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PARLATORIA OLEAE (COLVÉE), IN
CALIFORNIA BY IMPORTED APHYTIS
MACULICORNIS (MASI)
(HYMENOPTERA: APHELINIDAE)**

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C. B. HUFFAKER,² C. E. KENNETT,³ and G. L. FINNEY⁴

INTRODUCTION

OLIVE SCALE, *Parlatoria oleae* (Colvée), was first discovered near Fresno, California, in 1934 and soon became an extremely serious pest. Chemical control methods against this scale were then inadequate and in the latter part of the 1940's—at which time the currently used parathion treatments had not been developed—intensive efforts at biological control were initiated in California by the late H. S. Smith. In 1948 parasite material was received from Egypt, and from this the Egyptian *Aphytis* was obtained and apparently became established. In 1951 Boyce (1952)⁵ searched the world distribution of the scale for its natural enemies and sent many shipments of material to R. L. Doutt, who initiated the biological control program in California. Doutt's (1954) report of that early work indicated that the Persian *Aphytis* showed much promise; the report also noted the ineffectiveness or lack of establishment of several other introduced species.

In appraising results of a parasite introduction, it is important to consider both the status of the host pest and the natural enemies which may be found attacking it prior to such introductions. Such pre-release knowledge is needed to properly evaluate the mortality factors already existing and to estimate the relative importance of subsequent introductions. Pre-release checks also assure investigators that an eventual introduction is not merely the establishment of a parasite species already present in the area.

Bacon (1941a) reported studies on the action of *Hemisarcoptes malus* (Shimer) on *P. oleae* on olives and on several other host plants in the area

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⁵ See "Literature Cited" for citations referred to in the text by authors and date.

of Fresno, California. He found this predatory mite to be fairly widespread and attacking eggs and crawlers which had not issued from beneath the parental scale coverings. He suggested that the immature females may be too tightly attached to permit entrance of the mites—an observation in which we concur.

Bacon found this mite more commonly in older and more heavily encrusted infestations where high percentages of the eggs were often destroyed; it was not commonly present in new, light infestations. He estimated that where it was most numerous and where it was destroying nearly 100 per cent of the scale eggs present at the time of observation, only about 50 per cent total control was being exerted because about 50 per cent of the eggs had already hatched and the crawlers had escaped destruction by moving out. Bacon (1941a) found no mites attacking scales on the leaves of olive, Virginia creeper and lilac, but scales on the stems from the same plants were infested as follows: Virginia creeper 85 per cent, olive 70 per cent, and lilac 60 per cent.

Bacon's notes indicate the status as to natural enemies at a time when olive scale was very abundant in some places and was spreading rapidly in the Fresno area but before successful introduction of enemies of the scale had been made. Since that time, general observations by the present authors and by E. M. Stafford confirm Bacon's observations that this predatory mite thrives only at high densities of its scale prey; the mite either leaves or dies *en masse* when it has reduced a high infestation to rather low densities, and it does not immediately rebound with rebound of the prey population.

Since the general establishment of *Aphytis maculicornis* (Masi) from Persia the present authors have found this mite only rarely in the area studied—except in places where, because of insecticidal usage or other disturbance of *Aphytis* action, the scale has again developed heavily-encrusted infestations. This latter condition is now seldom encountered; *Aphytis* simply holds the scale at densities below the effective threshold for *Hemisarcoptes* success.

Bacon (1941b) also reported the parasitization of *P. oleae* by an internal aphelinid, *Aspidiotiphagus citrinus* Craw. However, he found it to parasitize only a small percentage of scales. In the one instance where a specific percentage (0.5%) was reported, it was in scales on Virginia creeper—obviously a dooryard infestation. Doult (1952) observed that an introduced *Aspidiotiphagus* was seldom found to parasitize more than a low percentage of hosts, although he noted one instance of 45 per cent parasitization. This also seemed to be limited to dooryard infestations in California's Central Valley. The species is now apparently established in the vicinity of Chico, California.

Extensive examination by E. M. Stafford, O. G. Bacon and their associates, of all stages of scales in the early 1940's in the Fresno area revealed no entomophagous parasite other than *Aspidiotiphagus citrinus*. This suggests that the so-called Californian form of *Aphytis maculicornis* studied by Hafez and Doult (1954) may be the "Egyptian" form which, so far as the limited evidence indicates, seems equivalent biologically and which was,

according to Douth (1951), colonized in 1949. Hafez and Douth did not report the "original" hosts of the presumed indigenous Californian form. It is noteworthy that *Aphytis maculicornis* was not known to occur in North America prior to the introduction of the Egyptian stock.

The first attempt to control olive scale by introduction of parasites was made by S. E. Flanders and E. M. Stafford (unpublished notes) through the liberation of *Habrolepis rouxi* Compere in Fresno, California. This started in March, 1940, and continued into 1942. Although *H. rouxi* parasitized the scale it was unable to maintain itself.

A number of other species of parasites and predators which attack olive scale were also liberated in Fresno and Merced counties in 1948 and 1949 by R. L. Douth (unpublished notes), who reported, "None of these species became established with the possible exception of an *Aphytis* sp. from Egypt which maintains itself at a low density." According to a later report of Douth (letter of September 25, 1951 to C. P. Clausen), this form, designated at that time as *Aphytis* "D," was released on March 10, 1949 at four locations in Merced and Fresno counties—a total of 5,000 being colonized. Recovery (5 per cent parasitization) was obtained at the Herndon location at Grantland and Barstow Road, Fresno County on June 6, 1949, and again on June 27. The species was also recovered at Ventura Avenue, Fresno (8 per cent parasitization) and in the city of Merced (13 per cent parasitization) on July 6, 1951.

The research reported in the present publication was carried out from 1955 through 1960 and is a continuation of studies reported by Douth (1954) which covered the introduction and initial results with Persian *Aphytis* first liberated in 1952. The presently reported field research was exclusively on olives. However, one group of tests was initiated on peaches and plums, but San Jose scale, *Quadraspidiotus perniciosus* (Comstock), was more abundant than was *P. oleae* at the initiation of the tests. Because *P. oleae* declined steadily and San Jose scale increased, the study shifted to one of San Jose scale.

In the first few years after introduction of Persian *Aphytis*, olive scale on commercial peaches, plums, apricots and other similar deciduous fruits declined, in general, to a minor status. The insecticides used on commercial plantings of many of these crops are such as would preclude the most effective *Aphytis* action, and in some instances may directly control *P. oleae* as well. E. M. Stafford, an authority on chemical control of olive scale, comments as follows in this connection:

I have felt that dormant sprays for control of olive scale on deciduous trees were not nearly as effective as sprays applied about the last of April. Comparisons of dormant sprays with April sprays were consistently in favor of the latter. The parathion-oil combination spray used for olive scale is the most effective dormant spray for San Jose scale. For some reason San Jose scale increased and olive scale decreased. I find it difficult to believe that the decrease in olive scale on deciduous trees was largely due to use of insecticides. If it was not due to parasitism, then some other factor was at work—and effectively at work. This factor does not detract from the importance of *Aphytis* in reducing olive scale infestations.

Aphytis, as Stafford suggests, may have been a key factor in the general decline of olive scale in sprayed deciduous orchards; its ability to increase so phenomenally during a short period in spring makes for such a possibility despite its high susceptibility to insecticides. It is also possible that under present treatment programs the natural enemies of San Jose scale are inhibited (as is Persian *Aphytis*) and, consequently, San Jose scale increases more rapidly than does *P. oleae*. This assumes that *P. oleae* inherently cannot compete with San Jose scale. However, around parks and dooryards where such treatments are not usually applied, Persian *Aphytis* must unquestionably be credited with an important role in reducing the previously heavy infestations to a relatively innocuous status.

When a given natural enemy continuously holds a pest at non-economic densities in all areas infested, it is not imperative to delve into the details of the ecology of the pest species. The role of such natural enemy action is not obscured by the other environmental forces influencing the pest species. This can readily be demonstrated by use of "check methods" of analysis (DeBach, 1958a, DeBach *et al.*; in press).

If a natural enemy is very effective only at times, or is effective only in certain areas, a delicate balance involving all the environmental forces which influence both the pest species and the natural enemy is indicated. In such cases it is necessary to study the whole environment of both organisms in order to appraise the reasons for the variable success and to discover possible ways of improving the biological control. Consequently, in this study we have considered a number of abiotic factors of importance in the dynamics of the host species, and have considered how these factors affect the parasite. While it was not possible to make a bioclimatic study (which would undoubtedly have permitted a more generally valid appraisal) the information obtained regarding the physical environment does throw some light upon the question of variable effectiveness of this small aphelinid. Weather factors can, for example, inhibit the host or cause a very high rate of increase, or can drastically curtail or enhance the effectiveness of the parasite.

In the present study, the host and then the parasite are first considered as separate biological units. Following this is a consideration of field and laboratory studies of the role of the parasite in the control of the scale. The study ends with a survey of the degree of control achieved and of possible methods for improvement.

THE HOST

Taxonomic Status

Olive scale, *Parlatoria oleae* (Colvée) was described by Colvée in 1880 from specimens collected from olives at Valencia, Spain. The scale covering of the adult female is somewhat circular, slightly convex, and measures approximately $\frac{1}{16}$ inch in diameter. It is a dirty white or gray color along the outer portions, but almost dirty black in the center, the latter incorporating the cast coverings of the 1st and 2nd stages. The body of the scale in the young stages is a pinkish to violet color, a deeper purple developing with age. This color characterizes the males, crawlers and eggs as well. Older male scales

are easily distinguished by their subovate, in contrast to the female's circular shape. (See Plate 1, *e* and *f*, center pages, but note that exit holes of the parasite are present in both male and female scale coverings).

This scale can be distinguished from other species of *Parlatoria* in California by the possession of four pygidial plates (instead of the three which are common in other species) between the third and fourth pygidial lobes (McKenzie, 1956).

World Distribution

According to McKenzie (1952), olive scale is widely distributed in the entire Mediterranean region and also occurs in Persia, Russian Turkestan, India, England, Argentina and the United States. In the United States its occurrence is limited to Maryland, California, and Arizona. In the United States it has posed a serious problem only in California; this applies to both the deciduous fruit and olive industries.

Distribution in California

Parlatoria oleae was first discovered in California near Fresno in 1934. It had been abundant at the site since about 1931 (Wymore, 1935) although its identity had not been determined. The authors are indebted to McKenzie (1952) for much of the following chronological history of the spread of this pest in California.

A survey conducted in Fresno County in 1935 indicated the distribution of *P. oleae* to be about 100 square miles (Mackie, 1938). A survey initiated in 1939 included Fresno, Kings, Kern, Madera and Tulare counties and the indications were that Fresno was the seat of the original infestation. The scale continued to spread, despite attempts at extermination and despite intensive enforcement of quarantine restrictions—by 1939 approximately 410,000 acres were infested, with 2,089 foci in Fresno, 18 in Tulare, and 2 in Madera counties. In 1941 the scale was found in Kings, Merced, Kern, and Santa Cruz counties; in the latter county the single infested plant was removed and the infestation apparently eradicated. In 1942 the scale was also found in the mountainous North Fork area of Madera County on native plants such as *Ceanothus* and manzanita. From 1942 to 1952 there was additional spread to include Stanislaus, San Joaquin, Sacramento, Placer, Sutter, and Yuba counties to the north, and Los Angeles, Orange, San Bernardino, and San Diego counties to the south. Incipient infestations were also discovered in Alameda County (San Leandro) and Santa Barbara County during this period but were immediately eradicated. Infestation was later discovered in Livermore, Alameda County; this still exists.

