference in habitat selection and low aphid density in the early growth phase minimized the effects of interspecific competition. Probably the factors involved in determining the early growth rates of the aphid population were differences in the individual physiological condition of the plants, in the genetic constituent of the aphids, and in the vigor and age of the colonizing adult aphids.

The distribution pattern of the mixed-species populations shown in figure 14 substantiates the habitat selection found in the first experiment. Up to August 10, over half of the *M. sanborni* population was found on the stem, and about 90 per cent of the *A. gossypii* population was found on the leaves. The stem did not grow, since the terminal growing point of each plant was removed, but the leaf area increased. The distribution graphs also indicated that *M. sanborni* maintained about the same density on the stem throughout the experiment, and the subsequent population increase took place on the leaves.

Single-species short-term population

Counts of the total populations were taken at frequent intervals in Experiment 1 to study the effects of competition and alate formation on population dynamics. Census of age distribution along with the total aphid counts would have been advisable but not practical, because the various instars of the aphids would have been difficult to distinguish without the aid of a microscope.

Single-species treatments were compared with mixed-species treatments to develop evidence of interspecific competition.

Single-species population growth curves of *M. sanborni* and *A. gossypii* are represented in figure 5 as the mean number of aphids per terminal. The means were based on seven replications. One replication from each treatment had to be omitted because of flower bud formation.

The initial increase of *M. sanborni* was greater than *A. gossypii;* however, during the latter part of the accelerated growth phase, *A. gossypii* displayed a steeper growth curve than *M. sanborni.* Since the experiment was terminated before environmental resistance could greatly influence the growth of the population, both species displayed approximately "J"-shaped growth curves. The *M. sanborni* growth curve was less steep than that of *A. gossypii* because more alates were produced. This will be discussed in the section on mixed populations.

At the termination of the experiment, *A. gossypii* outnumbered *M. sanborni* more than two to one. However, as Cook (1961) indicated, numbers alone may not be adequate to analyze population densities. Since *A. gossypii* is two or three times smaller than *M. sanborni,* it can have two or three times the density of *M. sanborni* in areas of comparable size. Therefore, in equal areas, one can expect a greater number of *A. gossypii* to be present before the same degree of crowding or competition will take place.

Long-term populations of *Aphis gossypii*

Reinhard (1927) reported that *A. gossypii* alate formation was strongly influenced by crowding. Other workers who have reported similar findings on

different aphid species are: Ackerman (1926), Bonnemaison (1951), Brittain (1921), Comstock (1950), Johnson (1965), Lees (1961), Lowe and Taylor (1964), Paschke (1959) and Wilson (1938).

Color variation in single colonies of *A. gossypii* has been reported by many early workers: Gillette (1908), Paddock (1919), Patch (1925), Pergande (1896), and Theobald (1926). Wall (1933) was the first to point out a direct correlation between the color of *A. gossypii* individuals and their body size and appendage length; the darker morphs were larger. Wall observed that sparse colonies maintained by fumigation and spray programs generally remained dark, but when colonies were allowed to increase, the light morphs became dominant under both field and greenhouse conditions. Conducting a series of individual rearings in the laboratory in which the alates produced the greatest number of light morphs (14 per cent), he reported that the light morphs produced an average of one-third the number of alates that the intermediate or dark morphs produced.

Shull (1932) studied the green and yellow morphs in *Macrosiphum euphorbiæ* and found that neither color was genetically inherited and that the yellow morph produced fewer alates. Lowe and Taylor (1964) reported that the red strain of *Acyrthosiphon pisum* (Harris) produced more alates than the green strain. Reinhard (1927), however, did not consider color variation in his studies of alate production in *A. gossypii*.

Swift (1958) in his study on host suitability for *A. gossypii* reported that cotton was the least suitable of all the plants used in his experiment, and he found the highest percentage of light morphs on cotton. This suggested a possible correlation between light morphs and unfavorable hosts.

Kring (1959) reported that *A. gossypii* passed the unfavorable summer period in Connecticut in the small, yellow morph on Catalpa when extremely hot, dry periods wilted the leaves during the heat of the day. He found that these diminutive yellow morphs did not grow or reproduce until conditions became favorable. To determine if this was the estivating form of *A. gossypii,* he conducted a laboratory test using Rose of Sharon cuttings as the alternate host. He found that the small morphs transferred to Rose of Sharon in nutrient solution gave rise to multicolored morphs characteristic of the species. When transfers were made to Rose of Sharon cuttings growing in distilled water, 90 per cent of all the transfers remained small and yellow, but did have limited growth and reproduction.

Lowe and Taylor (1964) reported that the red and green strain of *Acyrthosiphon pisum* became pale yellowish, on poor plants under crowded conditions, although the original color returned when the culture revived. They added that similar changes have been observed in many other aphid species. Although Lowe and Taylor (1964) made no mention of size change along with the color change, it is presumed that the size changes did occur, and these morphs were probably in estivation or semi-estivation as reported by Kring (1959) for *A. gossypii.*

Essig and Abernathy (1952, page 11) reported that certain *Periphyllus* species estivate in the first instar through the long, hot summer. Dixon (1963) reported that the sycamore aphid *Drepanosiphum platanoides* (Schr.) undergoes a reproductive diapause. He mentioned that the nutritive status of the host plant and population density are the most important factors causing the induction of reproductive diapause.

The first of two periods of *A. gossypii* alate production occurred between August 5 and September 21, with an average daily peak of 36 alates being

produced between August 13 and 17. The second alate production period was from November 5 to January 4, with its average daily peak of 23 alates being produced between December 7 and 14.

The first period of alate production occurred during the early accelerated growth phase of the population. Alate production gradually decreased as the population density continued to increase, which indicated that alate production was not caused by high aphid density.

No counts were made to determine the percentage of yellow and dark morphs before the decline in alate production; however, the percentage of small, yellow morphs observed was negligible. On September 14, a count was taken of small, yellow morphs that occurred in the populations described in figure 18. They comprised 73 per cent of the population on plant 1, 92 per cent on plant 2, and 30 per cent on plant 3. The difference between these light morphs and estivating morphs which are diminutive and yellow should be clearly understood. The yellow morph in the multicolored colonies on healthy plants are not as pale nor as small as the estivating or semi-estivating morphs.

The differences in the percentage of small, yellow morphs on the three plants was probably due to the differences in the initial accelerated growth rate. Both aphid colonies in plants 1 and 2 (fig. 18) rapidly increased at first and had high alate production. This initial acceleration would bring about unfavorable conditions sooner than on plant 3 (fig. 18) which harbored an aphid colony with a slower initial rate of increase. Kring (1959) showed that *A. gossypii* produced small and yellow morphs under unfavorable conditions.

The fast rate of increase during the early growth phase resulted in higher alate production, as was demonstrated in the second short-term experiment. On plant 3 (fig. 18) the initial rate of increase was low, and no prominent period of alate production occurred during the initial growth phase. In the other two replications, peak alate production occurred from August 13 to 20 when the densities were approximately 700 aphids per replication. However, during this period there were less than 100 aphids on plant 3, and it was not until September 9 that the aphid colony on plant 3 reached a count of 700 aphids.

In the populations described in figure 18, aphid colonies on plants 1 and 3 displayed a second peak period of alate production; however, the aphids on plant 2 did not display any prominent second peak. Plant 2 was the only replication on which 90 to 99 per cent small, yellow morphs occurred during the last three months of the experiment. Furthermore, plant 2 had a higher density during this period than did the other two plants. Thus, there is strong evidence that alate production was prevented by the high percentage of small, yellow morphs and/or by high aphid density. This suggests the small, yellow morphs were in semi-estivation and did not respond to the environmental stimuli that triggered alate production in the dark morphs.

The percentage of small, yellow morphs can also help explain the decrease in alate production of *A. gossypii* after the initial growth phase. The increase in the small, yellow morphs could be related to changes in plant physiology which subsequently resulted in morphological and physiological changes in the aphid populations. These changes that occurred in the plants and the aphid populations are a direct result of increases in aphid density. Since plants supporting a high aphid population are stunted, a high percentage of the aphids produced under these unfavorable conditions are the small, yellow morphs.

Accelerated growth phase. Odum (1959) distinguished a "J"-shaped growth form from a sigmoid growth form in graphs depicting population trends when environmental factors abruptly block population increase. In the sigmoid curve the asymptote is gradually gained as the environment becomes less conducive to aphid production—and finally an equilibrium level is reached and maintained. He mentions that the "J" curve displays no equilibrium level and that relatively unrestricted growth is usually suddenly halted when the population runs out of some resource, or when frost or other seasonal factors cause the population to crash abruptly.

By the definition above, the growth curve of *A. gossypii* in the single-species experiment fits the sigmoid category, because it reaches the equilibrium level (fig. 17). There was, however, no indication of reduced acceleration near the asymptote level, which characterizes a sigmoid growth curve. Just before the inflection point of the growth curve, the population was suddenly reduced because of a heat wave. This might be interpreted as an example of a physical factor temporarily causing a sigmoid curve on the graph to take on a "J" shape.

Equilibrium phase. In this experiment, the equilibrium position was maintained for a period of approximately 80 days before the plants finally collapsed (fig. 17). Although the number of generations that occurred during this period was not determined, a very rough estimate would be 10 overlapping generations during the 80-day period. This estimation was derived from the work of Paddock (1919) with *A. gossypii* on cotton. During the period the population maintained an equilibrium position, alate production was low, except near the termination of the experiment. The small number of alates produced certainly was not important in the regulation of the population. Moreover, the aphid colony on plant 2 had no second peak of alate production, but the aphid population had clearly achieved an equilibrium position (fig. 18).

One of the primary factors in the maintenance of the equilibrium position was the development of the small, yellow morphs. These aphids were probably in a semi-quiescent state of slow development and low productivity. As previously mentioned, Kring (1959) observed that *A. gossypii* on Rose of Sharon cuttings in distilled water remained small and yellow, developed slowly, and reproduced at a low rate. He also reported that unfavorable conditions were the primary factor that brought about the small, yellow morphs. In this experiment, the unfavorable host conditions were caused by high aphid densities on the plants. Although the plants had deteriorated, they were still sufficiently strong to maintain high aphid populations for several months.

Only a few counts were taken to determine the proportion of small, yellow morphs in the various replications. In the populations described in figure 18, the aphid colony on plant 3 contained 30 per cent small, yellow morphs on September 14 and 65 per cent small, yellow morphs on October 21. On plant 1, 70 per cent of the population was made up of small, yellow morphs on September 14. Although later counts were not made, this replication was observed to have the highest percentage of dark morphs near the end of the experiment. On healthy plants small, yellow morphs may be present in small numbers in *A. gossypii* populations during the early accelerated growth phase. Nevertheless, these small, yellow morphs became dominant during the equilibrium phase of the population and brought about regulation by reducing natality in the population.

Production of the small, yellow

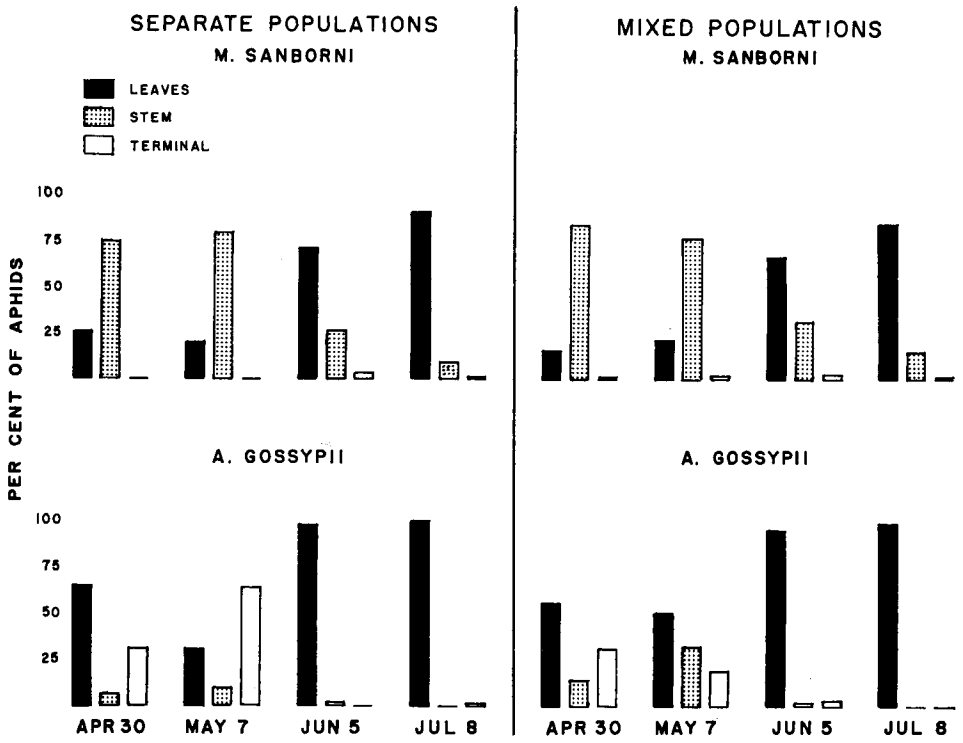


Fig. 1. Distribution of separate and mixed populations of *M. sanborni* and *A. gossypii* on the leaves, stem, and apical terminal.

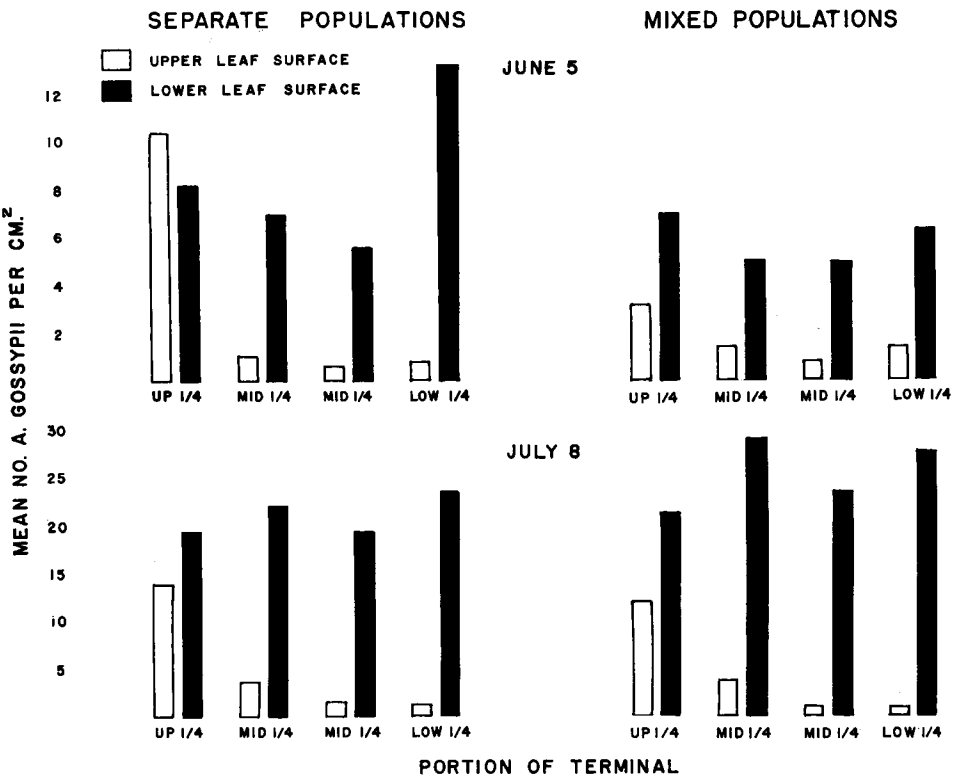


Fig. 2. Population distribution of *M. sanbornii* on upper and lower leaf surfaces when separate and mixed with *A. gossypii* on two different dates.

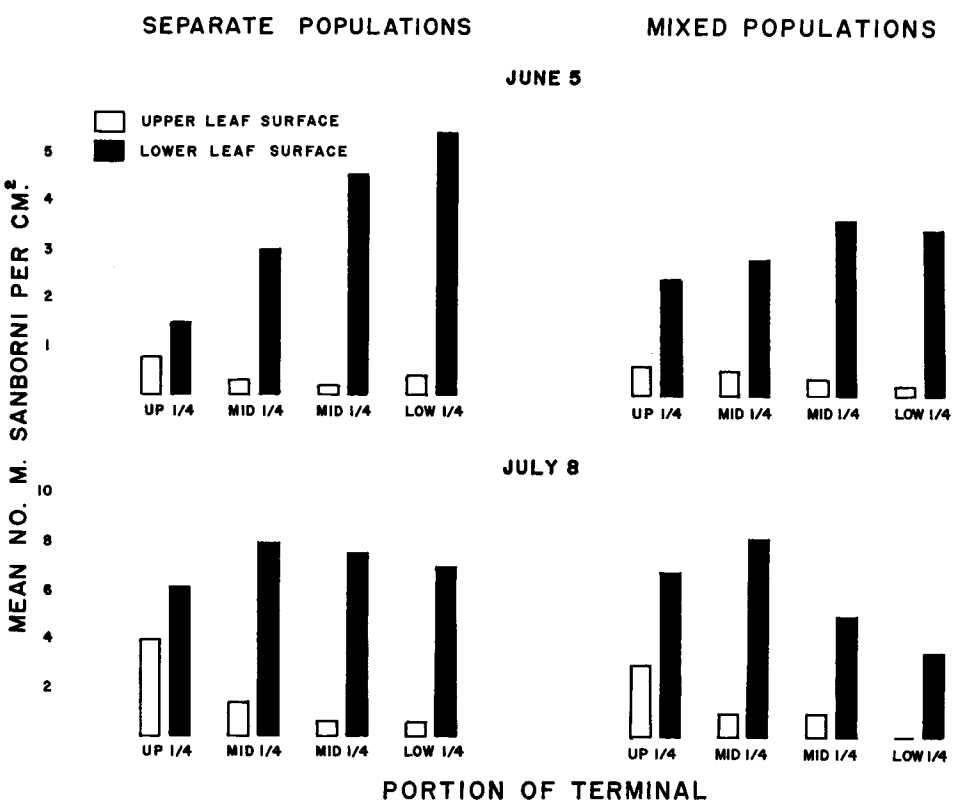


Fig. 3. Population distribution of *A. gossypii* on upper and lower leaf surfaces and various leaf sections when separate and mixed with *A. gossypii* on two different dates.

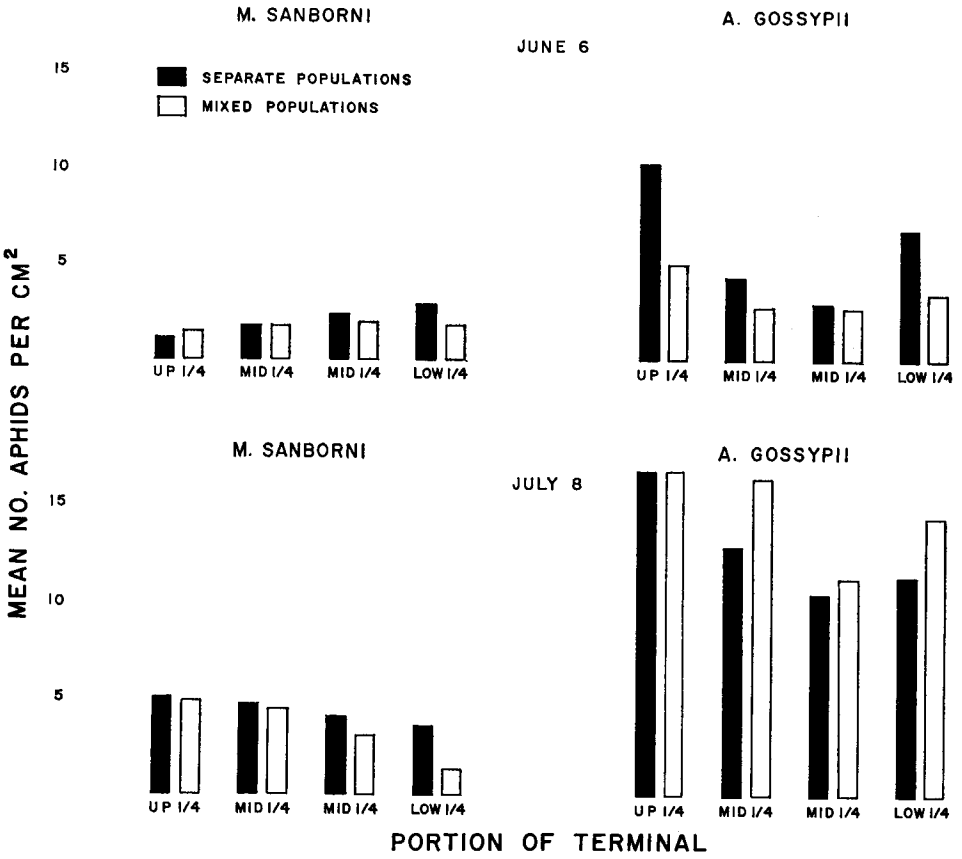


Fig. 4. Population densities of separate and mixed populations of *M. sanborni* and *A. gossypii* on various parts of the plant on June 6 and July 8.

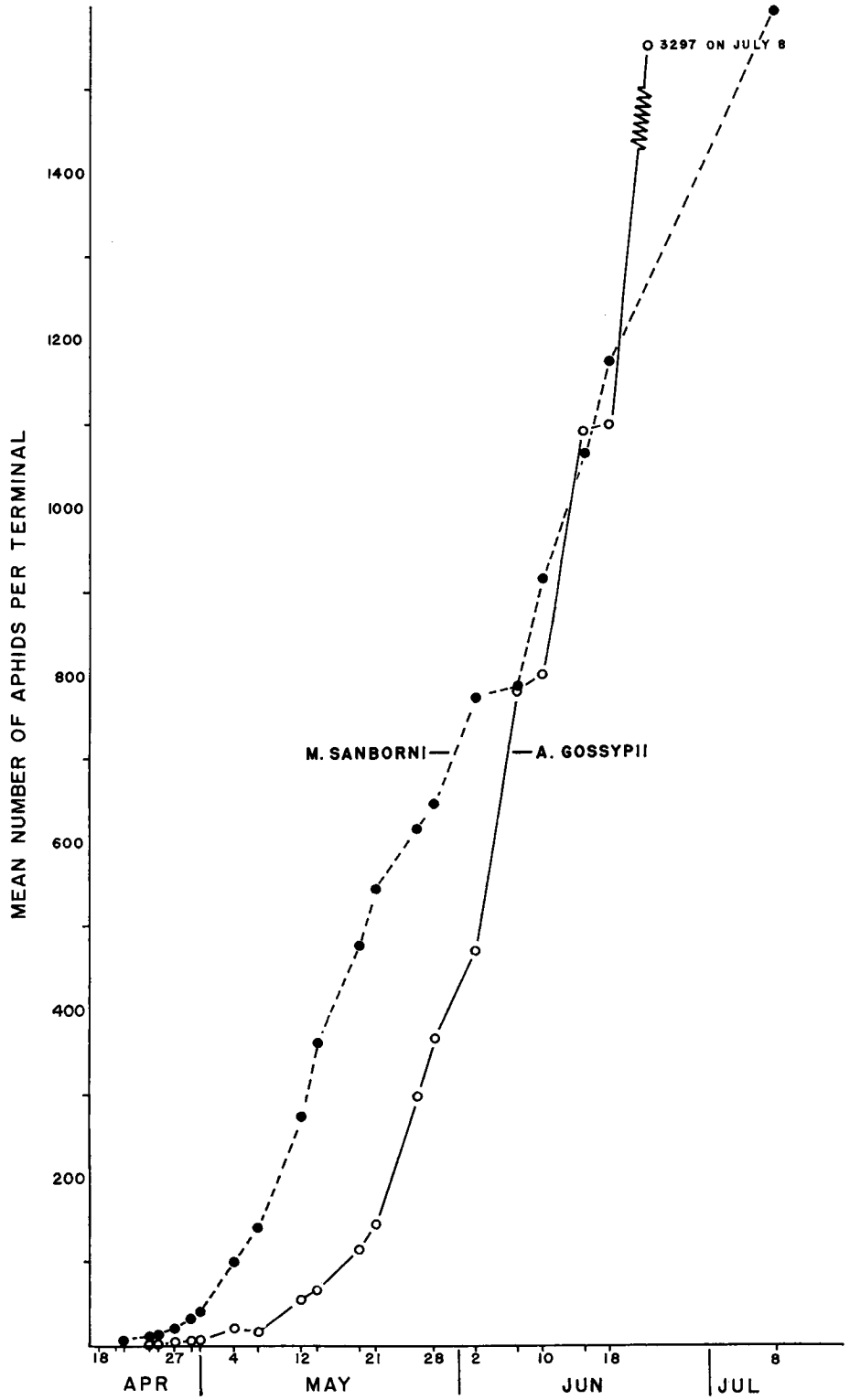


Fig. 5. Growth curves for separate populations of *M. sanborni and A. gossypii* with alates removed continuously before they deposited young.

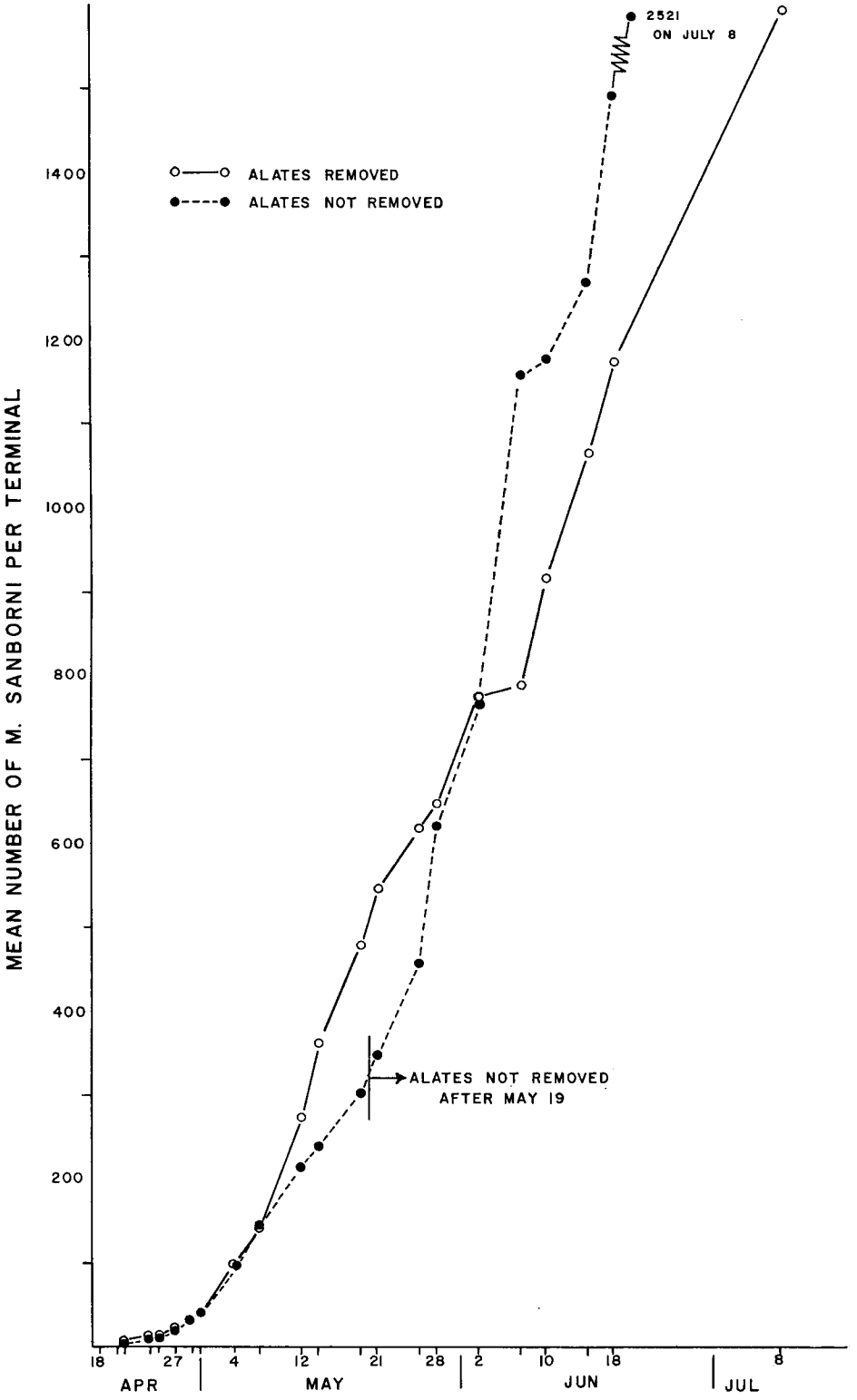


Fig. 6. Effects of alate removal on population growth curves of *M. sanborni*.

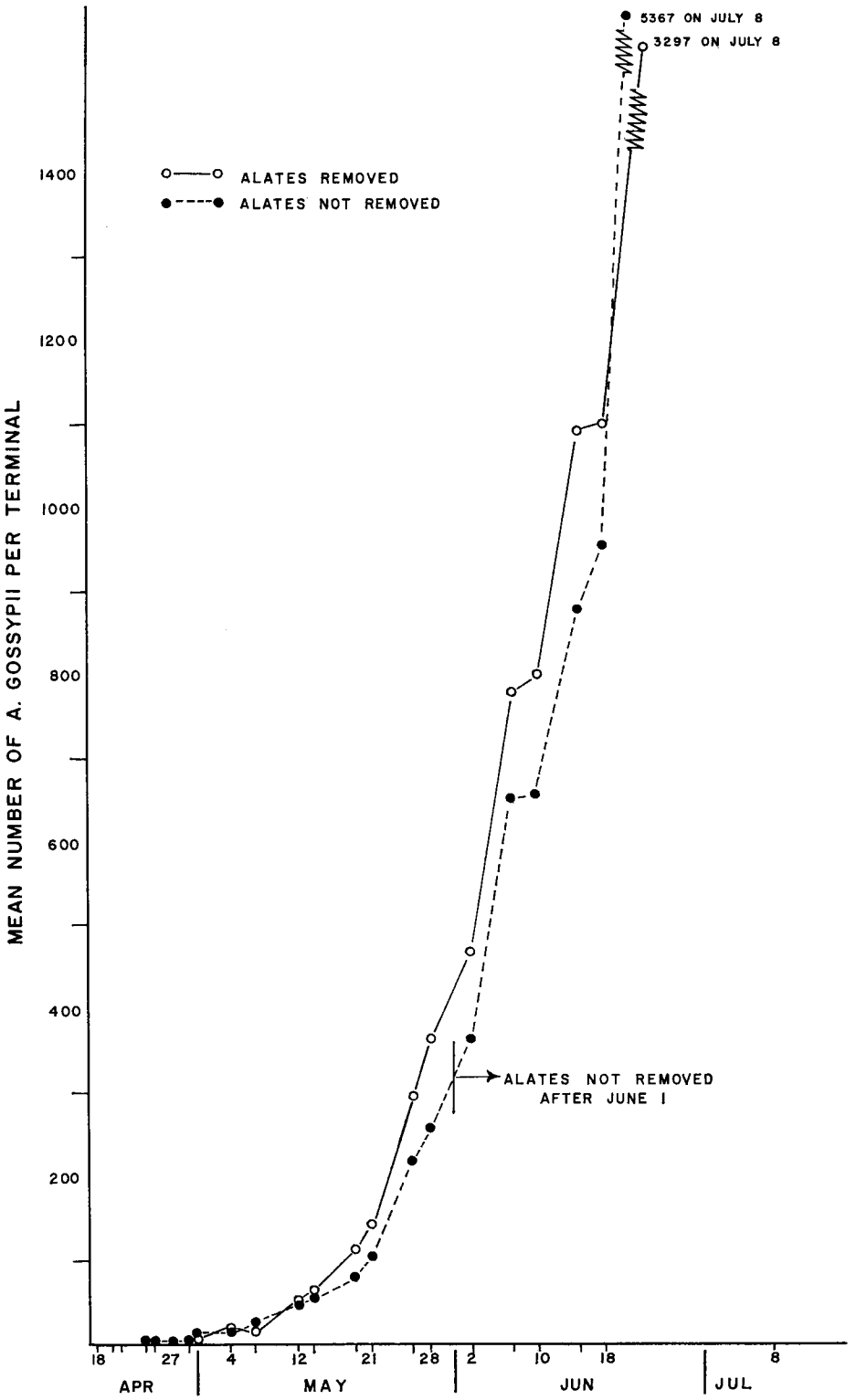


Fig. 7. Effects of alate removal on population growth curves of *A. gossypii*.

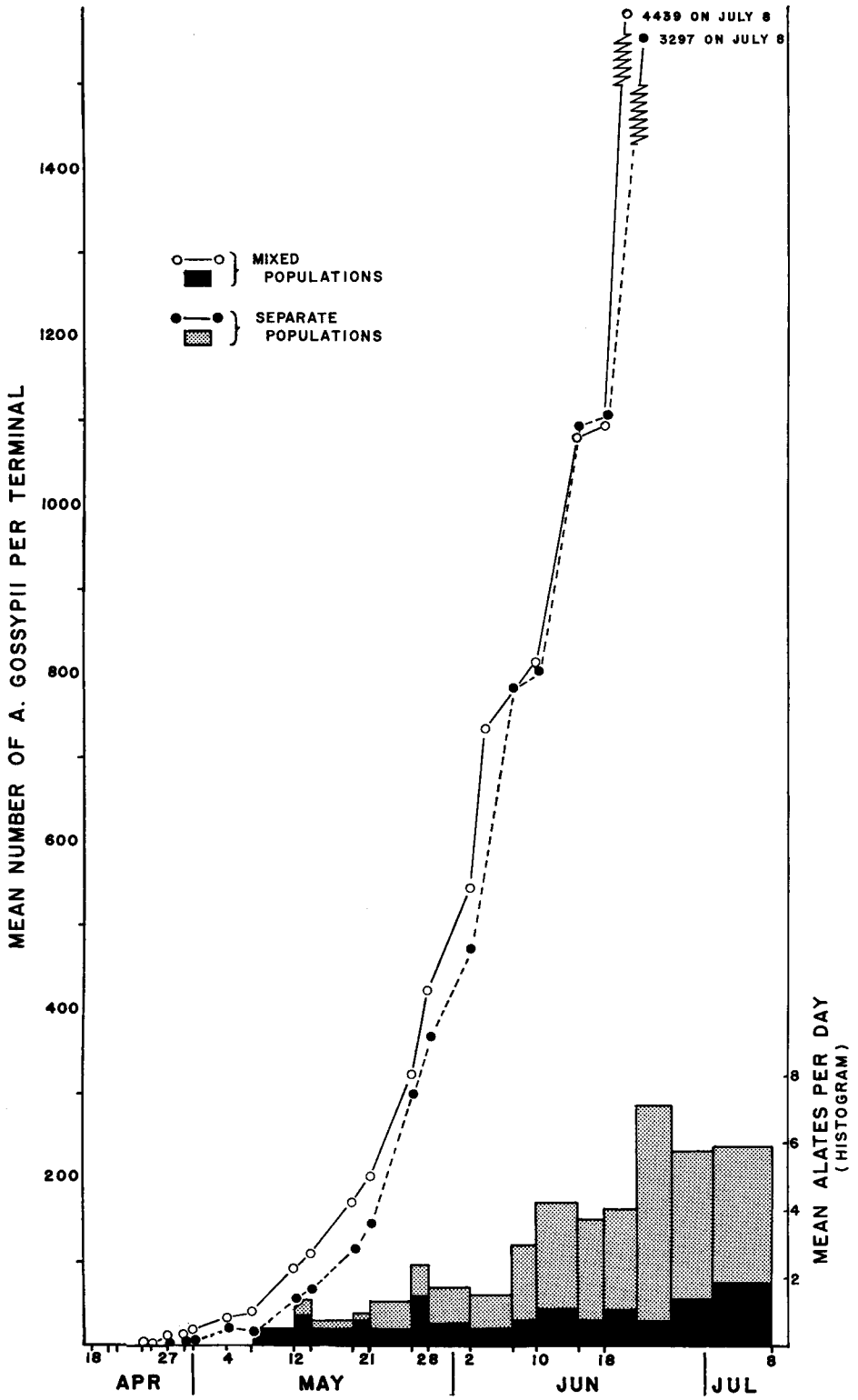


Fig. 8. Population growth curves and alate production for *A. gossypii* when separate from and mixed with populations of *M. sanborni*.