Subsequent to McKenzie's summary of 1952, infestations have been reported from Yolo, Glenn, Riverside, Tuolumne, Butte, Contra Costa, Colusa, Inyo, Solano, and Tehama counties, the latter three being discovered in 1959 and 1960.

Thus, in 25 years this pest has spread from the Fresno center northward to Tehama and southward to San Diego counties and is now found in an area which embraces most of the Central Valley counties and, to a lesser extent, south of the Tehachapi mountains. In all, the species has been re-

Fig. 1. Distribution of *Parlatoria olcae* (Colvée) in California—1960. Diagonal lines indicate area of general infestation; circles indicate isolated infestation. (Base map provided by Department of Entomology and Parasitology, Berkeley.)

ported from 29 counties with the Inyo County location being disjunct east of the Sierra Nevada. The pest seems to be naturally established in only 27 counties, however, as there is no direct evidence that it is now established in Santa Cruz and Santa Barbara, coastal areas of which seem not climatically suited to it. For discussion of the factors related to the varying success of this insect in various areas of the distribution see page 565.

Because this insect can move as a population only as active crawlers, its distribution between non-interlocking trees is normally accomplished by wind, birds, flying insects, and the like. However, the rapidity of spread which is exhibited by this record could only be accomplished by human means of transport. In fact, many of the original infestations in the various

counties were traced to purchases of nursery stock coming from Fresno and other heavily infested counties.

Status as a Pest

McKenzie (1952) reports that at the time of Colvée's original description of *P. oleae* from material collected in Spain in 1880, the insect was causing serious damage to olives. In this century, there have been occasional reports of its causing damage to deciduous fruits, as well as to olives, in a number of Mediterranean countries. However, explorers (such as A. M. Boyce, Paul DeBach, Robert van den Bosch, and J. K. Holloway) who have recently searched that region for natural enemies of the insect have found the scale to be rather scarce. This contrasts sharply with its general abundance on a very wide variety of host plants in California—particularly its abundance in the late 1940's prior to the introduction of Persian *Aphytis* (considering in each case host trees untreated with insecticides). To what extent this difference in abundance may be attributed to the action of natural enemies in the Mediterranean region, or to differences in climatic conditions or cultural practices, is not presently known.

Boyce (1952) searched the known world distribution of this insect for natural enemies in 1951, covering Thailand, India, Pakistan, and countries of the Middle East and the Mediterranean area. He considered Northern India, West Pakistan and the Middle East to constitute the native home of the scale. Collections and observations were made and material forwarded to California from India, Pakistan, Baluchistan, Afganistan, Iran, Iraq, Lebanon, Syria, Israel, Egypt, Tunisia, Cyprus, Greece and Spain. In personal correspondence with the authors, Boyce comments as follows regarding the status of *Parlatoria oleae* in these countries.

In practically all localities where the scale was found it was a very minor pest of deciduous fruit trees, that is, of apple, pear, apricot, plum and peach, and was exceedingly rare on olive. In only one country, Iran, does it periodically become very destructive on olive, but even there the infestations are ultimately controlled by natural enemies. These outbreaks are reported to occur at five to six year intervals. The high incidence of parasite attack in all areas and the very minor status of the olive scale as a pest in the countries of apparent origin give considerable promise that biological control by the same agencies can be accomplished in California.

In a report for April, 1952, to C. P. Clausen in which he had noted rapid increase in parasitization of *P. oleae* to 40–60 per cent by recently established Persian *Aphytis*, R. L. Doutt commented that the potential importance of *Aphytis* is obvious when it is remembered that during the past years rarely was parasitism above 5 per cent recorded. Most samples prior to the release of the new *Aphytis* yielded no parasitism.

Prior to introduction of *Aphytis*, *P. oleae*, though relatively innocuous along the Mediterranean, was a serious problem in California. Since its introduction into California, however, the scale has declined to a status much more nearly comparable to its status in the Mediterranean.

Regarding olive scale in California, McKenzie (1952) stated, "The aggres-

siveness of this scale in California would seem to place it at or near the top of the list as the State's most economically important scale species." Such a statement is not based upon the insect's potential damage to the olive crop alone; the fact that it attacks a wide variety of economically important hosts including the common deciduous fruits of the rose family, and many other trees and shrubs such as walnut, ash, cotoneaster, Toyon, privet, rose, lilac, *Syringa*, and Oregon grape, make it a potentially most serious pest. It is reported capable of development on some 211 different species of host plants, although many of these are not common or self-sufficient hosts (McKenzie 1952). In the early years of the California infestation the insect developed very heavy populations on the fruits, leaves, twigs, and limbs of many of its preferred hosts, including olive, peach, apricot, almond, plum, ash, privet, Oregon grape and Toyon.

Prior to 1951, serious infestations had developed in many parts of the San Joaquin Valley. The fruits of olives, plums and apricots, for example, were often so contorted and discolored by the scales that they were unmarketable, and the leaves, twigs and limbs of the trees suffered so severely from heavily-overlapping encrustations that die-back and a general sickly condition persisted (Pl. 2, *b, d, e*, center pages).

The most direct financial loss from this insect is due to the marking and discoloration of smooth-skinned fruits such as plums, apricots and olives. However, losses in quality otherwise and particularly in yield may be very great if high populations develop. Olives are particularly susceptible to economic losses because the fruits are smooth-skinned and because they are still present on the trees at the time of settling of the fall brood of crawlers which exhibit a marked preference or at least a differential success in settling on fruits as contrasted to the leaves and twigs. E. M. Stafford (personal communication to the authors) confirms that spring-produced crawlers certainly do not settle on fruits as much as do crawlers produced later in the season. Yet, in certain years and in certain orchards the fruit in the spring may develop faster than normal in relation to the crawlers. In such cases there may also be substantial fruit infestation in the spring. Attacked fruits develop a discoloration or darkening of the tissues surrounding the scale, and if the scales reach a late stage of development prior to harvesting there is a marked distortion of fruit. Only trace infestations of very young scales are tolerated by the olive packing and processing industry.

According to Stafford (1949), control of olive scale in California prior to development of effective treatment with parathion was rather difficult and unsatisfactory in some cases. Tent fumigation with HCN gas for olives, and oil sprays for both olives and deciduous fruits had been used. The development of parathion sprays for the pest has greatly alleviated the problem although there are hazards in the use of the material which many growers prefer to avoid, and there are some growers who cannot use it because of the locations of their groves.

From the time of its discovery near Fresno in 1934, and prior to the initiation of the present biological control program, olive scale in California was not *effectively* attacked by any parasites. The only external parasite known to have attacked this scale under field conditions prior to 1952 is the Egyp-

tian *Aphytis*, which was released in Fresno and Merced counties in 1949 by R. L. Doutt and K. S. Hagen (Doutt, 1951), and which apparently became established. Doutt also reports that the total parasitization observed by the Egyptian form, based on numerous field collections from olives and other hosts having heavy infestation, was never found to be much greater than 5 per cent.

It is obvious from the densities of the infestations that little control was exerted by natural enemies prior to the introduction of Persian *Aphytis*, except occasionally by *Hemisarcophaga*—a predator which did not prevent development of very high densities. Immediately after release of the Persian *Aphytis*, however, a phenomenal increase in the parasitization of olive scales occurred in instance after instance. Additionally, it was noted that within one year following release of Persian *Aphytis* in California densities of scales at release locations began a sharp decline, although the general trend since 1934 had been one of steady increase.

It seems clear that the natural enemies which were present in the infested area prior to 1952 were entirely unable to control olive scale and in fact had little impact upon it.

Life History and Ecology

Evaluation of Persian *Aphytis* as a biological control agent cannot be accomplished without close appraisal of both the host and the natural enemy in relation to their total environments. Because of this fact, useful data concerning the host were also obtained from detailed studies which, however, were concentrated on the parasite. It should be remembered that the data are exclusively from olives as the host plant. It has been noted (Stafford 1954) that egg-laying on deciduous fruits, for example, may occur two to three weeks earlier than on olives. But it is equally true that all seasonal phases of the life history may vary as much as two to four weeks from year to year, or from place to place, even on the same host plant (olives). Hence, the statements in this section regarding timing are given in general terms. This is particularly true when comparing Tulare and Glenn counties, for example, although the differences may vary almost as much within the same county or in the same orchards in different years.

The female scale and the number of generations. *Parlatoria oleae* in California has only two generations each year, although it is reported to have as many as four generations per year in certain Mediterranean countries (Grandi, 1951). This raises a question as to whether two or more distinct species may be involved—a question which a number of entomologists have asked, but which none has answered.

In California, *P. oleae* passes the winter largely as impregnated, immature to nearly-mature third-stage females. Some off-brood individuals of younger females and males may develop the following spring, but these represent only a small proportion of the brood's population. For example, in late April and early May there is a very marked single-stage condition, with mature females representing 95 per cent or more of the total population. These females also produce an even-brooded progeny, with the first settled stages representing up to 80 per cent or more of all the live settled stages during the middle of May or slightly later (figs. 2, 3, 4).

Fig. 2. Adult female *Parlatoria oleae* (Colvée) on orchard olives expressed as a percentage of live settled stages and the associated egg-laying periods. (Adapted in part from Stafford, unpublished data, 1941.)

Fig. 3. First and second nymphal stages of *Parlatoria oleae* (Colvée) expressed as a percentage of live settled stages. (Adapted from Stafford, unpublished data, 1941.)

Fig. 4. Male nymphs of *Parlatoria oleae* (Colvée) expressed as a percentage of live settled stages.

The fall brood is produced by females which usually peak in abundance in late July and early August, with the peak of the first settled stage being in middle to late August. This fall period is not characterized by such a pronounced single-stage condition. By this time each year there has occurred a considerable overlapping of stages so that in August, at the peak of first-stage abundance, this stage represents only 50 to 60 per cent of all live settled stages. The contrast is even more striking if we consider the peak in abundance of the egg-laying females, which at the early August period represent only 25 to 35 per cent of the total population, in contrast to 95 per cent or more in late April or early May.

Individual egg-laying females deposit eggs for a period of two to three weeks before they have exhausted their body contents and die. The mature female scales seem capable of withstanding the high temperatures and low humidities which often prevail in the San Joaquin Valley in mid-summer, but these factors are a potent cause of mortality of crawlers and the first settled stages. The older scales have thicker, more protective coverings against water loss and perhaps a greater ability to obtain water; such factors would contribute to superior tolerance of heat and dryness.

All stages of the scale may be markedly affected by unavailability of water in the tissues of the host plant, for, we have sometimes noted that olive

trees which had previously been under cultivation, irrigation and good care, and on which *P. oleae* succeeded well, would "clean up" following discontinuance of irrigation. This has been noticed especially in cases where the fruits and leaves on the trees became obviously shriveled and lacking in turgor, even if the condition were of short duration and the foliage reassumed a normal state after autumnal rains. All abandoned trees do not reach this state, and their internal turgor may remain adequate to sustain a continuing high density of this pest.

Contrasting examples have often been seen, however—for example, where a non-irrigated olive grove is next to a dwelling on the well-watered lawn of which a few olive trees having high scale populations are present. Mortality from such causes makes it impossible to use such groves in studies of biological control by *Aphytis*.

The nutrition afforded the scales may also have an effect on the success of a brood, or on the egg production of mature females. Obviously, some trees will support much higher populations than will others before this factor comes into operation. This could be a grove characteristic.