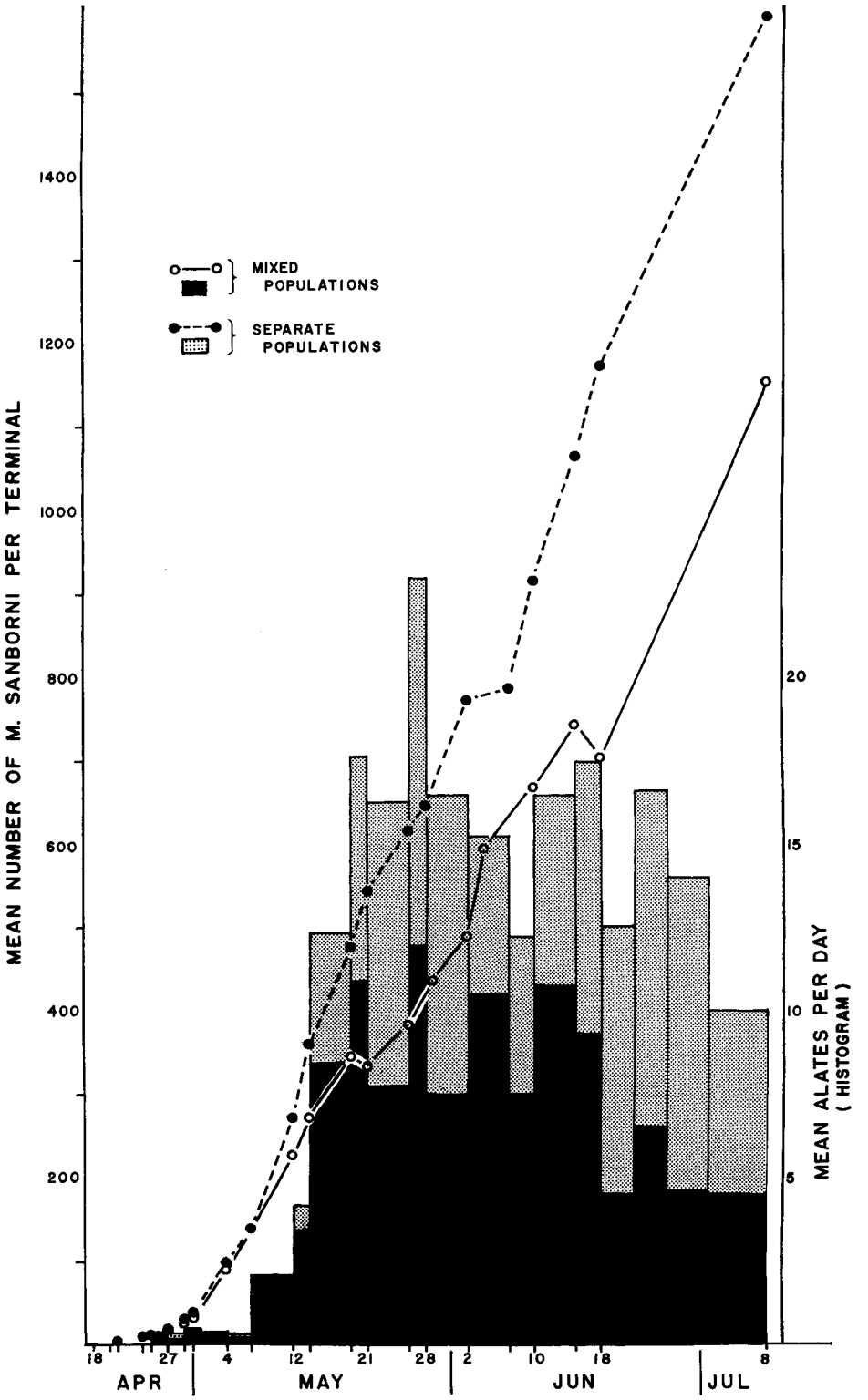


Fig. 9. Population growth curves and alate production for *M. sanborni* when separate from and mixed with populations of *A. gossypii*.

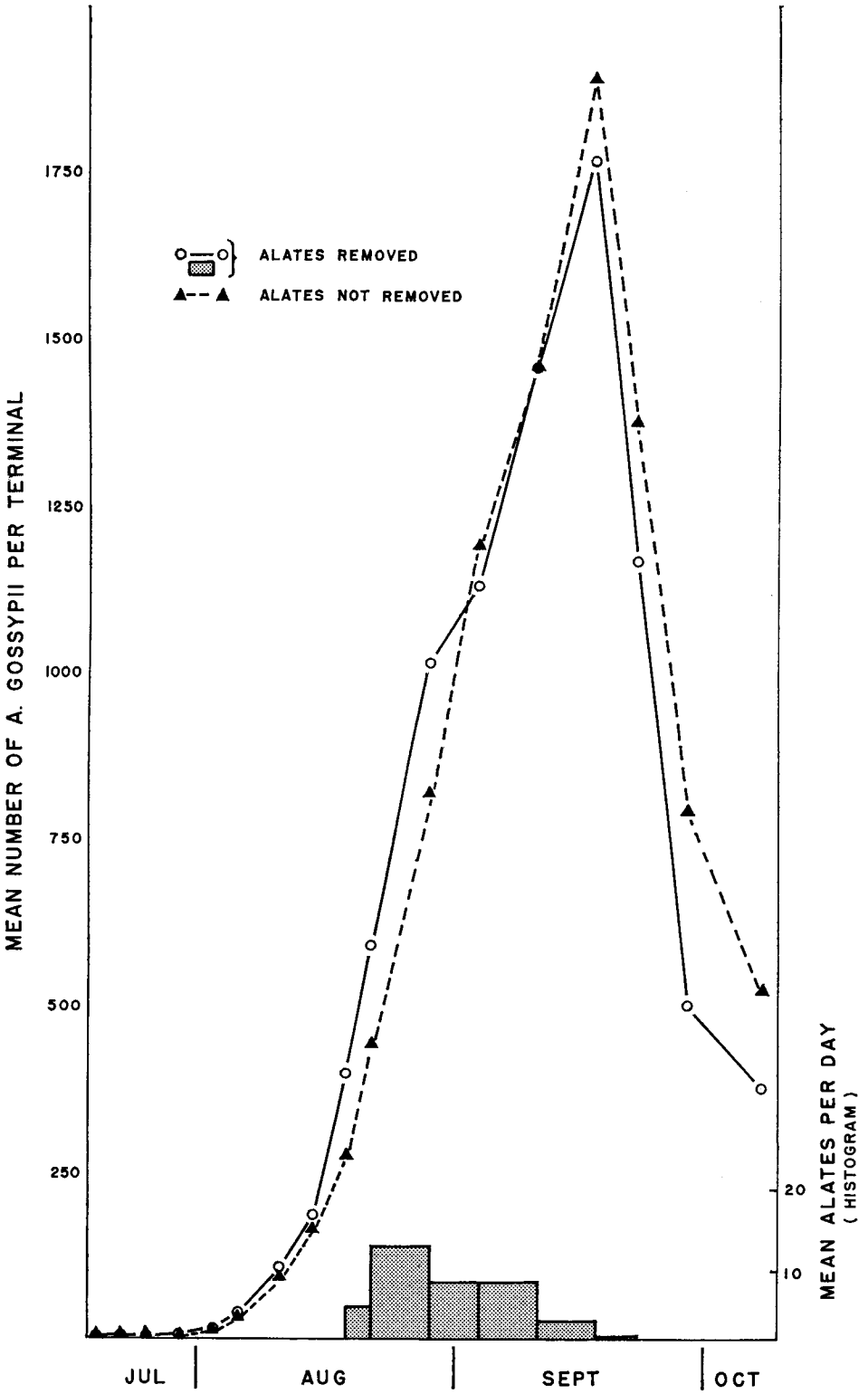


Fig. 10. Effects of alate removal on population growth curves of *A. gossypii*.

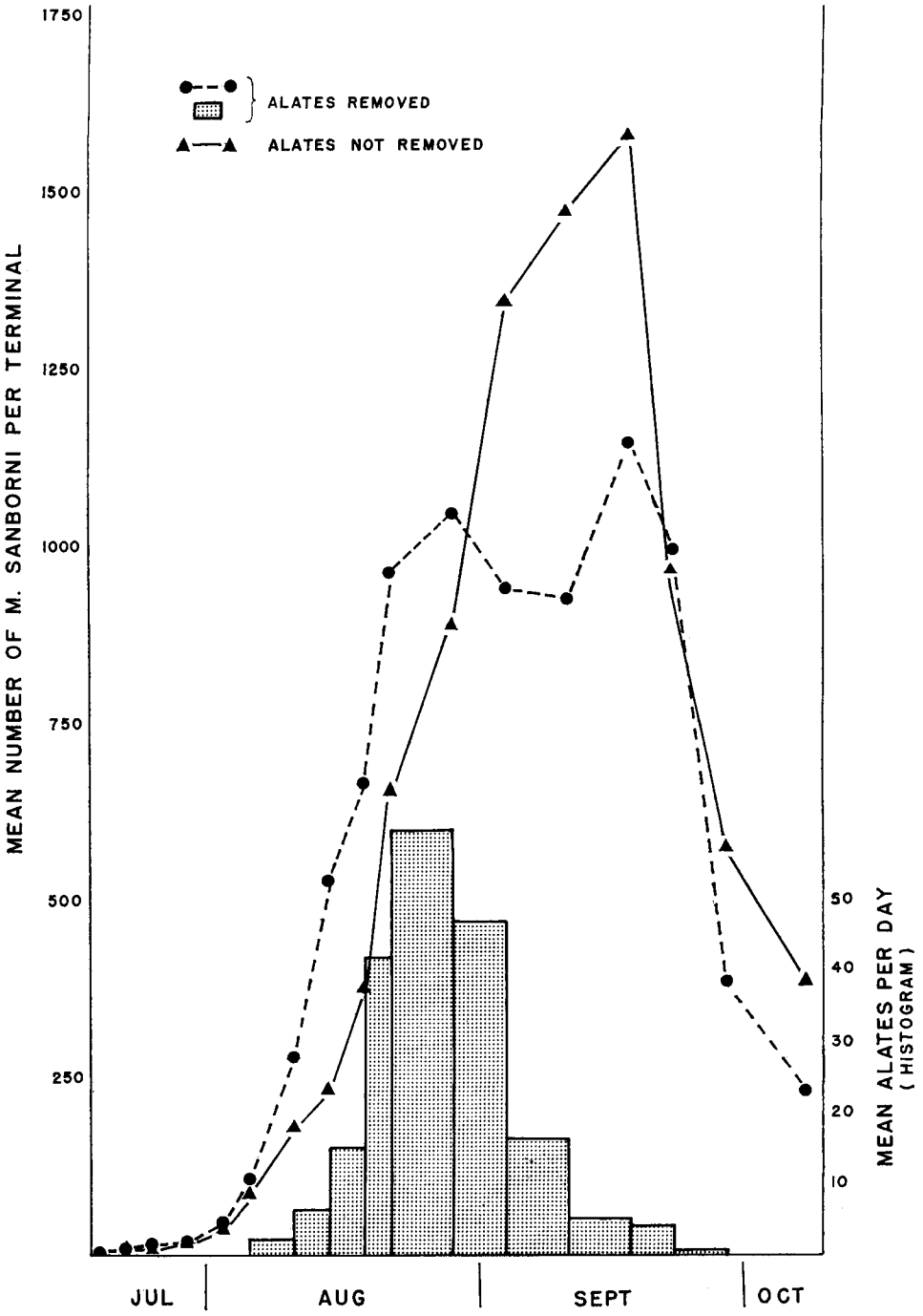


Fig. 11. Effects of alate removal on population growth curves of *M. sanborni.*

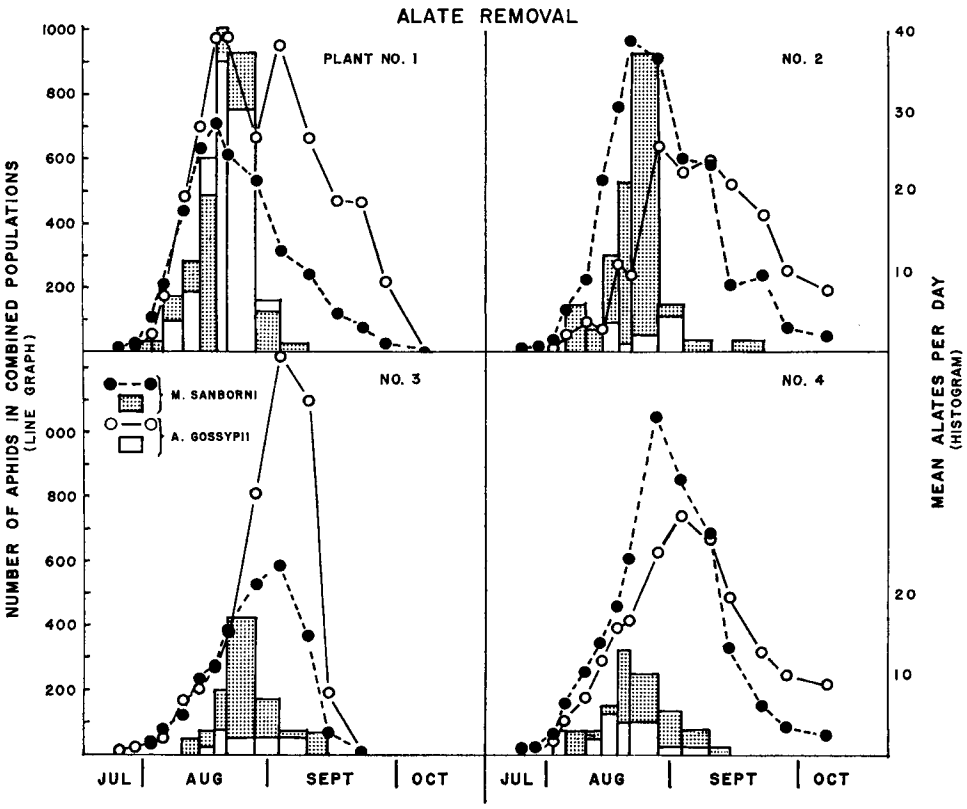


Fig. 12. Population growth curves and alate production for mixed populations of *M. sanborni* and *A. gossypii* on individual plants when alates were removed before depositing young.

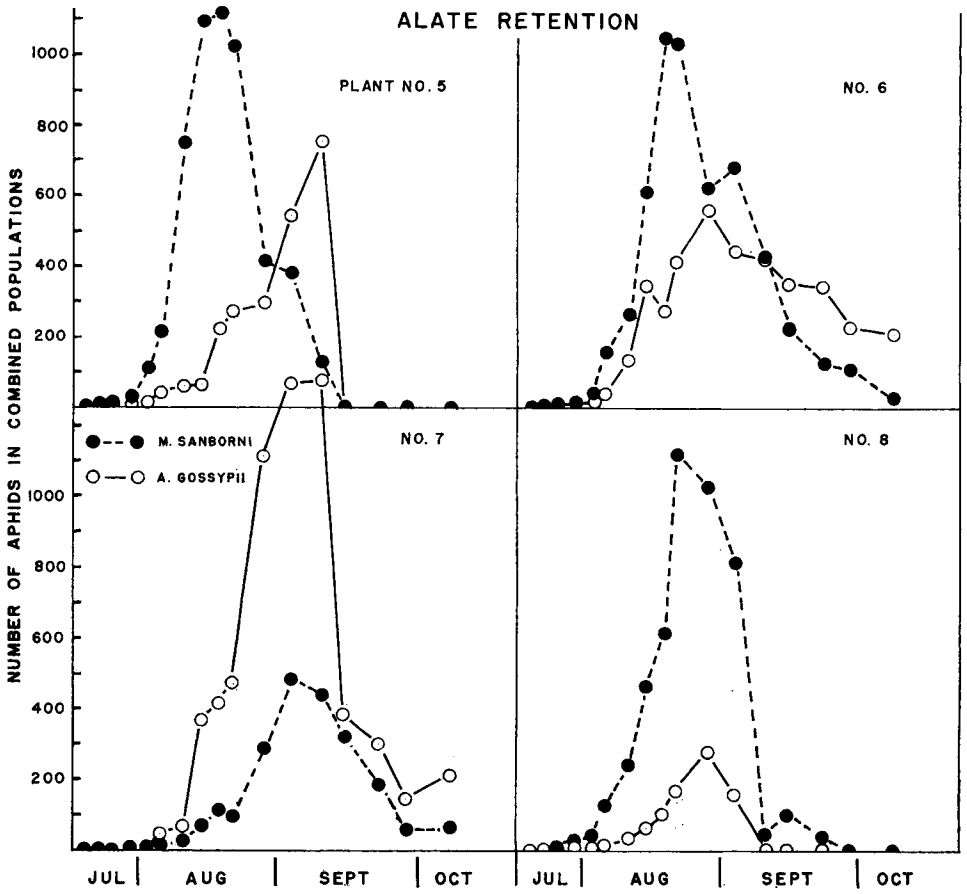


Fig. 13. Population growth curves for mixed populations of *M. sanborni* and *A. gossypii* on individual plants when alates were retained.