Referring briefly here to data from a later section, table 18 (p. 598) shows that egg production per female during the summer brood (when *Aphytis* effects are negligible) at the Bell grove was consistently higher than at either the Duncan or Whitney groves for the same years. Since, in general, the densities at the Whitney grove were highest, at the Bell grove lowest, and at the Duncan grove, intermediate, we might expect that this is a reflection of the influence of crowding or availability of food for egg production. A more specific analysis of this question does not support this explanation, however. It is unfortunate that data from the Whitney grove are available only for 1958 and 1959, and that a suitable comparison in several other respects is not possible. In considering the data shown in table 18, densities of mature female scales at the Bell grove in 1956 were about three times higher than at the Duncan grove (see table 17, p. 595) although in this respect 1956 was contrary to the order in other years. Also, the number of eggs produced per female in the summers of 1958 and 1959 (table 18) at the Whitney grove was not appreciably different from the Duncan grove, while densities of scales were much higher in the Whitney grove in 1958 but only somewhat higher in 1959 (table 17).

Furthermore, a direct comparison was made regarding the influence of density on fecundity by classing twig data (not presented here) according to high or low density classes for the Duncan and Whitney groves for 1958 and 1959. The production of eggs per female was then almost identical between the high and low density categories within each location. No twigs fell in the high density class for the Bell grove, so no comparison was possible for that grove.

Thus, while crowding can, under the most severe conditions, gradually reduce tree vigor and cause a nutritionally-induced lower scale fecundity in a grove, present data do not support this as an explanation of the differences in egg production per female (comparing populations at the groves studied). The more likely explanation is that tree vigor and physiology due simply to management practices and/or site potential at the Bell grove caused a higher fecundity at that location.

Another important point relative to the fecundity of the females is whether or not they are fertilized. Stafford (1947) inferred from observations and experiments that use of DDT to kill the males of this scale caused a lack of mating and the resulting females formed no eggs but instead remained non-gravid and formed abnormal, enlarged scale coverings. Under conditions encountered in this study this has not been a significant factor. It is suspected, however, that proper synchronization of male and female development may be a factor in the absence of this insect from cool coastal areas in California.

The male scale. Adult male *P. oleae* of the spring brood peak in abundance under Central Valley conditions in late June to early July—that is, about 15 to 20 days prior to the peak in mature females (fig. 4). In the fall brood the males develop to full maturity much earlier than the females, peaking in abundance in September, but at this time the spread in adult male appearance is considerably greater than in the spring brood. The females of the fall brood reach the third stage in some numbers about three weeks later, but do not reach a near-maximal abundance until late October or early November; in fact, a considerable portion of some populations may be retarded in this respect and persist in the second stage well into November or early December. Fully mature females do not peak in abundance until March or April of the following year in the absence of appreciable parasite activity, which latter creates a spurious timing of apparent peak abundance. Since some of the males are also retarded and might thus synchronize with the retarded females, this may not contribute significantly to infertility of the ensuing adult females in the spring. The question of synchronization of male and female development and other ecological factors relative to this insect's distribution and economic status is discussed on page 567.

The eggs. Female scales under very favorable conditions may deposit from 50 to 100 eggs (Lockwood 1950) although the range in number of eggs usually encountered under field conditions during this study has been considerably less, a common maximum being closer to 70 than to 100. See also Ezzat (1957).

The numbers of eggs produced may vary greatly with conditions, particularly with the nutritional qualities of the branches and with the activity of Persian *Aphytis*, which may completely or only partially curtail egg production. Although weather may be very significant for crawlers and the young settled stages, the weather conditions encountered in these study areas did not appear to have a decided influence on fecundity, or at least not nearly so great an influence as action of *Aphytis*.

The present population studies at three study areas reveal that the egg production per mature female varies from a low of about one per female (in cases where parasitization by *Aphytis* has prevented or greatly curtailed egg production by fully mature females) to a mean maximum of around 30 per female under favorable host plant condition and absence of curtailment by *Aphytis* (see page 598).

Tests on effect of lath protection versus full sun on development of young stages. For the spring brood, on May 23, 1957, two groups of 8 young olive trees grown in large redwood containers were arranged adjacently with like orientation to the sun, except that one group was left with full exposure

to the sun and the other was sheltered with a lath covering representing 67 per cent lath and 33 per cent open space. Fifty *P. oleae* crawlers were placed on each tree so that there was a total of 400 in full sun and 400 in the shade. After the scales had developed to maturity, examinations were made to determine the development to, and mortality in, the various stages. The tests were conducted at Orange Cove, California, on property of the late Henry Bell.

On August 21 a similar test was conducted with the fall brood of crawlers. The results of these tests, as presented in table 1, indicate that crawlers of

TABLE 1
MORTALITY AND SURVIVAL OF *PARLATORIA OLEAE* ON SPARSE-FOLIAGE OLIVES IN FULL SUN AND UNDER TWO-THIRDS SHADE BY LATH COVER

Brood	Sun or shade	Total crawlers	Settled stages	Settled successfully	Survival of settled stages	Crawlers reaching adult stage
				<i>per cent</i>	<i>per cent</i>	<i>per cent</i>
Spring.....	Sun	400	29	7.2	(5) 17.2	1.3
	Shade	400	33	8.2	(6) 18.2	1.5
Fall.....	Sun	326*	51	16.0	(35) 68.6	10.7
	Shade	355*	82	23.0	(64) 79.0	18.0

* These totals are adjusted from the original 400 crawlers used, due to an unnatural loss of leaves from the twigs.

the fall brood had most success in settling. The specific temperatures and humidities prevailing on the days the transfers were made is not the explanation, however, as temperature readings were high on August 21 (maximum of 95° F) and much lower (maximum of 75° F) on May 23. Relative humidities were not excessively low at the time of transfer of crawlers of either brood, averaging 58 per cent on May 23 and 37 per cent on August 21 for the hours during which the transfers were made.

A check was made to determine if there were any possibility of injury to the crawlers due to the transfer technique used. Similar transfers of crawlers were made onto olive branches which were then placed in cabinets kept at 70° F and 80–84 per cent relative humidity. Here, crawler settling and survival of settled stages was much higher; 151, or 37.7 per cent, settled, and of these 140, or 92.7 per cent, survived. This is 35.9 per cent final success from the crawlers used. Thus, mechanical injury caused only part of the high number of deaths occurring in the field tests.

Although crawlers and settled stages suffered severe mortality during the spring brood, crawlers and later stages survived moderately well during the fall period, which normally has less severe humidity patterns than the corresponding spring period although its maximal temperatures are not appreciably different. It is clear that the degree of shade used was not sufficient to offer an appreciable advantage under the conditions existing during the spring brood test, and only a moderate ameliorating effect is indicated for the fall brood (table 1). It is felt that a much greater protection from sun, wind and desiccation than offered here would have given a more striking contrast.

Densities on sparse and dense-foliage branches. Because olive scales usually seem more abundant on north and north-east sides of trees, on dense-foliage branches, or on branches which are located next to walls or structures offering shelter against wind or the most direct exposure to the sun, some time was spent in analyzing population densities of *P. oleae* under dense-foliage and sparse-foliage conditions. The study was made for the purpose of evaluating success of settled stages under the exposed and more protected conditions. Populations on new growth twigs were used because the dead scales from old leaves and wood would not be assignable as to current brood.

The sample dates chosen were such that the particular broods involved would not have experienced significant action of *Aphytis*, although of course the action of *Aphytis* on their progenitors is a factor not covered by these data. If *Aphytis* effectiveness were greater in dense foliage, this factor would tend to counteract the tendency of greater abundance of scales on dense foliage. Again, if *Aphytis* finds hosts more easily with increase in host density (the density-dependent relation) on either sparse or dense branches, this factor also would tend to counteract any tendency of an accumulating build-up on dense branches. Our analysis of data on the searching of *Aphytis* does not support the view of a differential effectiveness in sparse or dense branches. Hence, we may take the data only as an indication which supports other information relative to the role of physical adversity, although the analysis of variance for the populations did not reveal a significant difference. Tables 2 and 3 show that densities of all stages of scales on the twigs and leaves,

TABLE 2

P. OLEAE ON NEW GROWTH OF LEAVES AND TWIGS OF DENSE AND SPARSE BRANCHES OF OLIVES AT LOCATIONS IN TULARE, MADERA, AND FRESNO COUNTIES, CALIFORNIA (ON A 12-TWIG BASIS—72 LEAVES)

Dense or sparse branches	Tree	October 16, 1956				July 17, 1957*				Totals
		Whitney	Connor	Trafton	Bell	Whitney	Connor	Trafton	Bell	
Dense	1.....	528	2,176	454	55	35	26	10	0	3,284
	2.....	770	1,834	30	17	21	13	4	0	2,689
	Totals.....	1,298	4,010	484	72	56	39	14	0	5,973
Sparse	1.....	236	1,613	93	24	8	29	3	0	2,006
	2.....	874	710	8	15	9	17	1	0	1,634
	Totals.....	1,110	2,323	101	39	17	46	4	0	3,640

* Total sample size on this date was 24 twigs although the data are presented on a 12-twig basis. In spite of this, low numbers were obtained, and no scales were present at the Bell location.

and also on the fruits, were nearly twice as high for the dense-foliage condition as for the sparse-foliage condition (considering all the data combined).

The drastic action of *Hemisarcophyes* on the high densities of scales in the fall of 1956 (an action intensified in the dense-foliage condition) could have caused an equalizing or reversal effect the following summer. It is quite plausible that this is why the Connor location had slightly higher densities in the sparse-foliage branches than in the dense-foliage branches in July of

1957; however, densities were very greatly reduced as compared to 1956. This general indication of the important part played by protection from hot drying conditions is strongly supported by other data relative to the same question from the experimental standpoint.

TABLE 3

P. OLEAE ON 50 FRUITS OF OLIVES IN OCTOBER, 1956, FROM LOCATIONS IN TULARE, MADERA, AND FRESNO COUNTIES, CALIFORNIA*

Dense or sparse branches	Tree	Location				
		Whitney	Connor	Trafton	Bell	Totals
Dense	1.....	944	9,480	662	117	11,203
	2.....	2,690	5,558	105	48	8,401
	Totals.....	3,634	15,038	767	165	19,604
Sparse	1.....	846	4,217	125	59	5,247
	2.....	1,823	2,874	6	27	4,730
	Totals.....	2,669	7,091	131	86	9,977

* No fruits available for inclusion at sampling of July, 1957.

Laboratory tests on influence of temperature, humidity, and air movement on scale crawlers. Data obtained under experimental conditions support field data relative to protection afforded crawlers and young settled stages of *P. oleae* under shaded conditions or in dense-foliage areas where temperature, humidity and air movement may be somewhat ameliorated. A test was conducted in which 300 crawlers for each condition of exposure or protection were placed on small cut branches of olives, the branches being

TABLE 4

INFLUENCE OF CONSTANT TEMPERATURE, HUMIDITY, AND AIR MOVEMENT ON DEVELOPMENT OF *P. OLEAE* ON OLIVE BRANCHES HELD IN CONTROLLED CABINETS IN THE LABORATORY*

Number of scale crawlers used	Air blowing on branchlets	Temperature	R. H.	Living scales in 2nd or 3rd stage (no others alive)	
				Number	Success
		°F	per cent		per cent
300	None	90	17 ± 3	0	0
300	Fan	90	17 ± 3	0	0
300	None	72	70 ± 5	50	16.6
300	Fan	71	70 ± 5	28	9.3
300	None	91	70 ± 5	0	0
300	Fan	91	70 ± 5	0	0

* Period of test was 43 days ± 1 day. Temperatures varied ± 2 degrees and the figures given are averages. Relative humidities were controlled by use of salt solutions, and an electric fan reduced to very low speed was used to produce air movement in the closed cabinets. Light was maintained by fluorescent daylight tubes.

held in jars of $\frac{1}{4}$ strength Hoagland's solution. The jars were then maintained in cabinets for a period of time sufficient to permit development to mature males and immature third-stage females. Temperature, air movement and relative humidity conditions were controlled to give a gradation from unfavorable to favorable protection status in the six cabinets, each cabinet representing one combination of conditions (table 4).

The results of this experiment show that crawlers of *P. oleae* are very susceptible to continuously high temperatures; there was no survival at 90° to 91° F even when the relative humidity was 70 per cent and when no air movement was employed. Thus, at this extreme temperature there was no opportunity of expression of an expected favorable influence by increasing the humidity from 17 per cent to 70 per cent, for example. Unfortunately this latter comparison was not made using 80° F, a sufficient number of cabinets not being available. Table 4 shows that at 71° to 72° F, and a relative humidity of 70 + 5 per cent air movement apparently accounted for a lower survival in that cabinet, as contrasted to the cabinet in which there was no fan.

Population dispersion and sexual differences in dispersion and survival on stems, leaves, and fruits. Considerable information concerning the dispersion in the tree and the behavior of *P. oleae* has been accumulated during these studies. Regarding the differential success of males and females, or the two sexes combined, on fruits of olives or other parts of the tree, the data indicate a varied pattern.

Stafford (1947) reported that most of the females are found on the stems. Our data support his conclusion to some extent, but we did find a substantial percentage of females on the leaves and still larger numbers on the fruits. This has been true throughout the 5-year period of study, and the analysis of populations at five groves made for this purpose in October, 1956, may be considered somewhat representative (tables 5, 6). The data of table 5 reveal that there is a marked difference in the male and female occurrence on different parts of the olive tree.

The stems or woody parts of the branchlets contained 2,179 scales assignable to sexes of which only 469, or 21.6 per cent, were males. The individual figures at each location support the average result in every instance, but less so at the Bell location where the density of scales was so low that only 10 scales assignable to sexes were encountered. The leaves of the same branchlets contained more than twice as many scales assignable to sexes; 4,303, or 79.3 per cent, were males, and 1,126, or 20.7 per cent, were females. The data at each location support the general averages.

Fruits were sampled in a different way, being picked from the trees at random and independently of the branchlets used as the leaf and twig samples. Therefore, total numbers cannot be directly compared. Of 23,415 scales assignable to sexes on the fruits, 12,606, or 53.8 per cent, were males.

Table 6 presents these data according to the total male and female populations present in the samples. Of the 4,772 males on both stems and leaves, only 9.8 per cent were on stems, and 90.2 per cent on leaves, with the individual records for the five groves in each instance being of the same order. Considering total females present on stems and leaves combined, there was not so sharp a difference: 60.3 per cent of the females were on the

TABLE 5

P. OLEAE ON STEMS, LEAVES, AND FRUITS OF OLIVES, BY SEXES AT FIVE LOCATIONS IN TULARE, MADERA, AND FRESNO COUNTIES, OCTOBER 1956. (144 LEAVES, 24 TWIGS, AND 100 FRUITS PER TREE—2 TREES AT EACH LOCATION)

Plant part	Property	Total recognizable sexes*	Males		Females	
			Number	Per cent	Number	Per cent
Stems	Trafton	127	20	15.7	107	84.3
	Whitney	554	135	24.4	418	75.5
	Connor	1,430	288	20.1	1,142	79.9
	Bell	10	4	40.0	6	60.0
	Kearney Park	58	22	37.9	36	62.1
	Totals	2,179	469	21.6	1,709	78.4
Leaves	Trafton	248	209	84.3	39	15.7
	Whitney	1,626	1,339	82.3	287	17.7
	Connor	3,310	2,562	77.4	748	22.6
	Bell	43	36	83.7	7	16.3
	Kearney Park	202	157	77.7	45	22.3
	Totals	5,429	4,303	79.3	1,126	20.7
Fruits	Trafton	653	391	59.9	262	40.1
	Whitney	5,807	3,075	53.0	2,732	47.0
	Connor	16,413	8,814	53.7	7,599	46.3
	Bell	175	113	64.6	62	35.4
	Kearney Park	367	213	58.0	154	42.0
	Totals	23,415	12,606	53.8	10,809	46.2
Totals			17,378		13,644	
Stems				2.7		12.5
Leaves				24.8		8.3
Fruits				72.5		79.2

* At the time of year when sex is determinable for the great majority of the surviving brood population.

TABLE 6

PERCENTAGES OF TOTAL POPULATION OF EACH SEX OF *P. OLEAE* ON STEMS AND LEAVES OF OLIVES (FROM DATA OF TABLE 5)

Location	Recognizable male population			Recognizable female population		
	Totals	Per cent of totals on:		Totals	Per cent of totals on:	
		Stems	Leaves		Stems	Leaves
Trafton	229	8.7	91.3	146	73.3	26.7
Whitney	1,474	9.2	90.8	705	59.3	40.7
Connor	2,850	10.1	89.9	1,890	60.4	39.6
Bell	40	10.0	90.0	13	46.2	53.8
Kearney Park	179	12.3	87.7	81	44.4	55.6
	4,772	9.8	90.2	2,835	60.3	39.7

stems and 39.7 per cent on the leaves. At two of the three locations studied there were more females on the leaves than on the stems, but these were the places with the lowest population densities and the least contribution to the total record. Furthermore, the fact that females occur nearly as abundantly on the stem segments as on the leaves (which latter exhibit a much greater total surface area) is evidence of selectivity of the females for the stems. Again, the females were considerably more abundant on the stems at the two high density locations where pressure for movement onto leaves would naturally be great.

When we consider the populations on the fruits it is obvious that there is a considerable dispersion of both females and males on the different parts of a branch. The percentages given at the bottom of table 5 show only the percentages of the males and females, respectively, which occurred on the stems, leaves, and twigs as included in these samples. Six leaves were taken from each of twenty-four branchlets (144 leaves, in all) and the bearing stem internodes were included as the leaf and stem samples per tree. There were few fruits on the branchlets, so for the sample 100 fruits were taken at random from each tree.

An average-sized olive fruit has nearly the same surface area as a leaf. Thus, barring differential favorability for fruit or leaf, and regardless of whether a heavy or light fruit crop is set, there should be about the same number of scales on a fruit as on a leaf. The data show that this is not true, however. There were 4,303 recognizable male and 1,126 female scales on the 1,440 leaves taken at the five locations. This is a density of 3.0 male and 0.8 female scales per leaf. There were 900 fruits in the total sample taken at the four locations (only 25 per tree at Kearney Park). On these fruits there were 12,606 male and 10,809 female scales which reached recognizable sexual development—that is, there were densities of 14.0 and 12.0, males and females, respectively, per fruit. Densities of males on fruits were thus about 5 times as high as on leaves, and densities of females were about 15 times as high on fruits as on leaves. It is obvious therefore that, regardless of the specific accuracy of this approximation, the fruits are either very highly attractive to crawlers of both sexes or else there is a marked mortality of settled stages on leaves which does not occur on the fruits. The former assumption is in conformity with general observations that even at very low densities of scales per tree appreciable commercial marking of the fruits occurs.

From this, it can be concluded that at the time of maturing of the fall brood, scales on the leaves of olives are about 80 per cent males and only 20 per cent females, and that on stems the reverse is true. There is also a marked concentration of both sexes on fruits during the fall brood.

This raises the question as to whether this result is one of behavioral activity at the time of settling or whether it is due to differential mortality between the sexes after settling.

Data bearing indirectly on the initial sex ratio of this species, and derived directly from the numbers of males and females among the total numbers reaching recognizable sexual development, were summarized for the Duncan and Bell groves for the years, 1956–1960, inclusive. These data are based on

the numbers of males and females for the fall and spring broods at the single count dates when there was maximum differentiation of the sexes, but before an appreciable number of the early-maturing males had emerged and a weathering-off effect became more disturbing, and before the females were subject to the disparity caused by a longer period of mortality. The data so restricted included 3,563 recognizable sexual forms, 1,843, or 52.2 per cent, of which were females. For those yearly records which consisted of

TABLE 7
MORTALITY OF RECOGNIZABLE MALE AND FEMALE *P. OLEAE* ON NEW GROWTH PRIOR TO *APHYTIS* ACTION AT FIVE LOCATIONS IN TULARE, MADERA, AND FRESNO COUNTIES, OCTOBER, 1956

Plant part	Location	Males			Females		
		Total recognizable*	Living or emerged	Mortality	Total recognizable*	Living	Mortality
				<i>per cent</i>			<i>per cent</i>
Stems	Tafton.....	20	18	10.0	107	83	22.4
	Whitney.....	135	121	10.4	418	376	10.3
	Connor.....	288	86	70.1	1,142	933	18.3
	Bell.....	4	1	75.0	6	2	66.7
	Kearney Park.....	22	19	13.6	36	22	38.9
	Totals.....	469	245	52.2	1,709	1,416	17.2
Leaves	Tafton.....	209	159	24.9	39	33	15.4
	Whitney.....	1,339	1,179	11.9	287	245	14.6
	Connor.....	2,562	1,209	52.8	748	547	26.9
	Bell.....	36	26	27.8	7	6	14.3
	Kearney Park.....	157	131	16.6	45	21	51.2
	Totals.....	4,303	2,704	37.2	1,126	852	24.3
Fruits	Tafton.....	391	298	26.1	262	244	6.9
	Whitney.....	3,075	2,499	18.7	2,732	2,388	12.6
	Connor.....	8,814	2,883	67.3	7,599	5,529	27.2
	Bell.....	113	89	21.2	62	49	21.0
	Kearney Park.....	213	162	24.0	154	100	35.1
	Totals.....	12,606	5,931	47.0	10,809	8,310	23.1

* At the time of the year when sex is determinable for the great majority of the surviving brood population.

at least 300 individuals, the percentage of females ranged from 39.2 to 55.0. This general result does not include losses in early-stage mortality in the egg, crawler, or young settled stages, and does not include the numbers present on fruits or on larger woody parts of the tree. From other data we found that while there was, comparatively, a differential settling of males on leaves and of females on stems, both sexes rather equally settled with greater success on the fruits. The error in data which would result from this disregard of the settling on fruits would not materially change the final conclusions. Hence, unless there was initially a greater number of either males or females, and unless subsequent early-stage mortality served to *precisely match* the initial sexual disparity in the opposite order, the data as recorded signify an approximate sex ratio of 0.5.

Mortality of scales prior to *Aphytis* action on stems, leaves and fruits.

Table 7 shows the mortality of scales on new growth after scales reached a state of recognizable sexual distinction in October, 1956. In general, premature mortality during the recognizable male and female stages on the fruits was definitely low, varying between 6.9 per cent for females and 26.1 per cent for males at the Trafton location. This excludes the higher mortalities occurring at the Connor location which probably were due to action of the predatory mite *Hemisarcoptes malus*. This predator was very active on the male population and, although large numbers of males and some females were obviously dead because of *Hemisarcoptes* action, much of the work of the predator had occurred a short time prior to these observations, and thus it was not possible to identify all of the dead males with this probable cause. The earlier action of the predators occurred at a time when they could enter beneath the loose, open ends of the scale coverings of the early-maturing males and destroy them. But at this same time the female coverings were still closely attached and they could not be attacked by *Hemisarcoptes*, except for those unusual ones having scales overlapping others next to them. This accounts for the fact that at the Connor location mortality of male scales after reaching recognizable status was unusually high on all plant parts, while mortality of females was comparable to the mortality at the other locations.