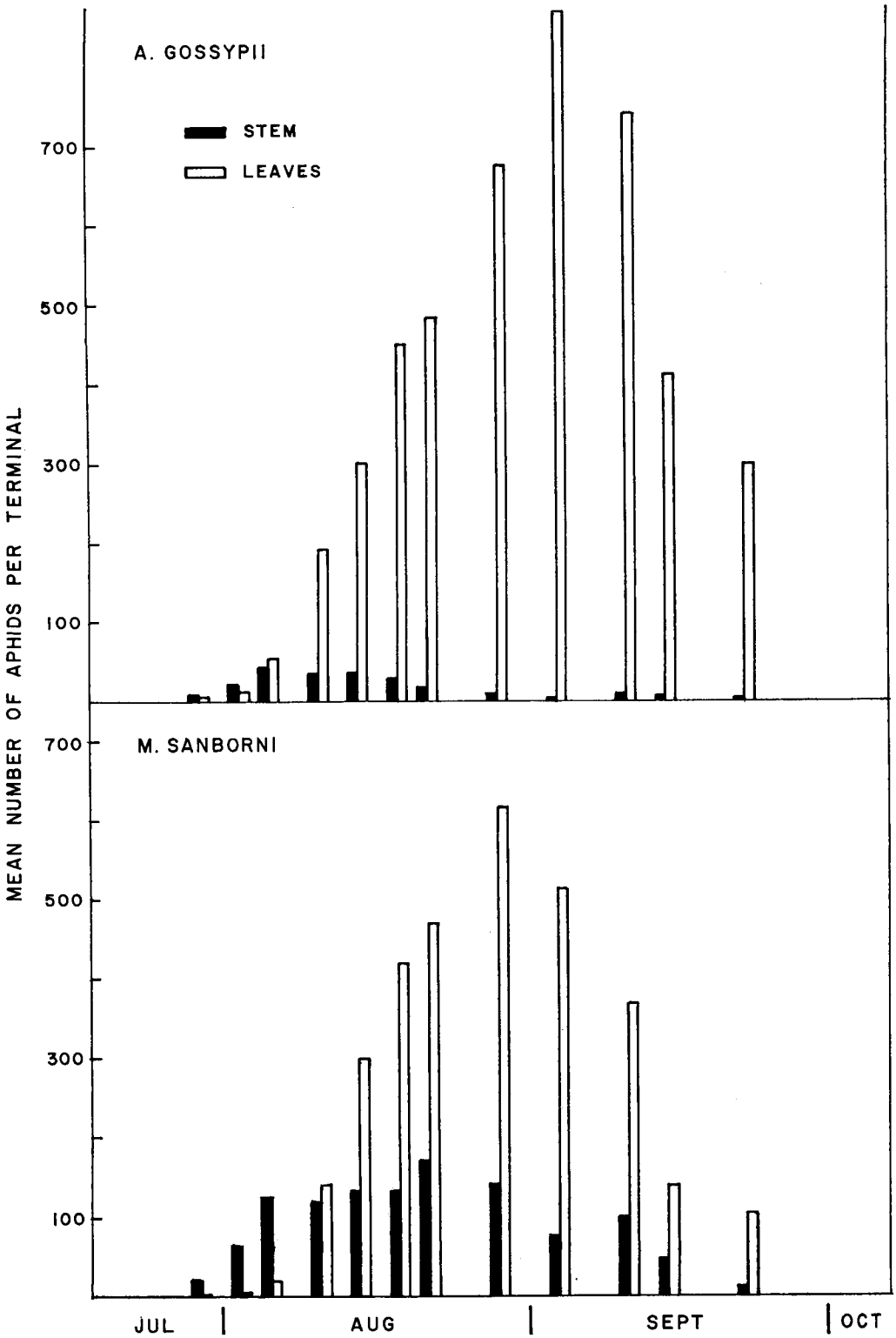


Fig. 14. Distribution of *M. sanborni* and *A. gossypii* on the stem and leaves of the plant.

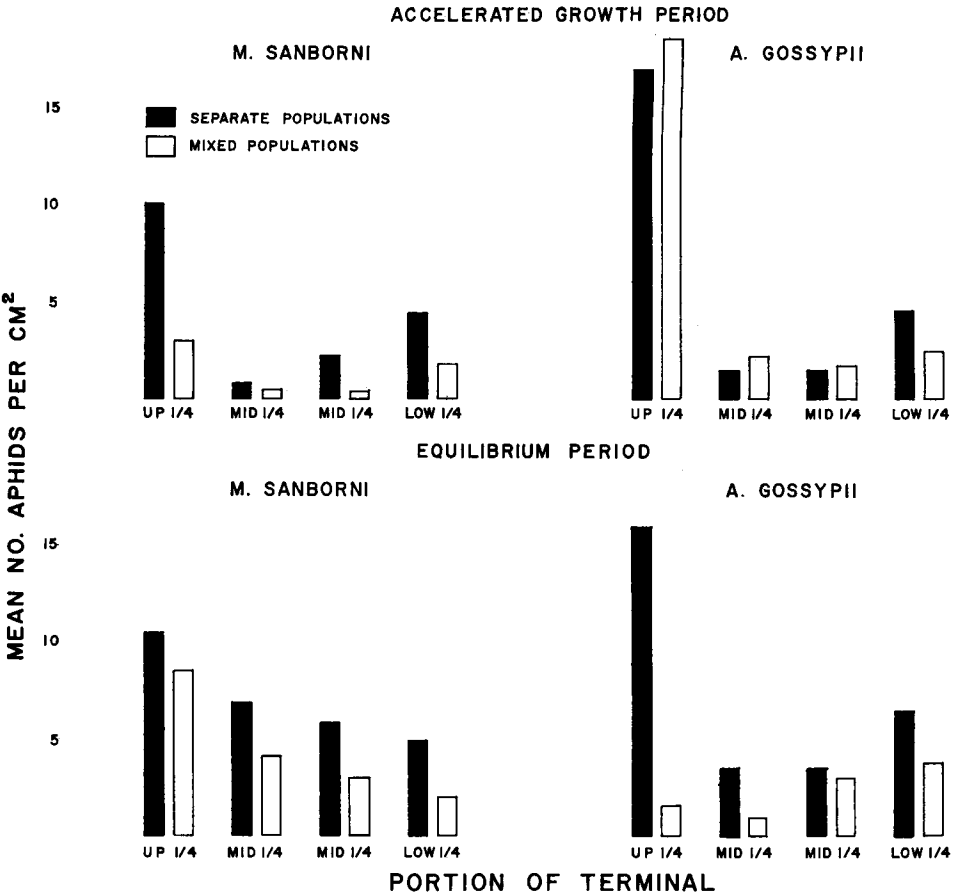


Fig. 15. Distribution of *M. sanborni* and *A. gossypii* on various parts of the plant terminal during the accelerated growth period and after population equilibrium.

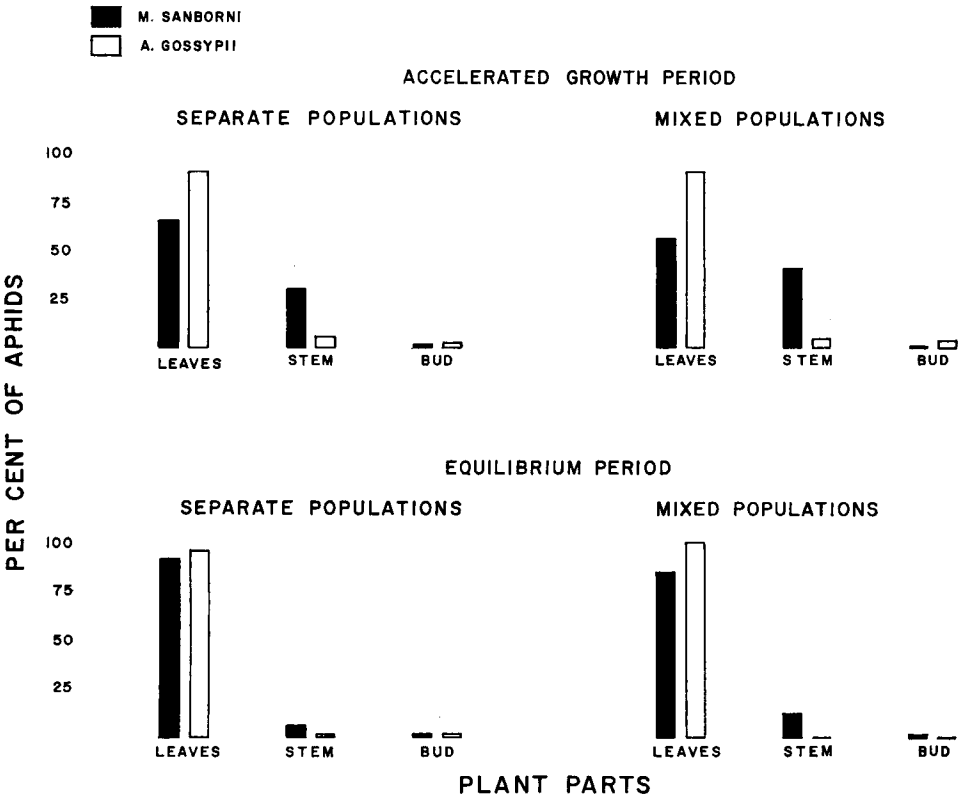


Fig. 16. Distribution of *M. sanborni* and *A. gossypii* on the leaves, stem, and bud during the accelerated growth period and after population equilibrium.

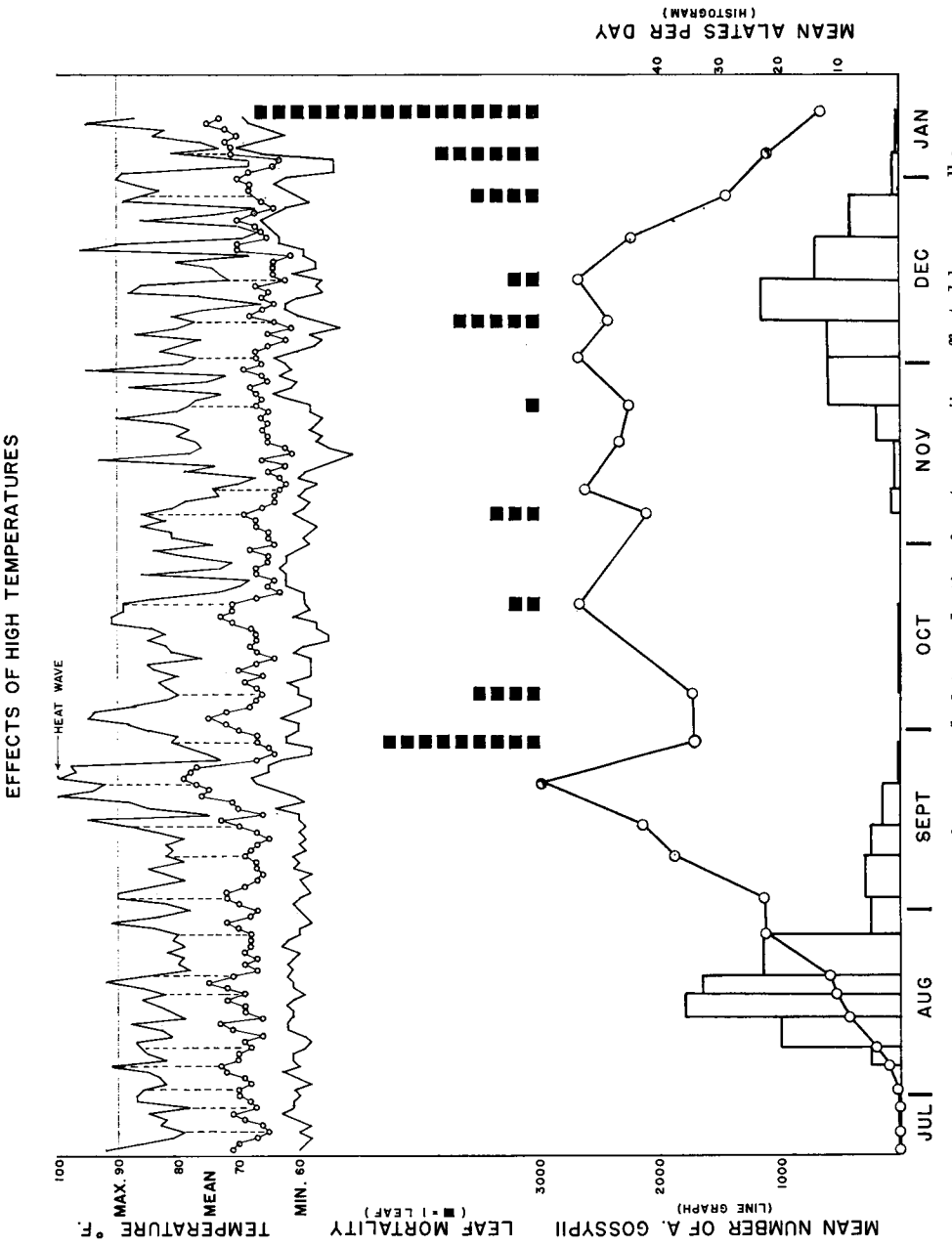


Fig. 17. Population growth curve and alate production for *A. gossypii* as affected by unusually high temperatures with subsequent leaf mortality.

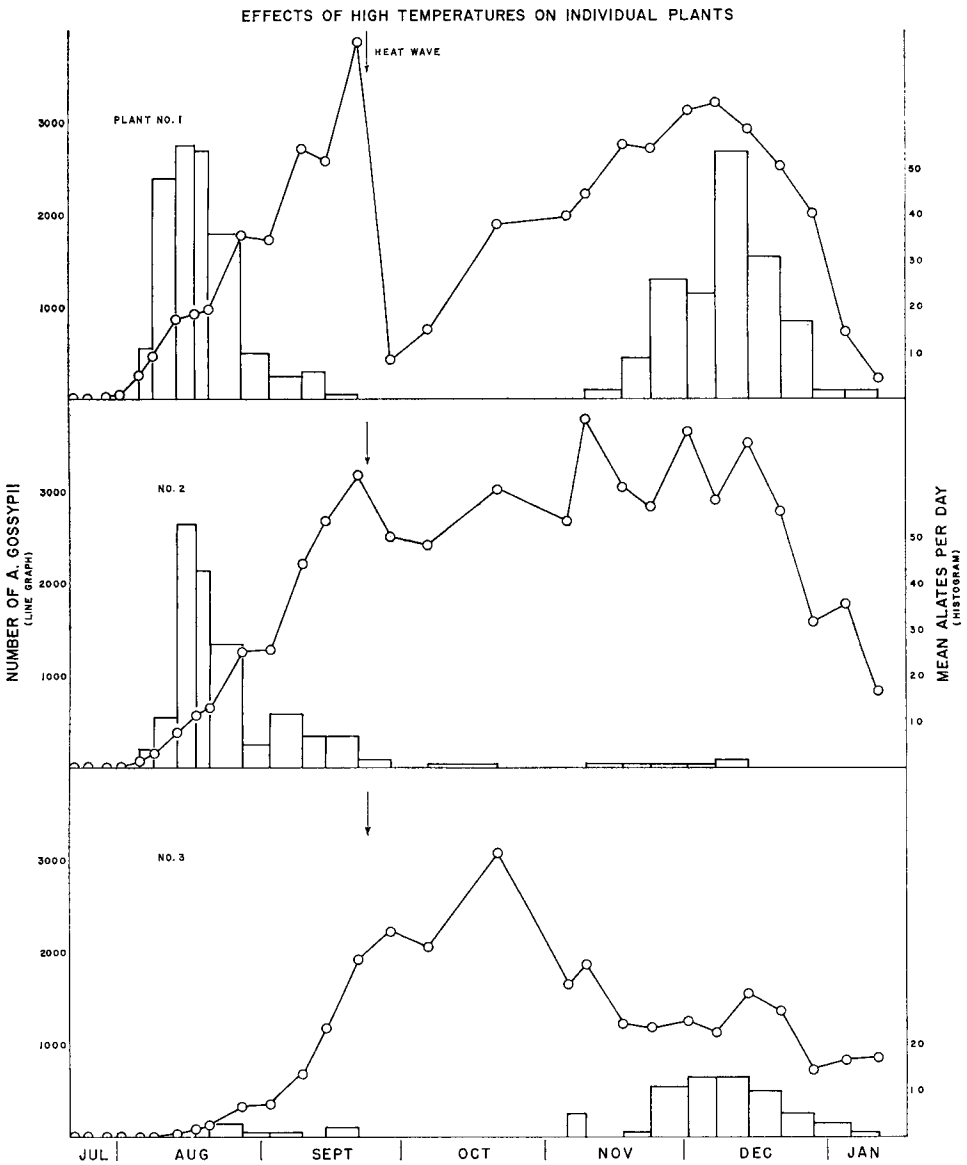


Fig. 18. Population growth curves and alate production for *A. gossypii* on individual plants as affected by high temperatures and population densities.