Mortality of males and females was also rather low on leaves, one exception being the case of males at the Connor location. In this category, the high mortality otherwise was 51.2 per cent for females at Kearney Park. This result is based on a low number (45) of scales.

Mortality of females on stems was not appreciably different from that on leaves and fruits, except at the Bell location where there were only six recognizable females in the sample. The data regarding mortality of males on stems are inconclusive because of the low densities at the Trafton, Bell and Kearney Park locations, and the predator action at the Connor location. Thus, it is unknown whether the low mortalities at the Trafton, Whitney, and Kearney Park locations are meaningful. It is known that the action of *Hemisarcoptes* such as occurred at the Connor location is very exceptional and that it does not occur at the low to moderate densities which normally prevail since introduction of Persian *Aphytis*. No *Hemisarcoptes* were active at the other locations.

If we disregard all male mortalities at the Connor location because of the unique action of *Hemisarcoptes*, the general mortalities are seen to be rather low, averaging 12.2 per cent on stems, 14.1 per cent on leaves, and 19.7 per cent on fruits. These mortalities are somewhat lower than those of the females, but the reverse is true if the Connor data are included (table 7). If we omit the individuals killed by *Hemisarcoptes* at the Connor location it appears that the mortalities of either males or females during the recognizable stages were not appreciably different on stems, leaves and fruits. The somewhat lower mortality of males (excluding *Hemisarcoptes* action) seems to be no more than could be explained by the fact that some females also were killed by *Hemisarcoptes* at the Connor location, and by the fact that, since males mature much sooner than females, they are exposed to causes of mortality a shorter period of time.

Table 8 gives the premature mortality data for the first and second settled stages as well as for recognizable males and females. At all locations this mortality in the recognizable male and female stages on the stems was low, varying from 2.4 per cent for males at the Whitney location to 12.5 per

TABLE 8
PREMATURE MORTALITY OF FIRST AND SECOND SETTLED STAGES AND
OF RECOGNIZABLE MALES AND FEMALES OF *P. OLEAE* BY ACTION
OTHER THAN *APHYTIS* AT FIVE LOCATIONS IN TULARE,
MADERA, AND FRESNO COUNTIES, CALIFORNIA,
OCTOBER, 1956

Plant part	Location	Total settled stages	Dead 1sts and 2nds		Prematurely dead males		Prematurely dead females		Total mortalities
			Number	Per cent	Number	Per cent	Number	Per cent	
Stems	Trafton.....	210	51	24.3	22	10.5	16	7.6	per cent 42.4
	Whitney.....	588	30	5.1	14	2.4	43	7.3	14.8
	Connor.....	1,924	405	21.0	202	10.5	209	10.9	42.4
	Bell.....	32	21	65.6	1	3.1	4	12.5	81.2
	Kearney Park..	118	50	42.4	3	2.5	14	11.9	56.8
	Totals.....	2,872	557	19.4	242	8.4	286	10.0	37.8
Leaves	Trafton.....	375	101	26.9	50	13.3	6	1.6	41.8
	Whitney.....	1,820	191	10.5	160	8.9	42	2.3	21.7
	Connor.....	4,409	1,030	23.4	1,353	30.7	201	4.6	58.7
	Bell.....	79	36	45.6	12	15.2	1	1.3	62.1
	Kearney Park..	295	88	29.8	26	8.8	24	8.1	46.7
	Totals.....	6,978	1,446	20.7	1,601	22.9	274	3.9	47.5
Fruits	Trafton.....	898	101	11.2	93	10.4	18	2.0	23.6
	Whitney.....	6,303	444	7.0	576	9.1	344	5.5	21.6
	Connor.....	22,129	4,881	22.1	5,931	26.8	2,070	9.4	58.3
	Bell.....	251	58	23.1	24	9.6	13	5.2	37.9
	Kearney Park..	699	163	23.3	74	10.6	54	7.7	41.6
	Totals.....	30,280	5,647	18.6	6,698	22.1	2,499	8.3	49.0
Totals	Trafton.....	1,483	253	17.1	165	11.1	40	2.7	30.9
	Whitney.....	8,711	665	7.6	750	8.6	429	4.9	21.1
	Connor.....	28,462	6,316	22.2	7,486	26.3	2,480	8.7	57.2
	Bell.....	362	115	31.8	37	10.2	18	5.0	47.0
	Kearney Park..	1,112	301	27.1	103	9.3	92	8.3	44.7
	Totals.....	40,130	7,650	19.1	8,541	21.3	3,059	7.6	48.0

cent for females at the Bell location. Mortality in the 1st and 2nd settled stages varied decidedly, from a low of 5.1 per cent at the Whitney location to 65.6 per cent at the Bell location. Total mortality at the Whitney location (where control by *Aphytis* failed) was only 14.8 per cent, whereas at the Bell location (where control by *Aphytis* has been excellent) total mortality was 81.2 per cent (based on low numbers).

On leaves, total mortality was highest at the Bell location (even if mortality due to *Hemisarcoptes* at the Connor location is included) and lowest at the Whitney location. On fruits, total mortality was again lowest at the

Whitney location, while the Bell location was intermediate. Mortality from causes other than *Aphytis* during this period was therefore lowest at the place where biological control has been decidedly inadequate (but see page 608).

In general, a good portion of the total mortality occurs in the young settled stages (and in the crawler stage, which is not covered by these data) and is probably due to adverse climatic conditions, sometimes aggravated by inadequate irrigation. These data indicate that there is some mortality in the first settled stage which was missed by this method of analysis, due perhaps to the sloughing off of the tiny scale coverings of individuals dying very young; the larger scale coverings are more firmly attached and more durable after death of the scales. Thus the losses during the egg, crawler and first settled stages contribute to a total mortality somewhat greater than indicated in table 8. Nevertheless, premature mortality due to causes other than *Aphytis* during this fall brood, though substantial, was not severe at these locations. At the Whitney and Trafton locations it was, in fact, fairly low.

It has been noted that males and females are disproportionately distributed on leaves versus stems. Since we find no significant evidence that differential mortality after settling is involved, the phenomenon appears to be due to differential behavior or success on the part of the crawlers at the time of settling. It seems likely that the female crawlers are adapted in a way which reflects the deciduous nature of many of this species' normal host plants, and that even on evergreen olive the females of the fall brood have a preference for stems over leaves. This preference is not exhibited by the male crawlers—a phenomenon compatible with the fact that male crawlers on leaves of deciduous trees usually mature prior to abscission and leaf drop, and pressure selecting for such behavior in the males would be lacking, whereas pressure for such selection would be intense in the females.

The premature mortality referred to in this section is caused by factors other than *Aphytis*, the samples being limited to populations on new growth and taken for the fall brood prior to normal *Aphytis* action; the spring brood is largely free of attack.

Table 9 gives data relative to the spring brood of scales. Although data were taken on the spring brood in July, 1957, at the same places and in the same manner as in the fall brood of 1956 (except that sample size was doubled and no fruits were included), the densities in the spring were so low at every location that presentation of the data by stem and leaf categories is not useful. In fact, the densities were so low that the combined figures on mortality are significant for comparative purposes only, as effective control by *Aphytis* had occurred during the elapsed interval.

Of the 136 recognizable males present, 44.1 per cent suffered premature mortality from causes other than *Aphytis*, and of the 80 recognizable females present, 40.0 per cent died from similar causes. There was therefore no indication of a sexual differential in mortality (table 9). However, the fact that 136 males and only 80 females reached recognizable sexual stages suggests (1) that the males, which differentiate earlier, may have escaped a period of severe mortality to which the females, still in the 2nd stage of

development, succumbed, or (2) that the original sex ratio of this small lot varied markedly in favor of males.

TABLE 9
MALE AND FEMALE *P. OLEAE* REACHING RECOGNIZABLE SEXUAL STAGES,
AND PREMATURE MORTALITY OCCURRING IN THOSE STAGES DUE
TO ACTION OTHER THAN *APHYTIS* AT FIVE LOCATIONS IN
TULARE, MADERA, AND FRESNO COUNTIES,
CALIFORNIA, JULY 17, 1957

Location	Recognizable males				Recognizable females			
	Total	Number alive	Per cent alive	Per cent dead	Total	Number alive	Per cent alive	Per cent dead
Whitney.....	44	25	56.8	43.2	38	24	63.2	38.8
Trafton.....	16	6	37.5	62.5	7	3	42.9	57.1
Connor.....	38	25	65.8	34.2	23	15	65.2	34.8
Kearney Park.....	38	20	52.6	47.4	12	6	50.0	50.0
Bell.....	0	..			0	..		
Totals.....	136	76	55.9	44.1	80	48	60.0	40.0

Table 10 presents the premature mortality in the combined population occurring in the early settled stages and in the sexual stages. It is seen that total mortality from causes other than *Aphytis* for the spring brood average 70.8 per cent, with results ranging from 65.3 to 76.3 at the five test locations. Thus, it appears there is a substantial natural mortality of the

TABLE 10
PREMATURE MORTALITY OF FIRST AND SECOND SETTLED STAGES AND
OF RECOGNIZABLE MALES AND FEMALES OF *P. OLEAE* BY ACTION
OTHER THAN *APHYTIS* AT FIVE LOCATIONS IN TULARE, MADERA,
AND FRESNO COUNTIES, CALIFORNIA, JULY 17, 1957

Location	Total settled stages	Dead in 1st and 2nd stages		Dead as recognizable males		Dead as recognizable females		Total mortality	
		Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
Whitney.....	143	60	41.9	19	13.3	14	9.8	93	65.0
Trafton.....	33	10	30.3	10	30.3	4	12.1	24	72.7
Connor.....	169	108	63.9	13	7.7	8	4.7	129	76.3
Kearney Park.....	75	25	33.3	18	24.0	6	8.0	49	65.3
Bell.....	0	...		..		..		...	
Totals.....	420	203	48.3	60	14.3	32	7.6	295	70.2

spring brood which develops during the early summer, probably because of high temperatures and low humidities. During the same time of the year, *Aphytis* is reduced to an entirely negligible status by the same severe conditions, although the scale, though markedly affected, is less affected than is the adult parasite.

Mortality in the first and second settled stages was 48.3 per cent of total mortality, while mortality in the recognizable male and female stages was

14.3 to 7.6 per cent, respectively. Mortality at the Connor location in the first and second stages was considerably higher than at the other locations. There was no evidence of *Hemisarcoptes* action at this time, although it may have caused some of the mortality somewhat earlier.

Mortality records of this brood, although based on much lower populations, may be compared with the previously discussed results for the fall brood. Mortality in the 1st and 2nd stages was rather consistently higher in the spring brood than in the fall brood. Total mortalities were also higher than those indicated at the time of sampling in the fall brood. For example, at the Trafton location there was 72.7 per cent mortality in the spring and 30.9 per cent in the fall; at Whitney, 65.0 and 21.1 per cent; at Connor, 76.3 and 57.2 per cent (in spite of an inflated mortality due to *Hemisarcoptes* in the fall); and at Kearney Park, 65.3 and 44.7 per cent. (There were no scales in the Bell sample in the spring, due to intensive *Aphytis* action in the interim period.) These data confirm the findings of other observations on mortalities; it seems probable that these mortalities are due particularly to the comparatively greater severity in humidity associated with the development of the spring brood. Climatic factors alone can serve to prevent an otherwise sudden resurgence of the population after decimation of the parent stock during the late winter and early spring by *Aphytis*, even in the absence of meaningful parasitization by *Aphytis* of the female progeny from this spring brood.

The data of tables 7, 8, 9, and 10 do not cover the parasitic action of *Aphytis*, as data were obtained at times of the year when *Aphytis* is a negligible mortality factor. However, the main reason why the populations in tables 9 and 10 were so much lower than those in tables 7 and 8, is the action of *Aphytis* during the intervening spring on the overwintered females of the populations reported in the latter tables. Parasitization was so heavy at each location that, in general, not enough scale parents escaped to produce a large spring brood.

It seems very probable that the success of *Aphytis* may hinge, in part, upon the normally high mortality of young scales during hot summer periods, particularly for the spring brood. Since the parasite is severely reduced in numbers in summer, and is ineffective on one brood of the scale, the rapidity of rebound of the host is a potent factor in the degree of control achieved by *Aphytis*. Normally, the scale's inability to increase in numbers because of weather stress, is not enough to negate the effective action of *Aphytis* in the spring, but if the scale survives these stresses much better than the parasite—rather than only slightly so—then control can be prevented.

Ecology of the insect relative to its geographic distribution and economic status. It is apparent from the data presented that the cool coastal areas of California are poorly suited to the establishment of this insect, in contrast to hot Central Valley areas. Although *P. oleae* made its appearance as early as 1942 in the cooler, mountainous North Fork area of Madera County (McKenzie, 1952) and later in mountainous locations in Tuolumne County, infestations there have never thrived as have those on the floor of the Central Valley, and the colonies are just able to survive, at least now that Persian

Aphytis is present. As to coastal areas north of Los Angeles County, the insect has been found only as isolated infestations at Santa Maria, Santa Barbara County; Santa Cruz, Santa Cruz County; on nursery trees at San Leandro and in Livermore, Alameda County; and at Antioch, Brentwood, and Pittsburg in Contra Costa County. Of these, the Contra Costa County and Livermore locations have some similarities to Central Valley conditions.

With general though lesser opportunity of vehicular transfer from the Fresno area coastward, it seems apparent that the relative absence of this insect as a pest in coastal areas of California is due to factors other than access or precautionary measures. Either natural enemies are more effective in suppressing the scale along the coast, or the climate in some way inhibits its development. The former idea is ruled out on the basis that the most effective natural enemies known to attack the insect were not present in California when the period of most rapid spread took place—and also because the activity of this parasite does not *prevent* infestation even on a single tree, but only greatly reduces densities.

R. P. Allen (personal conversations) has confirmed and enlarged upon the authors' observations that *P. oleae* does not thrive in cool coastal or mountain areas of California and is absent from Imperial Valley, where summer conditions may be too severe for the more susceptible stages of the scale. It is our belief that the susceptible crawler and early settled stages are fairly well timed in the Central Valley area to avoid the most severe, hot, arid conditions; these conditions would not be avoided in the Imperial Valley.

The hazardous existence of olive scale in foothill or coastal areas, despite its occasional occurrence in high densities, may well be associated with a phenomenon commonly referred to as "undercrowding" or "underpopulation effects." In these generally unfavorable (or marginally favorable) areas general infestation is usually spotty and very localized, but heavy infestation may occur here and there among the susceptible host plants, most of which remain almost (if not entirely) free of the scale.

Data presented in this paper show that the crawlers and earliest settled stages of this insect are very susceptible to hot, dry atmospheric conditions, whereas older scales are relatively more resistant. This is one of the important sources of mortality which must be overcome by the insect's natality in order that it can increase in density. The general environment in cooler coastal and Sierra foothill areas may be such that in the initial stage of colonization natality plus immigration is not sufficient to offset mortality. Hence, the majority of the plants remain uninfested. However, if here and there a particular branch or localized area may be even slightly more favorable the insect may gain a foothold. If this slight favorability persists, a steady but slow increase to higher densities would occur even if higher density did *not* favor survival. Since crawlers and earliest settled stages are greatly favored if they have old scale coverings under which to settle and develop, pre-existing high densities may proportionally increase the natality/mortality ratio in favor of further increase in density. This may result in very localized infestations somewhat comparable in density with the high densities in areas much more favorable climatically.

It is known that an increase in mortality from natural enemies and from

food depletion because of this increase in density can occur in the same area and time. The factor of food depletion would presumably not come into play in these marginal areas at densities any lower than they would be in climatically favorable areas. The increase in enemy action with increase in the host's density is quite variable with the situation, and this may or may not be sufficient to offset the increase in favorability from this social effect as density increases. Furthermore, in areas where Persian *Aphytis* is not usually effective, these localized infestations would be expected to stabilize at rather high densities unless other factors intervened. However, action by such predators as *Hemisarcoptes malus*, *Cybocephalus*, *Chilocorus*, insectivorous birds, or temporarily by *Aphytis*, for example, may from time to time drastically reduce such infestations, and they would "clean up." A shifting pattern in such infestations would be exhibited.

The fact that unfertilized females of this scale do not produce young and that males must emerge in synchrony as to timing with the proper sexual phase in the slower developing females is another point of theoretical importance. This led us to speculate that in cool coastal areas the synchrony may be disturbed by a differential effect of reduced temperatures on male and female development—thus leading to infertility. Consequently, a test was conducted at Albany, California to determine if this may be involved.

Scales from eggs placed on potted olive plants at Albany on April 29, 1960 (at which time eggs are normally abundant in the San Joaquin Valley) developed so slowly that first generation males did not begin emerging until late August and many were still immature in early September. Up to August 30 very few females had developed to a stage differentiable as to sex, but they had reached the nearly mature third stage by early December. In the San Joaquin Valley, females from the same brood of eggs developed fully, and by the last of July or early August were producing eggs of the next generation.

In April, 1961, the first generation females at Albany were depositing eggs—thus, there was a single generation depositing eggs in synchrony, seasonally, with the overwintered second generation females under Central Valley conditions. This pattern was repeated in 1961 and up to April, 1962. Furthermore, the trend of the population (artificially started) has been steadily downward, and although in this instance the cause may have been appreciably due to competition with black scale, it is felt that in such environments the insect's natality will be inadequate normally to match the mortality. No natural infestation of this insect is known which exhibits a single generation per year.

It is clear that in cool coastal or mountain areas there may be inadequate temperature accumulation in effective day-degrees for two full generations. Such situations might theoretically permit $1\frac{1}{2}$ full generations per year, for example, but this does not occur. If timing of temperature accumulation were such that females were only half-grown perhaps they would be much more subject to winter mortality; also, it is suspected that emergence of males would be at a very inopportune time, seasonally, for copulation to occur, and/or the females would not be in the right stage, developmentally, for copulation (the low temperatures *perhaps* having a differential, unsyn-

chronizing effect on the two sexes). Limited tests conducted to establish this last point have been negative, but it is now known that they should be conducted in areas other than Albany.

In these marginal areas of the insect's distribution the seasonal timing remains essentially constant year after year, even though on the basis of the temperature accumulations we would expect something more than one and something less than two full generations so that—barring selection against such marked irregularity—there would not be a constant seasonal timing in the egg deposition period, *et cetera*, from year to year. Since the constancy exists, it is assumed that factors operate to hold successful reproduction in constant timing seasonally. We have suggested various ways in which this could conceivably be brought about, and conclude that in these marginal environments, even though there is a timing corresponding to two generations a year and two generations per year *do* occur, these are only fragments of the two potential *full* generations.

It is the present authors' belief that only the first progeny produced by a generation in spring is able to produce the successful overwintering grandchildren, those grandchildren being again only from among the first progeny produced by *their* parents, and that they do so in proportion to the relative amount of effective temperature accumulation. The later-developing individuals of the second brood of young would in general be unsuccessful. In this connection, it is known that some immature scales do overwinter successfully, but with much less success than their mature sisters. Also, if crawlers and the earliest settled stages are off-season in timing they would more likely be subjected to severe summer conditions and so suffer a higher mortality. These factors might tend to retain a constant timing in sequence with two generations per year (with a possible diapause involved), but with the quantitative success being much less than the full two generations potential. This question needs detailed study in the environments concerned.

In conclusion, cold in winter, hot dry periods in summer, and total effective temperature accumulation during the growing season, may be factors of great importance in determining the degree of marginality in this insect's distribution. Close observations and counts made during all months of the year show that if the female scales have been poorly fed (because of crowding), or if they are delayed in their development and enter the coldest period in stages prior to the nearly mature or fully mature stage, they will suffer increased mortality during the winter. In cool coastal areas or in mountain locations it may be expected that a large proportion of the overwintering brood would so enter the winter period.

All of these circumstances may combine to present a situation of remarkable unpredictability in the pattern of infestations in marginal infestation areas, whereas in the climatically favorable areas very heavy infestations can be predicted with relative certainty if natural enemy action is seriously curtailed, judging by tests on olives as host and by past histories of infestations.

THE PARASITE

Taxonomic Status

For a description of *Aphytis maculicornis* (Masi) and the Proclia group to which it belongs, the reader is referred to the work of Compere (1955). Compere reviews the systematics of the genus *Aphytis* Howard, and applies the name *Aphytis maculicornis* (Masi) to the parasite which was introduced from Persia in 1951 and which has since become an important natural control factor of olive scale in California. According to Compere, "The species to which the name *maculicornis* is applied is not the same as that to which Mercet (1930, 1932) applied the same name." Agreeing with the opinion of A. B. Gahan (correspondence, 1932), Compere states that Mercet misidentified *maculicornis*, and he then applies the name *maculicornis* to a species which, he says, does not meet fully Masi's (1911) description. Compere adds that Masi's description is vague, but he assumes that Masi nevertheless did in fact describe the species to which he (Compere) applies the name *Aphytis maculicornis* (Masi). Compere's descriptions are based on specimens collected at Villa Rica, Italy. He also gives keys to the Proclia group to which the species belongs, further characterizes both the group and *A. maculicornis*, and provides an illustration of the antennae of *maculicornis*.

In the present paper, we are dealing with a complex of parasites which Compere and other systematists have not separated morphologically from the Italian form which Compere describes as *A. maculicornis*. In fact, Compere studied samples representing the "Persian" *Aphytis*, the "Indian" *Aphytis* and the "Spanish" *Aphytis* as well as the Italian stock, all of which attack *Parlatoria oleae*, and he states that he is unable to distinguish between them. However, Hafez and Doult (1954) present biological evidence that there are several sibling species of the *maculicornis* complex and that they include a "California" form. Whether or not these, or some of them, may eventually be accepted as "good species" on the basis of morphological distinctions, the biological differences seem to be sufficient for recognizing certain ones as biological entities. Hafez and Doult state:

These results . . . show the following: (1) An incubation period of three days occurs in all strains except in the 'Californian' which remains in the egg stage 4 to 5 days. (2) The larvae of the Persian and Indian strains develop faster than those of the Spanish and 'Californian' *Aphytis*; the same condition is true of the pupae. (3) The day of peak emergence may be an important criterion for separating these *Aphytis* biologically, and it should also be of practical importance as an indication of the voltinism of each strain. The Indian and Persian cultures emerged in greatest numbers 17 days after oviposition, whereas the Spanish required 20 days, and the greatest proportion of the 'Californian' strain did not emerge until 23 days after oviposition. (4) Three significantly different groups, (a) the Persian and Indian, (b) the Spanish, and (c) the 'Californian' are clearly indicated by this study of developmental stages.