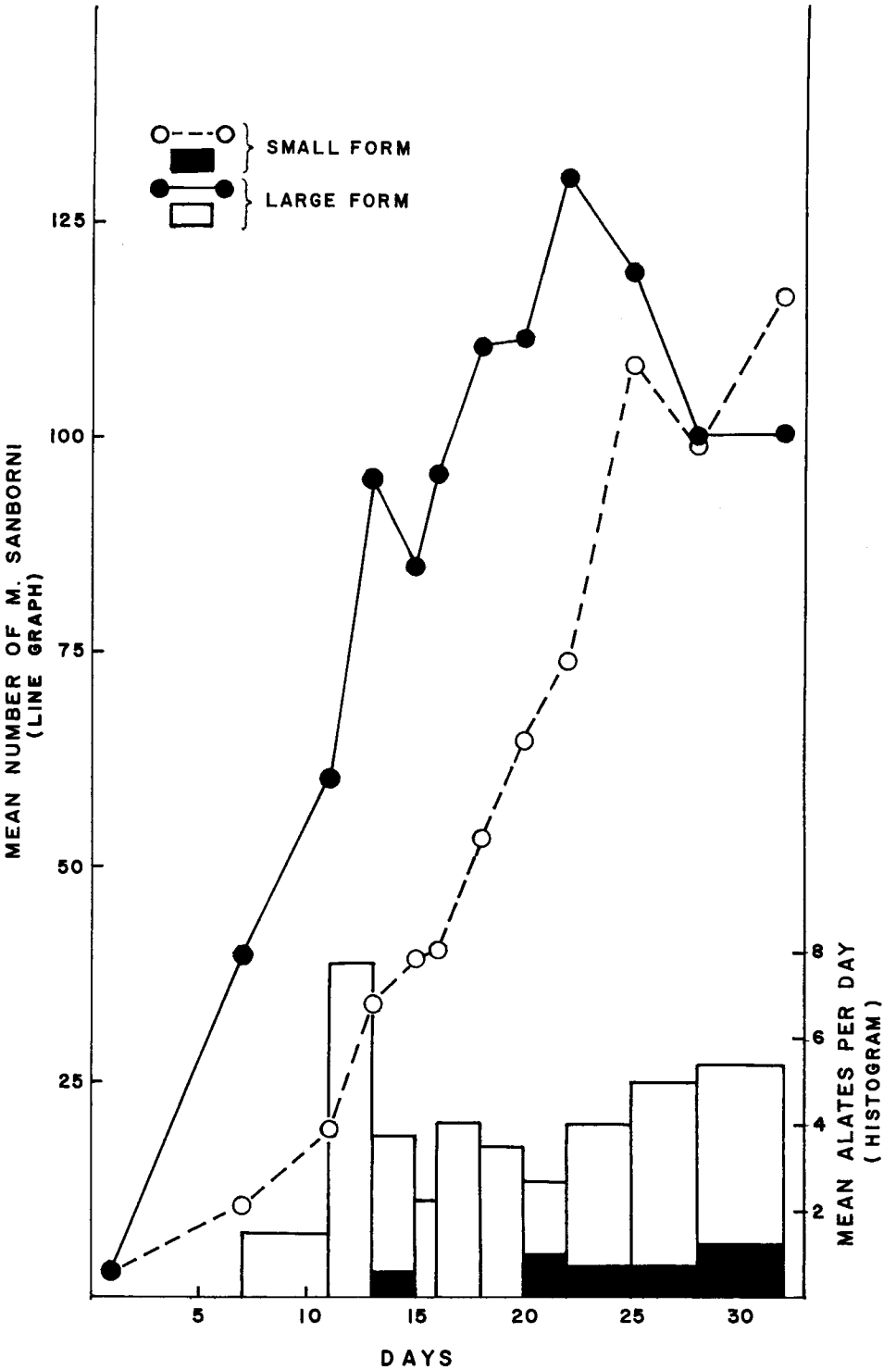


Fig. 19. Population growth curves and alate production by the progeny of large and small forms of *M. sanborni*.

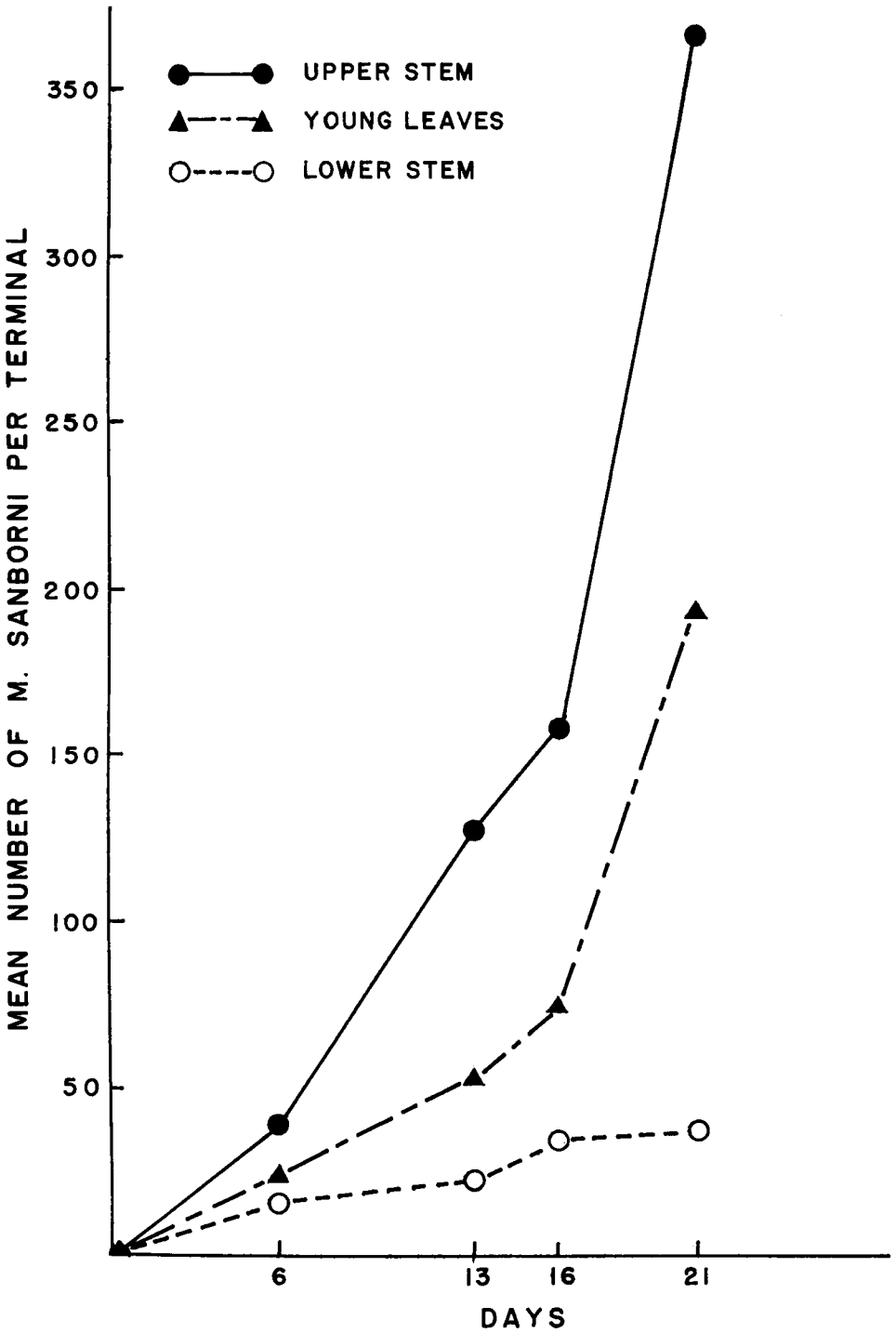


Fig. 20. Population growth curves for *M. sanborni* on young leaves and the upper and lower portions of the stem.

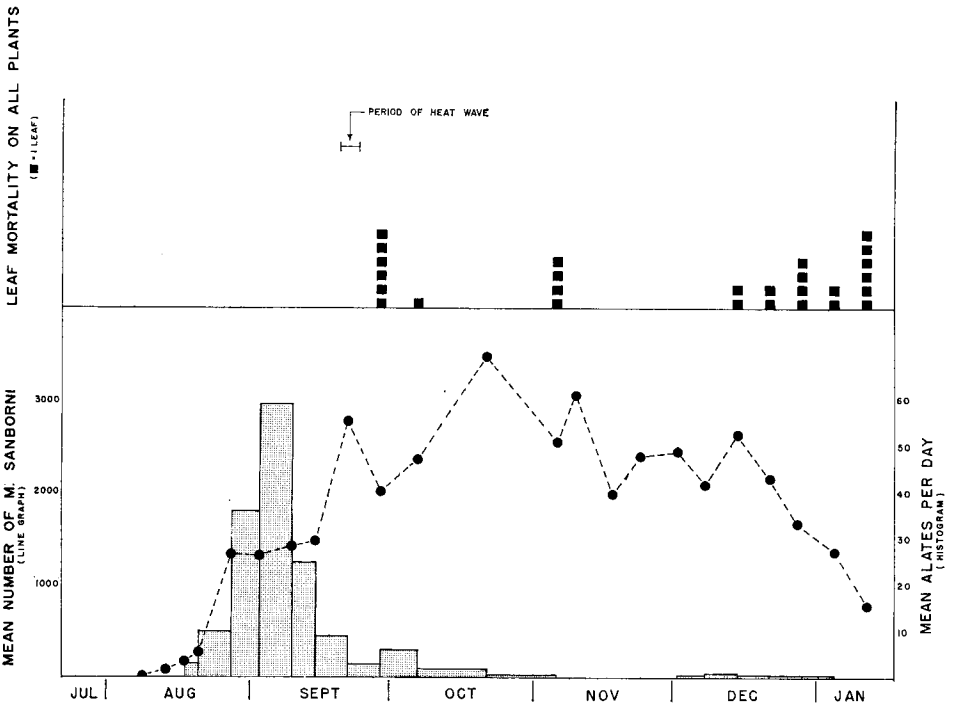


Fig. 21. Population growth curve and alate production for *M. sanborni* as affected by unusually high temperatures with subsequent leaf mortality.

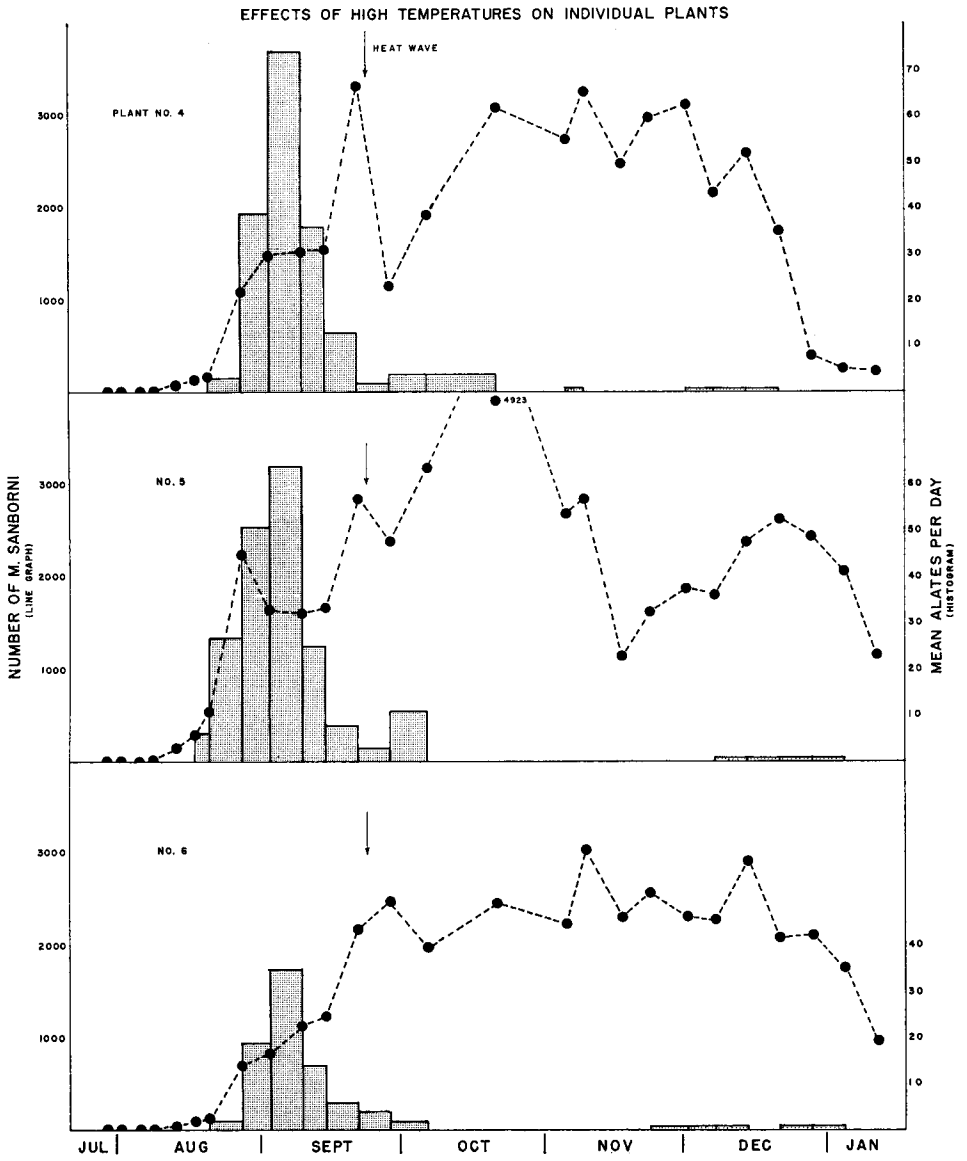


Fig. 22. Population growth curves and alate production for *M. sanborni* on individual plants as affected by unusually high temperatures.

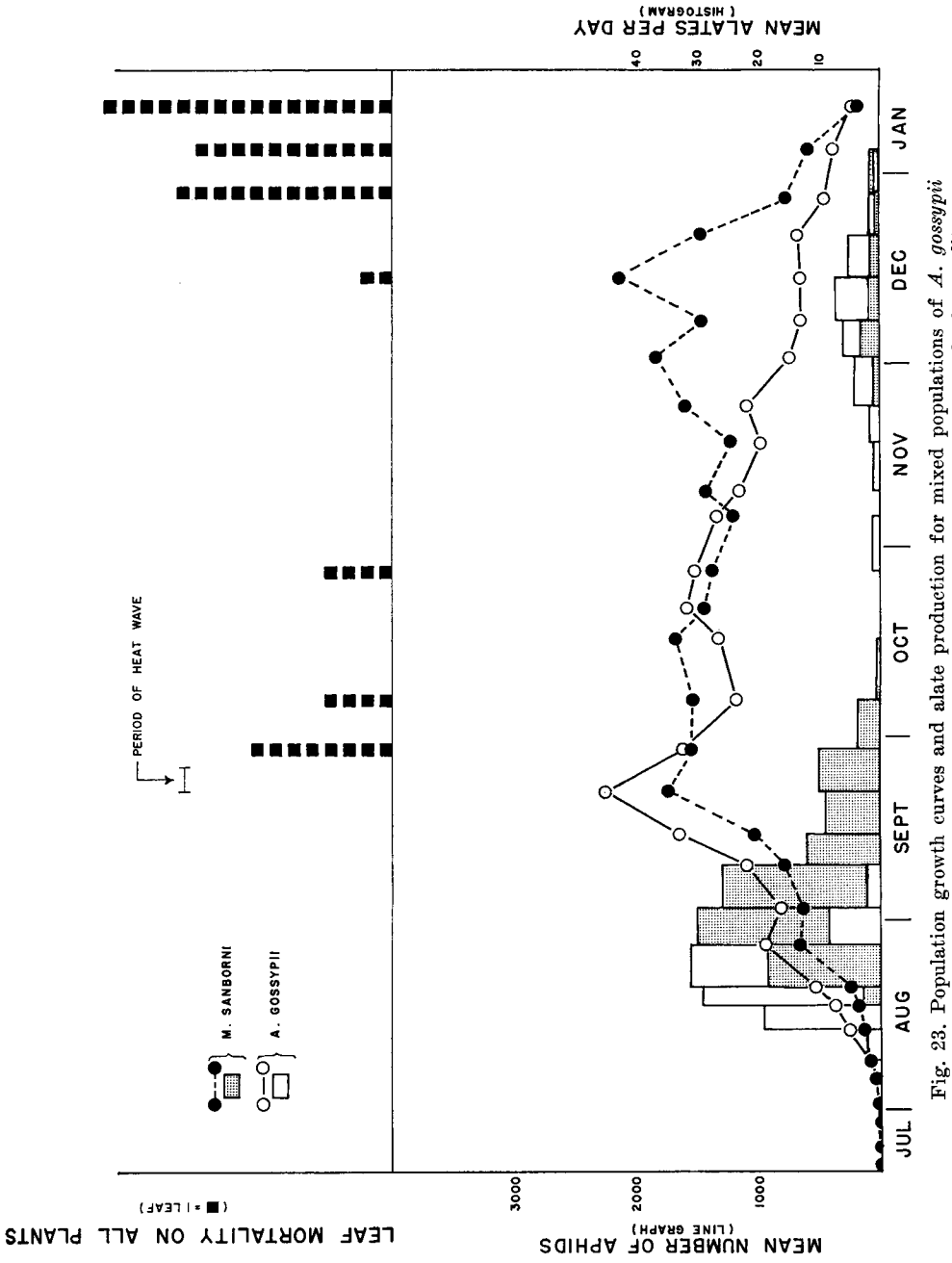


Fig. 23. Population growth curves and alate production for mixed populations of *A. gossypii* and *M. sanborni* as affected by unusually high temperatures with subsequent leaf mortality.