One of the striking differences among the sibling species according to Hafez and Douth, is the fact that two are thelytokous and one at least, is arrhenotokous. The Persian and Indian forms exhibited arrhenotoky with a tendency toward more females than males (63.3 per cent females in the Persian and 67.5 per cent females in the Indian populations). The Spanish form had 99.3 per cent females, while the Californian form "... is apparently completely thelytokous, for not a single male has been found." Hafez and Douth (1954) found that females isolated from the pupal stages produced only female progeny in the Spanish and Californian forms and males only in the Persian and Indian forms.

Compere (1955) observed that the Italian stock he examined (received from H. S. Smith in 1939) contained no males. This is one indication of similarities with the Californian form studied by Hafez and Douth. Similarly, the Egyptian and Spanish stocks studied at the time of their receipt in the insectary at Albany, California, exhibited a very great preponderance of females, although males did occur at a level of less than one per cent. It is thus not yet clear whether the Egyptian, Californian, Italian, and Spanish forms are differentiable from one another on the basis of cross-breeding tests, although Hafez and Douth point to biological differences between the Spanish and Californian (possibly Egyptian) stocks used.

Results immediately following release of the Persian, Egyptian, Spanish and Indian forms in the field in 1952 and 1953 support Hafez and Douth's belief in these biological distinctions. Upon release, only the Persian form exhibited an almost unfaillingly rapid increase to high abundance and an appreciable effect upon its host's populations.

Regarding the Persian and Indian forms, cross-breeding tests were conducted by G. L. Finney, who was in charge of the insectary production program, using single pairs of males and females of the Indian and Persian stocks early in the importation program before stocks had had an opportunity to become accidentally mixed. Three replicates each of Persian females with Indian males and three of Persian males with Indian females were used. Table 11 shows the results which indicate but do not prove (because of the small number of replications) that these two forms are not only arrhenotokous but are probably distinct species which do not interbreed.

Regarding the so-called Californian stock, Douth and Hagen (1953, unpublished report) stated, "In October and November parasites resembling *A. maculicornis* were taken in various localities in the San Joaquin Valley where no releases had been made." These *Aphytis* are a unisexual strain and consequently different from the Iraqi [= Persian] and Indian forms." This form Hafez and Douth (1954) later termed the "Californian strain."

To summarize: (1) Since no species of *Aphytis* was found to parasitize *P. oleae* prior to the introduction of such forms from Europe, Asia and Africa, beginning with the Egyptian stock in 1948 and 1949; (2) since the Egyptian form was recovered on a number of occasions in the general areas where the so-called Californian stock was later obtained by Hafez and Douth; (3) since *A. maculicornis* was unknown from North America prior

⁶ The ability of the Egyptian form to have spread to those localities cannot be precluded.

to the introduction of the Egyptian stock; and, (4) since all that is known about the biology of the Egyptian form conforms closely to what has been reported by Hafez and Doult (1954) for the Californian form, we are inclined to the belief that the Californian stock derives from the Egyptian importation.

TABLE 11
RESULTS OF CROSS-BREEDING TESTS USING PERSIAN
AND INDIAN *APHYTIS MACULICORNIS*

Replicate	Female	Male	Progeny	
			Number of males	Number of females
1.....	Persian	Indian	68	0
2.....	Persian	Indian	60	0
3.....	Persian	Indian	84	0
Totals.....			212	0
1.....	Indian	Persian	40	0
2.....	Indian	Persian	40	0
3.....	Indian	Persian	45	0
Totals.....			125	0
1.....	Persian	Persian	55	27
2.....	Persian	Persian	36	19
3.....	Persian	Persian	31	31
Totals.....			122	77
1.....	Indian	Indian	23	19
2.....	Indian	Indian	35	72
3.....	Indian	Indian	31	25
Totals.....			89	116

Distribution in California

Beginning in 1952, an intensive program of colonization and establishment of imported *Aphytis* which attack *P. oleae* has been carried out. Methods were developed for producing these parasites in large numbers for both experimental and field colonization purposes. The California State Department of Agriculture was interested in advancing this program as rapidly as possible and during 1953 and 1954 W. W. Wiard, of the Bureau of Entomology of that department, in cooperation with the respective county agricultural commissioners, effected a very wide-scale liberation of parasites of the several imported stocks. Table 12 presents a summary covering all the releases made of these parasites by university, state or county officials. The results do not include certain releases made in orchards where parasites were already established and where additional parasites were released purely for experimental purposes.

Table 12 shows that these stocks of *Aphytis* have been colonized in every area of marked infestation by *P. oleae*. No colonizations have been requested or made in the counties of Alameda, Inyo, Santa Cruz, Santa Barbara and Solano. While parasites have not been released in all localities where the host

is found, the coverage was very nearly complete and natural movements between release sites have largely completed the process. In some of the counties only more recently invaded by the scale, and where parasites were only recently colonized, the latter may not be present in all areas. In recent years we have seldom found the parasite absent in areas long infested, except

TABLE 12
COLONIZATION OF IMPORTED STOCKS OF *APHYTIS MACULICORNIS* FROM
1952 TO JUNE 30, 1960

County of release	Number of <i>Aphytis</i> released				Total	Years released
	Persian	Spanish	Indian	Egyptian		
Butte.....	254,500	32,500			287,000	1953, '59-60
Colusa.....	9,000				9,000	1956
Contra Costa.....	16,000				16,000	1955-56
Fresno.....	20,376,285	64,000	91,093	1,750	20,533,128	1952-59
Glenn.....	176,000				176,000	1952, '57, '58
Kern.....	311,900	85,000			396,900	1952-54
Kings.....	165,700	58,900			224,600	1952-53
Los Angeles.....	200,200	30,200			230,400	1952-53, '57
Madera.....	355,500	15,200			370,700	1952-53, '57
Merced.....	335,000	37,700	15,000		387,700	1952-53
Orange.....	125,000	11,700			136,700	1952-53
Placer.....	160,000	12,500			172,500	1952-53
Riverside.....	200				200	1953
Sacramento.....	10,000	16,000			26,000	1952-53
San Bernardino.....	90,000	7,500			97,500	1952
San Diego.....	24,275	7,700			31,975	1952
San Joaquin.....	502,300	15,000	52,000		569,300	1952-53
Stanislaus.....	145,000	8,500	8,000		161,500	1952
Sutter.....	88,000				88,000	1952, 1959*
Tehama.....	105,000				105,000	1954, 1959-60
Tulare.....	2,953,900	62,950	19,770	500	3,037,120	1952-59
Tuolumne.....	125,000	6,500			131,500	1953
Yolo.....	3,000				3,000	1953
Yuba.....	5,000	31,500			36,500	1953
Totals.....	26,536,750	503,350	185,863	2,250	27,225,223	

* Mainly 1959.

in groves where parathion or other detrimental insecticides are used. The present distribution of Persian *Aphytis* in particular is therefore presumed to be largely coextensive with the distribution of olive scale as shown in figure 1 (p. 546).

During 1953 alone nearly seven million *Aphytis* were colonized in approximately 300 locations in 21 counties (Doutt, unpublished report). Table 12 shows that from 1952 to July, 1960, a total of over twenty-seven million *Aphytis* were released for colonization in 24 counties. These were distributed among the various imported stocks as follows: Persian—26,536,750; Spanish—503,350; Indian—185,863; and Egyptian—2,250.

Life History and Ecology

Relationship to the host. All forms of *Aphytis maculicornis* considered in this study are essentially solitary arrhenotokous or thelyotokous ectopara-

sites of diaspine scales, and the natural host from which they were recovered was *Parlatoria oleae*. The females may superparasitize their host, but two eggs or larvae are only rarely found on a single host. It is rarer still that two parasites successfully develop on a single host. The sex ratios of the various stocks studied vary from all females to nearly 50 per cent of each sex—although there is a tendency toward a preponderance of females.

The adult parasite pierces the scale covering and places the egg on the

Fig. 5. Adult *Aphytis maculicornis* (Masi) examining a mature female scale.

surface of the scale body. Occasionally, hosts are observed with brownish shrivelled areas which later enlarge and cause the death of the host. These appear to be the result of probing action of the parasite's ovipositor. DeBach and White (1960) studied this phenomenon relative to the related species (*Aphytis lingnanensis* Comp. and *A. chrysomphali* (Mercet)) which attack California red scale, *Aonidiella aurantii* (Mask.). In the case of *Aphytis maculicornis* the additional mortality caused by this action, as distinct from parasitization as such, is not appreciable.

Plate 1 (center pages) shows the immature stages of the parasite in relation to the host; figure 5 shows the adult parasite.

Adult longevity. Under favorable cool temperatures adult *Aphytis* are rather long-lived. It has been a customary insectary practice to hold adults of all stocks of this complex in an outdoor cold-box maintaining usually a temperature of 45° to 55° F. Longevity under this condition has been very good. Hafez and Doutt (1954) report the following mean longevities for

TABLE 13
AVERAGE PROGENY OF *APHYTIS*, PER FEMALE, RESULTING FROM SUCCESSIVE DAYS OF EGG DEPOSITION

Stock	Number of females	Days																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Persian.....	18	1.28	2.94	2.67	3.33	2.39	1.94	1.39	0.78	0.94	1.22	0.94	1.22	0.89	0.83	0.61	0.78	0.67
Indian.....	15	1.73	3.80	3.60	2.87	2.60	1.40	1.60	1.26	0.73	0.47	0.53	0.27	0.80	0.53	0.27	0.27	0.20
Combined.....	33	1.48	3.33	3.09	3.12	2.48	1.70	1.48	1.00	0.85	0.88	0.76	0.79	0.85	0.70	0.45	0.55	0.45

four stocks held at a higher temperature (82° F) and approximately 65 per cent relative humidity: Persian—18 days; Indian—18 days; Spanish—16 days; and Californian—18 days. The longevity under field conditions would vary markedly from these figures depending particularly upon the temperature and humidity. Hafez and Douth found the longevity to vary from 32 to 83 days for these stocks during April and May under outdoor conditions at Albany, California (a cool, coastal location where the host does not occur). At the other extreme, we have found almost complete mortality of exposed adults to occur within 24 hours under midsummer field conditions at Orange Cove, California (where the host is a serious pest, but where *Aphytis*, nevertheless, is generally effective) under daytime temperatures of 100° to 104° F and a relative humidity of 15 to 18 per cent. During the period of most effective parasite activity in late March and April at such locations, the longevity would probably be somewhere between 15 and 30 days.

Hafez and Douth (1954) found that the adult parasites die within 24 hours if exposed continuously to temperatures of 35° F. This means that *adults* are very susceptible to the low winter temperatures of the Central Valley area of scale infestation. This does not apply to the immature stages.

Fecundity. Table 13 shows the number of progeny resulting from daily egg deposition per female for Persian and Indian stocks. Barring the very rare superparasitism or mortality during development, the data show the rate of egg deposition per female per day.

Fig. 6. Progeny of *Aphytis* per female, resulting from successive days of egg deposition. (Data of table 13.)

In general, egg deposition during the first 24-hour period was 1.3 per female for the Persian stock and 1.7 for the Indian stock. Egg deposition of both stocks doubled during the second day, was maintained at as high a level during the third and fourth days, and then declined, first more sharply and then gradually thereafter (fig. 6). The results do not reveal much difference between the Persian and Indian stocks in the rate of egg deposition, or in variations due to age. Although there were slight differences, the trends were very similar and variations between individual females of the same stock were sufficient to cause non-significance between the two stock means.

D. M. Maddox, formerly technician with the Department of Biological Control, has recently completed a more detailed unpublished analysis of the fecundity of the Persian form. He found that females held at approximately 81° F and 55 per cent relative humidity deposited an average of 30 eggs during an average ovulation period of 20 days. There was no significant difference whether or not males were present with the females. His study did not cover other temperature and humidity combinations.