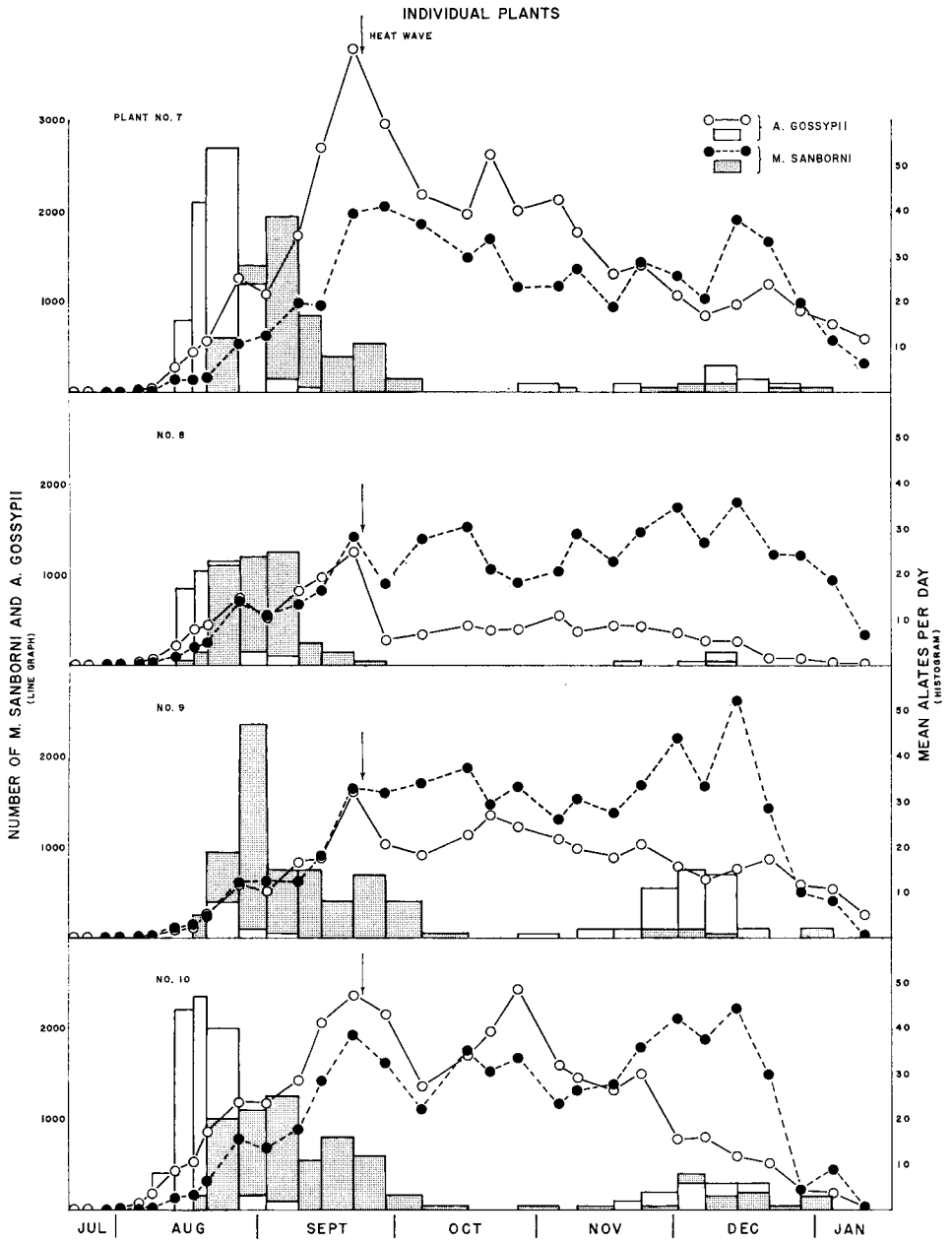


Fig. 24. Growth curves and alate production for mixed populations of *M. sanborni* and *A. gossypii* on individual plants as affected by high temperatures.

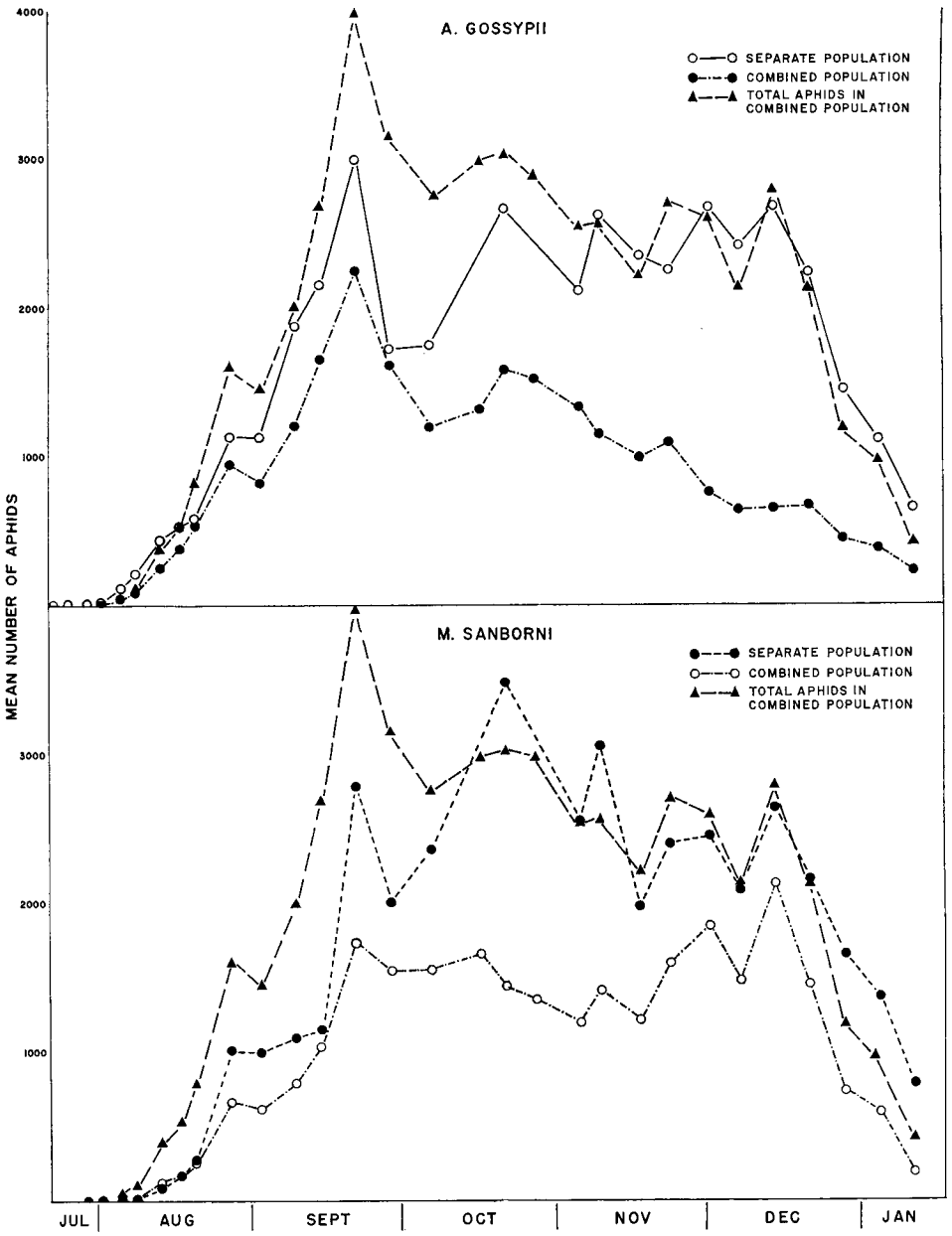


Fig. 25. Population growth curves for separate and combined populations of *A. gossypii* and *M. sanborni* and total aphids in combined populations.

morphs can be considered a density-dependent population regulating mechanism. The condition of the chrysanthemum plants in this experiment was strongly influenced by the number of aphids feeding on the plants. When the aphid densities increased, the plants lost their vigor and became stunted. This in turn caused development of the small, yellow morphs that had a reduced reproductive rate.

During the period of equilibrium, death of the older leaves was a primary cause of high aphid mortality (fig. 17). Hughes (1963) reported a similar phenomenon for *Brevicoryne brassicae* (L.). He found that hot, dry conditions in combination with high aphid populations caused rapid death of the leaves, and this would cause high mortality (10 per cent in two years) of the aphids that had been feeding upon the leaves.

In the experiment reported here, leaf distribution data taken on November 11 indicated that one older leaf had as many as 458 aphids, which represented about 16 per cent of the colony. This one leaf represented 10 per cent of the leaf area, but was only one out of 25 leaves on the terminal.

The most significant example of the aphid mortality due to death of older leaves was evident during the latter part of September (fig. 17), a period of unusually high temperatures which killed over one-third of the population. The aphid mortality was not directly due to high temperatures but was caused by death of the older leaves, which in turn was caused by high temperatures and high aphid densities. As the density of the colony increased in the individual replications, so did mortality (fig. 18). Table 1 shows this relationship between the actual number of aphids before and after the heat wave.

TABLE 1

INTERRELATION OF MORTALITY WITH APHID DENSITY WHEN POPULATIONS OF *APHIS GOSSYPII* WERE EXPOSED TO UNFAVORABLY HIGH TEMPERATURES

Plant number	Number of living aphids:		Mortality
	Before high temperature	After high temperature	
			Per cent
1.....	3878	418	89
2.....	3174	2502	21
3.....	1922	2238	0

Long-term populations of *Macrosiphoniella sanborni*

The purpose of Experiment 4 was to study the effects of aphid size on alate production and population growth. In addition, measurements on aphids taken from favorable and unfavorable plants were made before the experiment. At the end of the experiment, the measurements of all living adults were recorded (lower half of table 2).

Size variation. The mean measurements of the progeny from the small and large apterous adults were very similar, falling between the measurements of the small and large morphs before the experiment.

The large morphs of *M. sanborni* increased at a faster rate than the smaller morphs (fig. 19). During the initial growth phase, the larger morphs increased approximately three times as rapidly as the smaller morphs. Ten days after the initial count, both growth curves appeared to have similar growth rates. The reproductive rates, however, of the two populations were not the same; since the greater number of alates were removed from the cages with the large individuals.

The mean number of alates produced daily is shown in the histogram in figure 19. The total number of alates produced by all four replications of the large morphs was 381 compared to 52 for the small morphs.

At the time the count was taken dur-

TABLE 2

EFFECTS OF PLANT CONDITION ON SIZE OF *MACROSIPHONIELLA SANBORNI*

Original growth form of *M. sanborni*	Number of specimens	Influence of plant condition on aphids in terms of:		
		Total dimensions		Cornicle size
		Length ± S.D.	Width ± S.D.	Length ± S.D.
From originally favorable or unfavorable plants:				
		mm.	*mm.*	*mm.*
Apterous				
Large	25	2.13 ± .16	1.14 ± .12	0.30 ± .02
Small	25	1.20 ± .10	0.53 ± .07	0.19 ± .02
Alate				
Large	24	2.26 ± .17	1.20 ± .09	0.30 ± .02
Small	10	1.35 ± .15	0.56 ± .08	0.20 ± .01
After transfer to plants of intermediate favorability:				
Apterous				
Large	27	1.51 ± .23	0.81 ± .18	0.25 ± .04
Small	43	1.43 ± .12	0.74 ± .10	0.23 ± .02
Alate				
Large	40	1.37 ± .14	0.56 ± .20	0.21 ± .03
Small	17	1.35 ± .09	0.55 ± .40	0.20 ± .01

ing the last week, the aphid numbers and sizes were similar in both colonies; however, more alates were still being produced by the originally large aphids during this last week. Kitsmiller (1950) reported that wing determination in *M. sanborni* took place 90 hours before birth. The alates removed on the final day were determined (maternally) two to three weeks before, when the large-morph colonies were still numerically greater and were, presumably, still larger than the small aphids.

It should be mentioned that, although the aphids were initially caged on young stem growth, the terminal of the plant continued to grow, but the cages were not moved onto the new growth. When the experiment was terminated a month later, the enclosed stem was considered old-stem growth.

Unlike the apterous adults which varied in age as much as several weeks, the alate adults were of more similar age. Since all winged aphids were removed four days before the final sampling date, all the winged aphids measured were known to have molted to adults within a four-day period. These winged adults, from both small- and large-aphid colonies, were similar in size at the end of the experiment, and the mean size of these alates from both types of colonies were similar to the original, small, winged aphids (table 2).

These changes in aphid size from large to small occurred because the aphids were not allowed to go to the new growth but were restricted to the slowly-aging stem tissue. These data suggest that high aphid densities stunt plants, prevent new growth, and cause aphids to change from large to small morphs within a month. Also, during the early part of this experiment, the early progeny of the small morph presumably increased in size, but the aging stems prevented later progeny from becoming larger.

The extreme size variation of *M. sanborni* found in the previous experiment casts some doubt upon many workers' claims of seasonal polymorphism based

TABLE 3

VARIATION IN SIZE OF LARGE AND SMALL APTEROUS ADULTS OF *MACROSIPHONIELLA SANBORNI* COMPARED TO OTHER APHID SPECIES REPORTED BY BODENHEIMER AND SWIRSKI (1957)

Species	Body length		Size difference*
	Maximum	Minimum	
	mm.	*mm.*	*per cent*
M. sanborni	2.13 ± .16	1.20 ± .10	44
Hyalopterus sp.	2.34	2.03	13
Rhopalosiphum sp.	2.37	1.80	24
Pterochloroides sp.	2.54	1.97	22

* Size variation in *M. sanborni* was due to unfavorable host conditions; size variation in remaining species was due to seasonal variation.

on body length alone. From other workers' data, Bodenheimer and Swirski (1957, p. 80) discussed seasonal variation based on the total body length of three species *Hyalopterus pruni, Rhopalosiphum maidis,* and *Pterochloroides persicae.* In all three cases, significant differences occurred in the sizes of aphids collected in favorable and unfavorable months. Bodenheimer and Swirski (p. 80) suggest:

> If we regard body size as the expression of good growth conditions for the plant lice, we can say in general that in Israel the late winter is favourable and the late summer unfavourable for maximum body growth. It remains to be studied, however, whether nutritional conditions of the host are directly responsible for these differences, or whether—as in vertebrates—seasonal changes of endocrine activity inducted by environmental stimuli are responsible.

Table 3 lists the maximum seasonal size variations in body length of the three species used by Bodenheimer and Swirski (1957, p. 80), along with the body lengths of large and small apterous adults of *M. sanborni.* The percentage differences show that size variation of *M. sanborni* in unfavorable host conditions was greater than the seasonal variation of size reported for the other three species.

These extreme size variations found in *M. sanborni* are not new for aphids. Ackerman (1926) and Ewing (1916) reported extreme size variations in two aphid species. Ewing reported that variations in body length in *Aphis avenae* Fab. were due largely to differences in temperature and food. Ackerman, on the other hand, found that *Rhopalosiphum prunifoliae* Fitch grown on freshly germinated seedlings were 25 per cent longer than aphids grown on four-day-old plants. In addition, he found that these aphids were 70 to 100 per cent longer than aphids grown under overcrowded conditions.

Although measurements were not made of the aphids in the last experiment, aphids on the older stems were observed to be smaller than those on the younger, growing portions of the stems, even though more crowded conditions existed on the young growth. The changes in *M. sanborni* were due to the favorability of the feeding sites. Overcrowded conditions that caused extreme size differences in Ackerman's studies might be explained by changes in host physiology, which were brought about by high aphid densities. Weatherly, Peel and Hull (1959) reported that aphid feeding drains the sap from surrounding cells. Perhaps, under crowded conditions, starvation could be the primary cause of decreased aphid size. Yet, until more is known about the "group effect" proposed by Bonnemaison (1951)

in his hypothesis on alate production, endocrine activity stimulated by crowding cannot be discounted as the cause of size changes.

Influence of feeding site. In Experiment 5, population growth curves were determined for isolated aphid colonies on different parts of the plants (fig. 20). *Macrosiphoniella sanborni* increased in numbers most rapidly (366 per cage) on the younger portion of the stems, increased at an intermediate rate (194 per cage) on the young leaves, and increased most slowly (37 per cage) on the older portion of the stem.

Alate production was positively correlated with population increase. On the younger portion of the stems, a total of 236 alate adults were produced, whereas 85 alate adults were formed on the young leaves, and only four alate adults were found on the older portions of the stems. In this instance, alate production could be correlated with many factors such as aphid crowding, feeding sites, and aphid size. Probably all three factors determined the intensity of alate production.

The conditions of the various feeding sites affect population growth. Different-aged tissues have variously tough or thick epidermal tissues which prevent aphids from maximum feeding, because they cannot readily insert their stylets. Franz (1956) reported that after two years, *Adelges piceae* (Ratz.) populations declined, because the external layer of cork cambium died and was no longer a suitable site for aphid feeding. Another site condition that might affect populations is the difference in phloem sap nutrient content in the different sectors of a plant (Kennedy, 1958). Zimmerman (1963) suggested that the concentration of photosynthetic products which decreases from the top to the bottom of a tree trunk, is removed when the tree is defoliated.

Alate production. *Macrosiphoniella sanborni* in the single-species population reached its maximum alate production between September 2 and 9, and alate production gradually decreased after that time (fig. 21). Since the population density continued to increase after the decrease in alate production, it can be concluded that alate production of *M. sanborni,* as with *A. gossypii,* was not caused by high population density alone.

White (1946) reported that continuous light and a low temperature of 12° C were the most conducive for alate production in *M. sanborni;* however, she did not investigate the effects of crowding on alate production. Changes in the physical environment were not the explanation for the decrease in alate production in the experiment reported here, for during the period of minimum alate production a larger number of alate adults were produced in another experiment that was being conducted at the same time. In all the replications, there was only one major period of alate production in the *M. sanborni* single-species treatment (fig. 21). One might expect a second alate production period to occur as the plants slowly succumbed to the high aphid populations, but this was not the case. One explanation could be that like the small, yellow morph of *A. gossypii,* the small morph of *M. sanborni* is in a state of semiquiescence. Thus, as the leaves slowly die these small morph aphids are crowded onto decreasing areas of living tissue, but they are unable to produce winged progeny in response to the crowding effects because they are semiquiescent. It is also possible that these small morphs of *M. sanborni* produce a smaller percentage of alate morphs as is the case with the small, yellow morphs of *A. gossypii.*

Population trend. The combined populations of *M. sanborni* in the various replications followed a sigmoid growth curve that was interrupted by a plateau and a dip during the accelerated growth

phase (fig. 21). The plateau that occurred between August 27 and September 14 coincided with the period of peak alate production. This indicates that alate production and removal clearly affected the growth rate of the population. The dip in the growth curve that occurred on September 28 was due to the high temperatures, as discussed for *A. gossypii* (fig. 17).

After the accelerated growth phase, *M. sanborni* populations maintained an equilibrium level for about 80 days. The density-dependent factors in the regulation of the population were similar to those discussed in the regulation of *A. gossypii* populations.

During the period that the *M. sanborni* population was maintained at the equilibrium position, only small adult morphs were present. It has been shown that the smaller aphids produced fewer progeny than the large morphs (fig. 19). These small morphs with reduced natality were one of the primary factors that aided in regulation of the population. About December 14, the plants showed signs of succumbing to high aphid densities as can be seen from the mortality of old leaves represented by shaded squares in figure 21.

Evidence of the period of extremely high temperature acting on the *M. sanborni* population in a density-dependent manner is shown graphically in the growth curves of the individual replicates (fig. 22). Table 4 presents data on the population levels before and after the high temperatures and shows the direct relationship between aphid mortality and aphid densities.

Differences in the intensity of alate production show a direct relationship to the initial growth rate of the aphids. In figure 22 it can be seen that alate production on plant 6 was much lower than on either of the other two plants, and that the growth rate on this plant was much lower than on the other two replications. Here, again as with *A. gossypii*, the steeper the early growth curve, the greater the intensity of alate production.

TABLE 4

INTERRELATION OF MORTALITY WITH APHID DENSITY WHEN POPULATIONS OF *MACROSIPHONIELLA SANBORNI* WERE EXPOSED TO UNFAVORABLY HIGH TEMPERATURES

Plant number	Number of living aphids:		Mortality
	Before high temperature	After high temperature	
			per cent
4	3313	1145	65
5	2848	2389	16
6	2173	2485	0

Mixed-species population

In Experiment 3, these populations exhibited a similar pattern to both of the single-species populations (fig. 23).

Alate production in the first period from August 6 to October 6, *A. gossypii* reached maximum alate production approximately a week before *M. sanborni*. This difference was probably due to the introduction of *A. gossypii* onto the terminals a week before that of *M. sanborni*. This enabled *A. gossypii* to attain an initial numerical advantage in three of the four individual replicates (plants 7, 8, and 10; fig. 24).

The second period of alate production occurred between November 17 and December 4. Alate production of *M. sanborni* was greater at this time in the mixed-species populations than in the single-species populations, but the level was still very low. A second alate production period also occurred with *A. gossypii* at this time, but it was considerably less than in the single-species populations. This could have resulted from a gradual decrease of *A. gossypii* numbers in the mixed-species populations due to interspecific competition.

TABLE 5

ALATE FORMATION BY SEPARATE AND COMBINED POPULATIONS OF *MACROSIPHONIELLA SANBORNI* AND *APHIS GOSSYPII* DURING TWO DISTINCT PERIODS OF WING FORMATION

Treatment	Mean number of alate aphids during population peaks:		
	First peak	Second peak	Total
Single-species:			
M. sanborni	996	27	1023
A. gossypii	646	538	1183
Mixed-species:			
M. sanborni	725	68	793
A. gossypii	455	196	651

Table 5 shows the mean number of alates produced per caged terminal for each treatment during the first and second periods of alate production. These data clearly show that alate production was greater in the single-species populations, except for *M. sanborni* in the second alate production period. However, the number of alates for the two species combined in the mixed-species population was greater than the alate production for either of the individual single-species populations.

Population growth curves of single- and mixed-species populations of *A. gossypii* in Experiment 1 were similar until June 18 (fig. 8). This probably indicates that the effects of interspecific competition during this period were less than the effects of intraspecific competition.

The histogram in figure 9 represents the daily average number of aphids removed from each caged terminal. Paddock (1919) found that the average age at which *A. gossypii* reproduced was 6.5 days after the final molt. Therefore, to minimize the possibility of alates reproducing on the plants in our experiment, the alates were removed every three to five days.

The shaded histogram represents the number of alates produced in a mixed-species population, and the unshaded bars represent the single-species population. It can be seen that under the single-species treatment more alates were formed, even though the total aphid count with the mixed-species was much higher. Apparently, the higher density of these two aphid species together did not increase alate formation; on the contrary, it appeared to decrease alate production.

At the termination of this experiment, *A. gossypii,* in the mixed-species population had a higher total count than in the single-species population. At first, it might be expected that *A. gossypii* in the mixed-species population would have a lower count because of the suppressing effect of interspecific competition. As explained earlier, however, there was little evidence of interspecific competition (fig. 4).

A possible explanation might be the difference in alate production: In the single-species treatment alate aphids were produced at a rate of 48 per day in seven replications. Thus, over a period of 20 days from June 18 to July 8, a total of 961 alate aphids, or an average of 137 alate aphids per terminal were removed. Under the mixed-species treatment alates were produced at a rate of 15 per day; consequently 294 alates (or an average of 37 alates per terminal) were removed during the same period from eight repetitions. Thus, a total of 667 more alates, or an average of 100 more alates, were produced per terminal in the single-species treatment as compared with the *A. gossypii* in the mixed-species population. If it can be assumed that both treatments produced a similar number of adults, then *A. gossypii* in the mixed-species population had a reproductive advantage, because the apterous adults were not removed. This could explain why the mixed-species populations of *A. gossypii* increased more rapidly.

Single- and mixed-species population growth curves of *M. sanborni* displayed different rates of increase throughout the experiment (fig. 9). In this case, the single-species population increased at a faster rate than the mixed-species population. It was evident that interspecific competition affected the growth rate and the distribution pattern of *M. sanborni* (fig. 4).

Again, except for the very early period of this experiment, alate production in the single-species treatment was higher than in the mixed-species. In contrast to *A. gossypii* which had a steeper population growth rate in the mixed-species population, the *M. sanborni* mixed-species population had a slower growth rate than the single-species population. This probably indicates that interspecific competition had a greater effect on *M. sanborni* than on *A. gossypii.*

Macrosiphoniella sanborni produced more alates than *A. gossypii,* even though populations were somewhat lower at the end of the experiment (figs. 8 and 9). It is also evident that alate production in *M. sanborni* was not directly associated with the population increase. Alate production showed a positive relationship with population increase of *M. sanborni* up to May 28, but after this time, production of alates gradually decreased, even though the aphid population continued to increase. On the other hand, alate production in *A. gossypii* appeared to be more strongly correlated with the population increase throughout the experiment. Later, in the long-term experiment, however, alate production was not directly associated with population increase.

In the mixed-species populations, the two species displayed different accelerated growth rates (figs. 8 and 9). Initially, *M. sandborni* increased most rapidly, but as the experiment progressed *A. gossypii* was able to overtake and surpass *M. sanborni.* At the end, *A. gossypii* outnumbered *M. sandborni* in all the replications. This was true even with treatments that had originally been planned with the two species plus *Myzus persicae.* Thus *A. gossypii* was numerically superior in all 16 replications.

In Experiment 3 both species in the mixed-species populations displayed sigmoid growth curves (fig. 23). High temperatures during the latter part of September caused both aphid populations to decline, by killing the older leaves along with the aphids that were feeding on them. Furthermore, the high temperatures seemed to affect the carrying capacity of the plants so that the combined aphid populations never did surpass the maximum number of aphids that were present before the high temperatures.

Populations of *M. sanborni* seemed to be regulated until the plants finally began to collapse in mid-December, as illustrated by the number of dead leaves in figure 23. Over-exploitation by high aphid populations rather than high temperature was responsible for this final plant decline.

Aphis gossypii, on the other hand, continued to decline after a temporary recovery from the high temperatures, because it could not compete for the resurgence of new growth that occurred during the last half of the experiment.

Interspecific competition. Both species had similar growth patterns during the accelerated growth phase. The high temperatures affected both populations and caused an abrupt decline in aphid numbers, but *A. gossypii* was the most severely affected, since it was more numerous than *M. sanborni* on the older, more heavily infested leaves killed by high temperature.

In the short-term experiment, *A. gossypii* in the mixed-species populations reached a higher numerical count in all 16 replications, with the growth pattern

still in its accelerated growth phase at the end of the experiment.

In the long-term experiment, the plants had been stunted by the heavy aphid populations, but recovered and resumed new terminal growth on November 5. The more mobile of the two aphids, *M. sanborni,* quickly took advantage of the new food and entirely covered the new plant tissues before *A. gossypii* was able to move to this new food source. In one instance (plant 9), *M. sanborni* became so abundant on the new growth that the terminal leaves and growing point died before the older leaves. This resurgence of new growth was again stunted, however, by an increase of *M. sanborni,* while the *A. gossypii* population continued to decrease gradually.

Aphis gossypii was numerically superior during the accelerated phase on plants 7 and 10, but near the end of the experiment *M. sanborni* colonies had the numerical advantage in all of the replications.

Intra- vs. interspecific competition. During the accelerated growth phase, the combined number of aphids in the mixed-species populations was greater than either of the single-species populations. This might be expected because of the difference in habitat preference at the beginning of the experiment. Initially, *A. gossypii* infested the terminal buds and leaves, whereas *M. sanborni* preferred the stems and young leaves. Therefore, each species remained segregated in its own preferred habitat until it became overcrowded. Crowding not only caused the aphids to move from the preferred habitat, but also caused these favorable habitats to disappear by stunting the plants.

One striking similarity for both aphid species, whether under single- or mixed-species treatments, was the time at which the plants could no longer maintain high aphid populations (fig. 25). Except for the *A. gossypii* populations under interspecific competition that gradually declined over a long period of time, the other populations, whether alone or together with different species, displayed similar equilibrium levels. The average density of the two species alone was probably near the carrying capacity of the host plants; thus, it would appear that the effects of these populations at their equilibrium positions placed more or less equal stress on all the plants.

When means for the two species in the mixed-species treatments were combined, the resulting population growth curves were very similar to those for the single-species populations (fig. 25). Except for a higher initial peak, the equilibrium levels were approximately the same for all treatments. Each species, however, in the mixed-species populations showed a different growth curve; *A. gossypii,* after reaching a peak in September, gradually decreased in numbers. On the other hand, *M. sanborni* tended to reach an equilibrium level, but then increased in November and early December when there was a temporary flush of new growth.

DISCUSSION AND CONCLUSIONS

Bodenheimer and Swirski (1957), Kennedy and Stroyan (1959), and Hille Ris Lambers (1960), have all cautioned researchers about making generalizations from studies on a few aphid species. Therefore, the following hypotheses are restricted to these two species with the chrysanthemum as the host plant.

Alate production

Although emphasis was not placed on the cause of alate formation in these studies, the data obtained help explain

some of the factors that influence the intensity of alate production in *M. sanborni* and *A. gossypii* on chrysanthemums. In the long-term experiment, alate production at first increased with density, but as the aphid populations continued to increase, alate production declined. In some *A. gossypii* colonies, there was a second peak of alate production; but with *M. sanborni*, only one weak second peak was noted in one of the replications in the mixed species treatment. Physical factors such as light, temperature, and relative humidity were not important in the decline of alate production, because during the period of extremely low alate production, high alate production occurred in a separate contemporary experiment.

Crowding of aphids has been accepted by most aphidologists as the primary cause of alate formation. Crowding was defined by Reinhard (1927) as "a relative condition which varies from a comparatively small colony of aphids situated on contiguous position with a restricted area, to a maximum infestation in which the insects cover practically the entire stem, petiole or leaf of the food plant." Bonnemaison (1951) also studied crowding or "group effect" in relation to both local and average densities.

In the early accelerated growth phase, both species were found on the young growing tip of the terminal; *A. gossypii* was on the young leaves and *M. sanborni* was on the stems. When the different aphid populations increased in their own preferred habitats, the plants became stunted, the aphids became crowded; then they changed their distribution more uniformly over the entire plant. However, no more young, vigorous growing areas were available to produce the high degree of crowding necessary for alate production.

This change from a clumped distribution to more uniform distribution is not unique. Naylor (1959) reported that *Tribolium confusum* had a tendency to aggregate at low densities, but gradually changed to a very uniform distribution at high densities. This change to uniform distribution pattern was not related to preferred microhabitats but to female beetles repelling other females and attracting males.

When *M. sanborni* populations reached the carrying capacity of the plant, their sizes were markedly reduced. This size decrease was accompanied by physiological changes which lowered the reproductive rate. Morphological and physiological changes were probably due to unfavorable host conditions, which resulted from high aphid populations and were similar to those found with the small, yellow morphs of *A. gossypii* that Kring (1959) referred to as the quiescent stage. On chrysanthemums, however, the aphids were in a semi-quiescent state in which reproduction and development were still taking place but at a lower rate than normal.

The changes that occurred in the aphids were responsible for the decrease in alate production. For instance, the *A. gossypii* replication that changed from a multi-colored population to over 95 per cent small, yellow morphs did not have a second peak of alate production. Similarly, the small morphs of *M. sanborni* that were present in all replications late in the experiment did not have a second peak of production. Bonnemaison (1951) mentioned that when a leaf begins to wilt, the aphids are crowded onto the living part of the leaf, which in turn will cause a sudden increase in alates. In this experiment, Bonnemaison's theory would explain the second peak of alate production in the multi-colored *A. gossypii* colony, but it does not explain why the other, small-aphid colonies did not have a second peak.

It is believed that crowding on vigorously growing plants is the main cause of alate formation, but unfavorable

host conditions cause changes in the aphids, so that alate production is ultimately decreased by high populations. Small aphids required a much higher number of individuals per unit area to have the same intensity of crowding. Since preferred microhabitats on these plants are limited in area, crowding can take place; but with the loss of the preferred habitats, crowding is no longer stimulated. Even if aggregation was an instinctive behavior of the species, the lack of favorable feeding sites would cause relatively uniform distribution. For instance, when a resurgence of new terminal growth occurred late in the experiment, *M. sanborni* quickly converged on this new growth. The new growth of one to two inches was entirely covered with aphids, so that little if any green tissue remained exposed. Since the new plant growth was the favorable feeding site, it was overexploited and in this one instance the younger part of the plant died before the older leaves. Generally the younger parts of the plant can maintain higher densities of aphids because of their vigorous and healthy condition. If this gregarious behavior was not stimulated by favorable growing sites, the aphids would overexploit other areas that are in a weaker condition, such as older leaves, and hasten the death of the plant. Overexploitation of the older leaves did not seem to occur, for death of older leaves usually took place over a long period of time; only when the extreme high temperatures caused excessive stress, did the older leaves suddenly die.

Workers who have used cages to isolate portions of leaves to compare the effects of different leaf ages on alate production have been able to show that crowding causes alate production, but these studies did not give any indication of the actual intensity of alate production on various-aged leaves. Crowding would take place in the small, favorable areas on young leaves even without cages, but on older leaves crowding would only result under caged conditions and may not give a true expression of the aphid densities on these types of leaves. If the area on the older leaves was not limited, the populations would probably distribute themselves more uniformly than on the younger leaves. Under such conditions, the populations would probably reach the carrying capacity of the leaf before the crowding threshold was reached, and the leaves might die before large numbers of alates were produced.

Competition and distribution

According to Hairston *et al.* (1960), interspecific competition is usually less in herbivorous animals, because the limiting factor is generally predators, not food. Bodenheimer and Swirski (1957, p. 5) stated that "host condition and enemies are controlling factors, but in aphids the former predominates, so that when the enemy populations have grown to significant size the aphid populations are already in steep decline due to unfavorable host changes." In this experiment, predators and parasites were excluded in order to study other factors that reduced the intensity of competition.

During the accelerated growth phase, all factors that decreased the growth rate, even temporarily, delayed the effects of competition. They were: habitat segregation, dispersal, weather, and plant growth.

Habitat segregation was displayed in both aphid species during their initial population growth phase. *Macrosiphoniella sanborni* preferred the growing stem, and *A. gossypii* preferred the young leaves. The aphid populations continued to increase until the plant was stunted which led to the removal of the preferred habitat site which was the young, growing portion of the plant.

Physical factors can either delay or

hasten competition. For instance, high temperatures were shown to delay competition by decreasing the population. But it may also have promoted competition by weakening the plant, thus lowering its aphid-carrying capacity.

Alate aphid dispersal has been shown to delay population growth in many instances, and Ito (1960) reported that apterous emigration kept aphid numbers below competitive levels on barley plants. (The aphid species were: *Rhopalosiphum maidis* (Fitch) (=*Aphis maidis* Fitch)) *Macrosiphum granarium* (Kirby) and *Rhopalosiphum fitchii* (Sanderson) (=*Rhopalosiphum prunifoliae* Fitch). In the study reported here, alate production in both species at first increased with crowding and caused a temporary delay in population increase, but when high populations made the plants unfavorable, alate production declined.

In the long-term experiment, the two single-species populations and the total aphid count of mixed-species populations displayed similar equilibrium levels. There was no great difference between the effects of intra- and interspecific competition on the total aphid number. Both species appeared to affect the plants similarly, or the differences in stress that each species placed on the plant did not noticeably affect its carrying capacity.

Nevertheless, the presence of one aphid species affected the other species, even though the total aphid count was the same as in the single-species colonies. In the long-term experiment, *A. gossypii* in the mixed-species population decreased in number during the period of population equilibrium as displayed by the total aphid count. At the same time, *M. sanborni* was able to increase, because it could take advantage of the temporary resurgence of new plant growth.

In the short-term experiment, *A. gossypii* was numerically superior to *M. sanborni* in the mixed-species population because new side shoots were removed mechanically when they started to grow. Thus, *M. sanborni* can probably achieve numerical advantage when a plant temporarily recovers, because this species can cover new growth entirely before *A. gossypii* is able to move.

Under unfavorable plant conditions, *A. gossypii* was found to be dominant on the older leaves, whereas *M. sanborni* was dominant on the younger portion or the upper half of the terminal. As populations increased, and if growth did not resume, the entire terminal would become old growth. Under such conditions, *A. gossypii,* the species dominant on the older growth, would probably exclude *M. sanborni.* Since neither of these aphid species produced any toxic products that interfered with the population growth of the other species, the host plant condition in this experiment was the major factor in determining if both species would co-exist, or if competitive exclusion would result.

To distinguish between the effects of intra- and interspecific competition, Svardson's (1949) study on birds showed that under intraspecific competition the habitat ranges tended to increase. The competing individuals under crowded conditions would be forced into the periphery of the range. Under interspecific competition, however, the species would have a narrower habitat range, because competition takes place in areas of overlap. The information obtained in this study was analyzed to test Svardson's principle as it applied to aphid distribution patterns. It was found that aphids were not completely excluded from the areas of overlap as were Svardson's birds; however, at the end of the experiment, *M. sanborni,* under interspecific competition, was being forced from the least preferred area under intraspecific competition (fig. 4). Distribution patterns changed,

with increases in density that indicated that exclusion might have resulted if the experiment had been continued. Although *M. sanborni* densities were lower in the presumably less favorable area of interspecific competition, the distribution patterns did not indicate any movement from the unfavorable to the more favorable zones, for no increase was apparent in the other sectors of the plant compared to the single-species population. Consequently, it seems likely that *M. sanborni* was at its maximum capacity in the favorable zone or area of least interspecific competition, and only the excess of the population was to be found in the unfavorable zone.

Regulating factors

Ito (1960) reported that under the laboratory conditions of his study, barley apterous aphids maintained the population equilibrium by emigrating. His observations of leaf-to-leaf and plant-to-plant dispersal indicated that density on individual plants was regulated by movement rather than by the directly harmful effects of overcrowding. Focusing his study on the movement of the apterous aphids, Ito found that emigration increased with density.

In most aphid species, the apterous adults are not the true dispersal form; their movements to different parts of the plant or to other plants only allows the aphids to discover new feeding sites on which to reproduce and increase the total population. Therefore, apterous dispersal is primarily related to the accelerated growth phase of the population, but it is not a major factor in the maintenance of an equilibrium position after the habitat has become saturated. When unconfined aphids on a single plant are regarded as the population, apterous emigration can be a significant population regulator. However, when aphids on a large number of plants or aphids confined are considered as the population, apterous migration becomes much less important in population regulation. This latter condition seems to reflect most closely the conditions that occur in nature.

Alate aphids can move from one population area to another or spread beyond the immediate range of their population. Although not emphasized by Ito, alate production should be considered as a factor in population regulation; the majority of the alate forms can leave the immediate population, and take with them a large reproductive potential. In a short-term experiment, Wyatt (1965) concluded that regulation of green peach aphid populations on chrysanthemums was brought about by emigration of alatae.

As the aphid densities approached the carrying capacity of the plant, competition became one of the major regulating factors. However, this occurred only when the populations were allowed to increase without the interference of other regulating factors, such as predators, parasites, and pathogens. Under these conditions, food was the limiting factor. Although the chrysanthemum plants under severe pressure from high aphid densities were able to maintain aphid population over a period of eighty days, vigor and growth were visibly reduced, and the plants were contaminated with honeydew.

This, in turn, caused individuals of both aphid species to decrease in size and to change physiologically. The smaller morphs of *M. sanborni* had a lower natality rate, and as Kring (1959) had shown earlier, the small, yellow morphs of *A. gossypii* were quiescent. In this experiment, however, the small, yellow morphs were semiquiescent. The change to the small morphs was an important factor in lowering natality.

Death of the older leaves, which killed most of the aphids feeding on them, was the primary factor that in-

creased the mortality rate. Data on aphid mortality, during the period of high temperatures, indicated that death of the older leaves was correlated with the number of aphids feeding on them. A similar density-dependent effect of temperature was found for the walnut aphid *Chromaphis juglanicola* Kalt. under field conditions (Sluss, 1966). Sluss also found that the higher the populations the more severe were the effects of high temperature.

ACKNOWLEDGMENTS

The authors wish to express their thanks to R. F. Smith and P. S. Messenger, Professors of Entomology and Parasitology, and A. S. Leopold, Professor of Zoology, for their critical reviews of the manuscript.

LITERATURE CITED

ACKERMAN, L.
1926. The physiological basis of wing production in the grain aphid. Jour. Exp. Zool. **44**(1): 1–61.

ANDREWARTHA, H. G., and L. C. BIRCH
1954. The distribution and abundance of animals. Chicago: Univ. of Chicago Press, 782 pp.

BIDDULPH, S., and O. BIDDULPH
1959. The circulatory system of plants. Sci. Am. **200**(2):44–49.

BIRCH, L. C.
1957. The meaning of competition. Am. Nat. **91**(856):5–18.

BODENHEIMER, F. S., and E. SWIRSKI
1957. The Aphidoidea of the Middle East. Jerusalem: Weizmann Science Press of Israel. 378 pp.

BONNEMAISON, L.
1951. Contribution à l'étude des facteurs provoquant l'apparition des formes ailées et sexuées chez les Aphidinae. Ann. Épiphyt. (**C**) 2:1–380.

BRITTAIN, W. H.
1921. Some factors influencing the occurrence of alate forms in certain Aphididae. Proc. Acadian Ent. Soc. (Nova Scotia) **7**:7–29.

COMSTOCK, J. H.
1950. An introduction to entomology. 9th edition. Ithaca: Comstock Publishing Co., Inc. 417 pp.

COOK, S. F., JR.
1961. Coexistence and competition in two species of legume aphids. Ph.D. Thesis. University of California, Berkeley. 106 pp.

CROMBIE, A. C.
1947. Interspecific competition. Jour. Anim. Ecol. **16**(1):44–73.

DEBACH, P., and R. A. SUNDBY
1963. Competitive displacement between ecological homologues. Hilgardia **34**(5):105–66.

DIXON, A. F. G.
1963. Reproductive activity on the sycamore aphid, *Drepanosiphum platanoides* (Schr.) Jour. Anim. Ecol. **32**(1):33–48.

DOUTT, R. L., and P. DEBACH
1964. Some biological control concepts and questions. Pp. 118–42. *In* Biological control of insect pests and weeds. P. DeBach and E. I. Schlinger (ed.), London: Chapman and Hall Ltd., 884 pp.

ESSIG, E. O., and F. ABERNATHY
1952. The aphid genus *Periphyllus* (Family Aphidae). A systematic, biological and ecological study. Berkeley and Los Angeles: Univ. of California Press, 166 pp.

EWING, H. E.
1916. Eighty-seven generations in parthenogenetic pure line of *Aphis avenae* Fab. Biol. Bull. (Woodshole, Mass.) **31**(2):53–112.

FRANZ, J. M.
1956. The effectiveness of predators and food in limiting gradation of *Adelges* (*Dreyfusia*) *piceae* (Ratz.) in Europe. Proc. 10th Intl. Congr. of Ent. **4**:781–87.

GAUSE, C. F., and A. A. WITT
1935. Behavior of mixed populations and the problem of natural selection. Am. Naturalist 69(725):596–609.
GILLETTE, C. P.
1908. *Aphis gossypii* Glover and its allies. Jour. Econ. Ent. 1(3):176–81.
GRANT, V.
1963. The origin of adaptations. New York and London: Columbia University Press, 606 pp.
HAIRSTON, N. G., F. E. SMITH, and L. B. SLOBODKIN
1960. Community structure, population control, and competition. Am. Naturalist 94(879): 421–25.
HARDIN, G.
1960. The competitive exclusion principle. Science 131(3409):1291–97.
HILLE RIS LAMBERS, D.
1960. Some notes on morph determination in aphids. Ent. Berichten (Amsterdam) 20(6):110–13.
HUGHES, R. D.
1963. Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). Jour. Anim. Ecol. 32(3):393–424.
ITO, Y.
1952. On the population increase and migration in three species of barley aphids. Studies on the mechanics of ecological segregation in barley aphids I. Oyo-Kontyu (Tokyo) 7(4): 169–76.
1954. Sympatric occurrence of two species of aphids and their leaf preference, with special reference to the ecological significance. Studies on the mechanisms of ecological segregation of barley aphids. II. Bul. Nat. Inst. Agr. Sci. (Japan) Ser. C(4):187–99.
1960. Ecological studies on population increase and habitat segregation among barley aphids. Bul. Nat. Inst. Agr. Sci. (Japan) Ser. C(11):45–130.
JOHNSON, B.
1965. Wing polymorphism in aphids. II. Interaction between aphids. Ent. Exp. and Appl. (Amsterdam) 8(1):49–64.
KENNEDY, J. S.
1958. Physiological condition of the host-plant and susceptibility to aphid attack. Ent. Exp. and Appl. (Amsterdam) 1(10):50–65.
KENNEDY, J. S., A. IBBOTSON, and C. O. BOOTH
1950. The distribution of aphid infestation in relation to leaf age. I. *Myzus persicae* (Sulz.) and *Aphis fabae* Scop. on spindle trees and sugar-beet plants. Ann. Appl. Biol. (Cambridge) 37(4):651–79.
KENNEDY, J. S., and T. E. MITTLER
1953. A method of obtaining phloem sap via the mouth-parts of aphids. Nature (London) 171(4351):528.
KENNEDY, J. S., and H. L. G. STROYAN
1959. Biology of aphids. Ann. Rev. Ent. 4:139–60.
KITZMILLER, J. B.
1950. The time interval between determination and differentiation of wings, ocelli, and wing muscles in aphid *Macrosiphum sanborni* (Gillette). Am. Nat. 84(814):23–50.
KLOMP, H.
1961. The concepts "similar ecology" and "competition" in animal ecology. Arch. Neerl. Zool. (Leiden) 14(1):90–102.
1964. Intraspecific competition and the regulation of insect numbers. Ann. Rev. Ent. 9:17–40.
KRING, J. B.
1959. The life cycle of the melon aphid, *Aphis gossypii* Glover, an example of facultative migration. Ann. Ent. Soc. Am. 52(3):284–86.
LACK, D.
1945. Ecology of closely related species with special reference to cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*). Jour. Anim. Ecol. 14(1):12–16.
LEES, A. D.
1961. Clonal polymorphism in aphids, p. 68–79. *In* Insect polymorphism. (Symposium no. 1). Roy. Ent. Soc., London.
LOWE, H. J. B., and L. R. TAYLOR
1964. Population parameters, wing production and behavior in red and green *Acyrthosiphon pisum* (Harris) Ent. Exp. and Appl. (Amsterdam) 7(4):287–95.

MAYR, E.
1963. Animal species and evolution. Cambridge, Mass.: Belknap Press of Harvard Univ. Press. 797 pp.

MITTLER, T. E.
1954. The feeding and nutrition of aphids. Ph.D. Thesis, University of Cambridge, London. 234 pp.
1957. Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) I. The uptake of phloem sap. Jour. Exp. Biol. **34**(3):334–41.
1958. Studies of the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. Jour. Exp. Biol. **35**(1):74–84.

MITTLER, T. E., and R. H. DADD
1966. Food and wing determination in *Myzus persicae* (Homoptera: Aphididae). Jour. Econ. Ent. **59**(6):1162–66.

NAYLOR, A. F.
1959. An experimental analysis of dispersal in the flour beetle, *Tribolium confusum*. Ecology **40**(3):453–65.

ODUM, E. P.
1959. Fundamentals of Ecology. 2nd edition. Philadelphia and London: W. B. Saunders Co., 546 pp.

PADDOCK, F. B.
1919. The cotton or melon louse: Life history studies. Texas Exp. Sta. Bul. **257**:1–54.

PARK, T.
1962. Beetles, competition and populations. Science **138**(3548):1369–75.

PASCHKE, J. D.
1959. Production of the agamic alate form of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton) Univ. of California Publ. Entomol. **16**(4):125–80.

PATCH, EDITH M.
1925. The melon aphid. Maine Agr. Exp. Sta. Bul. **326**:185–96.

PERGANDE, T.
1895. The cotton or melon plant-louse. Insect Life **7**(4):309–15.

PLAUT, N.
1949. Ecological and biological studies of aphids in Israel (in Hebrew with English summary), Ph.D. Thesis, Jerusalem. Cited in Bodenheimer and Swirski (1957).

PRITCHARD, A. E., and R. E. BEER
1950. Biology and control of *Asterolecanium* scales on oak in California. Jour. Econ. Ent. **43**(4):494–97

REINHARD, H. J.
1927. The influence of parentage, nutrition, temperature, and crowding on wing production in *Aphis gossypii* Glover. Texas Agr. Exp. Sta. Bul. **353**:1–19.

SHULL, A. F.
1932. An internal but non-genetic character affecting wing production in response to light in an aphid. Am. Naturalist **66**(703):180–83.

SLUSS, R. R.
1967. Population dynamics of the walnut aphid, *Chromaphis juglandicola* (Kalt.) in northern California. Ecology **48**(1):41–58.

SMITH, H. S.
1935. The role of biotic factors in the determination of population densities. Jour. Econ. Ent. **28**(6):873–98.

STERN, V. M., R. F. SMITH, R. VAN DEN BOSCH, and K. S. HAGEN
1959. The integration of chemical and biological control of the spotted alfalfa aphid. Hilgardia **29**(2):81–101

SVARDSON, G.
1949. Competition and habitat selection in birds. Oikos (Copenhagen) **1**(2):157–74

SWIFT, J. E.
1958. Factors influencing the distribution and seasonal abundance of *Aphis gossypii* Glover in California. Ph.D. Thesis, University of California, Berkeley. 175 pp.

SWIRSKI, E.
1951. Fruit-tree aphids in Israel (in Hebrew, with English summary). Ph.D. Dissertation, Jerusalem. 148 pp. Cited in Bodenheimer and Swirski (1957).

THEOBALD, F. V.
1926. The plant lice or Aphididae of Great Britain. Vol. 2:411 pp. London: Headley Brothers.
WAGNER, R. P.
1944. The nutrition of *Drosophila mulleri* and *D. aldrich* growth of the larvae on a cactus extract and microorganisms found in cactus, p. 104–28. *In* Studies in the genetics of *Drosophila.* J. T. Patterson (ed.) IV. Papers dealing with the taxonomy, nutrition, cytology and interspecific hybridization in *Drosophila.* Univ. Texas Publ. no. 4445, 223 pp.
WALL, R. E.
1933. A study of color and color variation in *Aphis gossypii* Glover Ann. Ent. Soc. Am. 26(3):425–60.
WEATHERLY, P. E., A. PEEL, and G. P. HULL
1959. The physiology of the sieve tube. Preliminary experiments using aphid mouth parts. J. Exp. Bot. 10(28):1–16.
WHITE, W. S.
1946. The environmental conditions affecting the genetic mechanism of wing production in the chrysanthemum aphid. Am. Naturalist 80(790):245–70.
WILSON, F.
1938. Some experiments on the influence of environment upon the forms of *Aphis chloris* Koch. Trans. Roy. Ent. Soc. Lond. 87(6):165–80.
WYATT, I. J.
1965. The distribution of *Myzus persicae* (Sulz.) on year-round chrysanthemums. I. Summer season. Ann. Appl. Biol. 56(3):439–59.
ZIMMERMAN, M. H.
1963. How sap moves in trees. Sci. Am. 208(3):132–42.

4m-2,'69(J5757)P.A.V.

factor was high temperature, which killed more of the older leaves when they were infested with high aphid densities.

Alate production was associated with high populations on vigorously growing plants. Later, however, as aphid populations rose and plants became less favorable, alate production decreased. *Aphis gossypii* had two peak periods of alate production—one during the accelerated growth phase, and the other during the equilibrium phase. *M. sanborni* displayed one strong alate production peak during the accelerated phase and a very weak production peak during the equilibrium phase.

Aphid size varied with host condition. Size varied greatly between two *M. sanborni* colonies reared on chrysanthemums with different aphid densities and host-plant conditions. The large morphs of *M. sanborni* had a higher reproductive rate and a higher alate production rate than did the small morphs.

ABSTRACT

Competition and other factors influencing the population dynamics of *Aphis gossypii* and *Macrosiphoniella sanborni* on greenhouse chrysanthemums were studied. Single- and mixed-species populations after an accelerated growth period, reached a moderately stable equilibrium phase. Removal of alate forms, which simulated dispersal, reduced the rate of population growth, but did not stabilize the populations. Because they were strongly influenced by aphid density, the main population regulating agents were aphid size (related to birth rate), and leaf mortality (related to death rate). Another indirect, regulating factor was high temperature, which killed more of the older leaves when they were infested with high aphid densities. Although *Myzus persicae* is the major aphid pest of greenhouse chrysanthemums in California, this study suggests that, in the absence of insecticides, *M. sanborni* and *A. gossypii* are better adapted to chrysanthemums.

The journal HILGARDIA is published at irregular intervals, in volumes of about 650 to 700 pages. The number of issues per volume varies.

Single copies of any issue may be obtained free, as long as the supply lasts; please request by volume and issue number from:

Agricultural Publications
University Hall
University of California
Berkeley, California 94720

The limit to nonresidents of California is 10 separate titles. The limit to California residents is 20 separate titles.

The journal will be sent regularly to libraries, schools, or institutions in one of the following ways:

1. **In exchange for similar published material on research.**
2. **As a gift to qualified repository libraries only.**
3. **On a subscription basis—$7.50 a year paid in advance. All subscriptions will be started with the first number issued during a calendar year. Subscribers starting during any given year will be sent back numbers to the first of that year and will be billed for the ensuing year the following January. Make checks or money orders payable to The Regents of The University of California; send payment with order to Agricultural Publications at above address.**