Number of generations and winter tolerance. Various factors, in part previously discussed, are involved in considering the number of generations of *Aphytis* per year under California conditions. Obviously, the rate of development of the immature stages, the length of any pre-ovipositional period, the average period of egg deposition per female, and any periods of inactivity of either a reproductive or developmental nature, are important parameters.

The data of Hafez and Doult (1954) show that the Persian form has a short incubation period of only 3 days, a larval period of 7–9 days, and a pupal period of 6–9 days, the mean time to peak emergence from time of egg deposition being 17 days at 82° F and 65 per cent relative humidity. The pre-oviposition period is less than 24 hours, and peak oviposition occurs when the females are from 3 to 4 days old (fig. 6). Thus, under these conditions, a generation is completed in about 21 days. Night temperatures in the areas of infestation are usually lower than 82° F and daytime temperatures, although consistently higher than 82° in summer, are much lower in winter. Although a few individuals may complete their development in less than 17 days during mid-summer, there is no effective multiplication of the population at this time because of heavy adult mortality caused by high temperatures and low humidities.

During mid-winter, adult females are unable to withstand the cold and as a rule not many eggs are deposited from December to early February. However, the immature stages are well adapted to survive the winter conditions encountered. There is no marked adversity imposed by winter conditions, although reproduction nearly ceases. The immature parasites are almost invariably more abundant in late February than they are in November or December, despite the reduction in egg deposition. Development of larvae continues at a slow rate during the warmer periods in the winter months until the pupal stage is reached. The population concentrates rather markedly in the late larval and, particularly, in the pupal stages during late winter, and emergence is pronounced in late February and early March. Due to unseasonable weather specific occurrences may vary from these rule-of-thumb approximations.

Because of the factors just discussed we conclude that for practical purposes there are no "effective multiplicative" generations during July, August and part of September, or in December and January—although there may be some reproduction. It is likely that four to six effective multiplicative generations are completed each year, two or three in the fall, and a like number in the spring and early summer. The rapid increase in spring is shown in figure 7.

Fig. 7. Rapid spring increase of Persian *Aphytis*. (Redrawn from Doutt, 1954.)

Searching efficiency and discrimination. Persian *Aphytis* is a very efficient searcher in natural environments. Detailed records from monthly samples taken over a period of five years, involving thousands of olive branchlets infested with varying densities of *P. oleae*, show that the parasite effectively parasitizes the host in all situations in which it is found on the tree, whether in the center, southwest or northeast sides, for example. Two locations were studied and data were obtained regarding (1) searching efficiency when the host was present at low and at high densities, (2) effi-

ciency in finding hosts in protected or exposed positions (beneath older scale coverings or bark, for example), and (3) activity at different positions in the olive trees.

Not all of the scales included in the data presenting the population dynamics of this pest and its parasite were appropriate for the present analysis. Thus, only those scales which were classified as definitely in either exposed or protected positions are included for this purpose. Further, only those months during which *Aphytis* are active and abundant (April, May and June) and those months when they are active but scarce (October, November, February and March) were included. It had been expected that when parasites were abundant relative to the number of hosts available, any differential in searching efficiency for protected and exposed hosts would be decidedly reduced if, in fact, such a differential success were indicated.

TABLE 14
PARASITIZATION BY PERSIAN *APHYTIS* IN NORTHEAST, SOUTHWEST,
AND INSIDE POSITIONS IN OLIVE TREES AT TIMES OF SCARCITY
AND ABUNDANCE OF PARASITES DURING A 5-YEAR PERIOD,
1956-1960, IN TWO OLIVE GROVES*

Orchard	Parasite density	Northeast			Southwest			Inside (half sample size)		
		Hosts	<i>Aphytis</i>	Per cent parasitized	Hosts	<i>Aphytis</i>	Per cent parasitized	Hosts	<i>Aphytis</i>	Per cent parasitized
Bell	Low.....	215	26	12.1	163	11	6.8	121	12	9.9
	High.....	66	45	68.2	54	34	63.0	126	79	63.0
Duncan	Low.....	594	32	5.4	1,250	40	3.2	...	..	
	High.....	188	162	86.2	225	204	90.7	...	..	
Totals	Low.....	809	58	7.2	1,413	51	3.6	121	12	9.9
	High.....	254	207	81.5	279	238	85.3	126	79	63.0

* Two additional orchards were lost to the study prior to accumulation of adequate data.

TABLE 15
PARASITIZATION BY PERSIAN *APHYTIS* OF EXPOSED HOSTS AND HOSTS
RELATIVELY PROTECTED BY COVERINGS OF OLD OR OVERLAPPING
SCALES, BARK, ET CETERA, AT TIMES OF SCARCITY AND ABUN-
DANCE OF PARASITES DURING A 5-YEAR PERIOD, 1956-
1960, IN TWO OLIVE GROVES*

Orchard	Parasite density	Exposed hosts			Protected hosts			Ratios of per cent parasitized, exposed to protected
		Hosts	<i>Aphytis</i>	Per cent	Hosts	<i>Aphytis</i>	Per cent	
Bell	Low.....	248	36	14.5	251	13	5.2	2.8 to 1
	High.....	146	120	82.2	100	38	38.0	2.2 to 1
Duncan	Low.....	1,391	68	4.9	447	4	0.9	5.4 to 1
	High.....	349	329	94.3	64	37	57.8	1.6 to 1

* Two additional orchards were lost to the experiment prior to accumulation of adequate data.

Tables 14 and 15 present results of this phase of the study. Within the two parasite-density classes (table 14) for the northeast and southwest positions on the tree (and the inside position for the Bell location), there was no meaningful difference in parasitism associated with position in the tree. Therefore, position of scales in the tree did not seem to be a factor in control of the host as it might have been if parasites were not active, or only slightly so, at one or more positions. There was no change in this respect with different seasons of the year.

The most striking feature of this parasite's action is its very pronounced seasonal abundance, associated with resurgence in numbers mainly during the spring following a severe decimation during the previous summer. Data for this period, April, May and June, cover the period of characteristic high abundance and it is seen from table 14 that, contrasted to the period of low parasite abundance in October and November, February and March, there was a striking and consistent difference in parasitization achieved. This was true at all positions in the tree and in both orchards and has been a general occurrence.

Table 15 presents data on the parasitization of exposed and protected hosts and shows the same striking difference in parasitization between normal periods of high and low parasite densities. Parasitization of exposed hosts was definitely higher than that of protected hosts in every instance (including a further breakdown according to positions on the tree, not presented here). This was also true in nearly every instance, year by year, by the sub-categories, although the data on this are summarized collectively for the five-year period. Observations of parasites attempting to oviposit in scales beneath overlapping old scale coverings make this result an expected event. Yet, the very high degree of parasitization—90 to 99 per cent—often encountered under field conditions, indicates that such protected scales are nevertheless attacked successfully if densities of parasites are very high and longevity is good. The results here show that protected scales (fewer in numbers than exposed ones) and those only partially protected, are in fact attacked in much greater numbers when parasites are abundant, but the relative advantage of protected hosts was not narrowed as much as might be expected by an increase in parasite density. For example, at the Bell location, at low parasite densities the ratio of percentage of exposed hosts parasitized to that of protected hosts parasitized was 2.8 to 1, while at high parasite densities the ratio dropped only slightly to 2.2 to 1 (table 15). The high density category at the Bell grove was not nearly as high as that category at the Duncan grove because of the much lower densities of hosts and parasites per twig at the Bell grove. This is seen as compatible with the results of this comparison. At the Duncan location, the ratio at the low parasite density was 5.4 to 1, and this was reduced to 1.6 to 1 at high parasite densities.

No controlled tests have been conducted on the discrimination exhibited by ovipositing females of Persian *Aphytis*. However, extensive examinations and detailed records on the parasitization of hosts in all stages of development at various levels of density of hosts under *natural* conditions, reveal conclusively that this parasite has a very acute sense of discrimination. It rarely deposits more than one egg on a single host even though parasite

density in relation to host density is so high that 99.5+ per cent of susceptible hosts are parasitized. Population pressure, even if severe, does not "confuse" the parasite in its discrimination or prevent high efficiency in parasitization by causing it to neglect those hosts previously visited but not parasitized; nor does such pressure cause a much higher degree of superparasitization than is encountered at lower parasite densities.

This acute discrimination has other facets. Persian *Aphytis* almost never oviposits on a second-stage scale, and never on a first stage. The younger third-stage female scales are not suitable either, although when under pressure because of absence of older females or suitable males such females may be somewhat accepted by *Aphytis*. Since the male scales develop earlier than the females, there are two periods in the year in California when the parasites are dependent largely upon these males, although a very few precocious or retarded mature females may also be present at that time. These rather short periods are particularly critical in June, and much less so in September and October. During the remainder of the year, because of sufficient overlap in brood development, acceptable females are present in adequate numbers for maintenance of, if not for rapid increase in, the parasite populations.

Influence of low humidity and high temperature. Early in this work it became apparent that *Aphytis* activity is greatly retarded during the summer, as contrasted with the spring period. Doutt (1954) had speculated that the marked decline in abundance is associated with the evenly brooded condition in the host. Following the great preponderance of mature females in April and May, the age structure of the host population shifts to eggs, crawlers and first-stage scales which are immune to attack. As Doutt also noted, some early-maturing males are present in this critical period, and this serves as a cushion against a more drastic reduction in numbers.

In early July of 1955, *Aphytis* adults were observed to be fairly common on the leaves and twigs of olives even though the most critical shortage of suitable hosts had already passed. After this period, parasite populations should have increased again as a result of the increasing numbers of female scales which were again becoming highly suitable as hosts. But such recovery did not occur, even though adequate numbers of parent stock were present in early July. Instead, the decline continued throughout July, and through most if not all of August in most groves.

With this fact in mind, a test was conducted to learn if absence of liquid nutriment for the adults, or severely low humidity (associated with high temperatures), could explain the continued decline in *Aphytis* during the summer. Observations of the parasite's immature stages, which are protected beneath the scale coverings of the host and adequately supplied with both food and water, indicated that it faces no substantial adversity at this stage in its life cycle—even in a hot dry environment. Consequently, we concluded that the key factor very probably was the environment of the adult. To test this idea, an experiment was conducted at the Bell olive grove at Hills Valley, Fresno County on August 23, 1955, using 180,000 Persian *Aphytis* and three trees of similar size and appearance. In one tree, numerous strips of wax paper on which were dispersed thousands of droplets of honey were wound in and out through the branches; a second tree was kept humidified by use

of a fine-mist spray nozzle; and the third tree served as the control. Examinations of 50 branchlets from each tree just prior to release of the *Aphytis* showed no parasites on any tree. At 5:00 p.m. on a hot day (102° F) with low humidity (18 per cent), 60,000 *Aphytis* were released in each tree. The humidifying nozzle was run continuously.

Examination of 50 twigs from the humidified tree at 11:00 a.m. the following day revealed that *Aphytis* were still present at a ratio of approximately 1 *Aphytis* to each 10 branchlets examined. Equal samples showed that there were no *Aphytis* present on branchlets from the tree having honey added or from the control. A similar count the following day gave the same result.

In an effort to increase parasite activity during this same summer releases of *Aphytis* were made in midsummer after the period of shortage of suitable hosts had passed, but no increase was noted. This is in conformity with the results from the tests just described. In the San Joaquin Valley, the summer climate is decidedly hazardous for the parasite, as it is to a somewhat lesser degree for the host. Data for all localities studied confirm the conclusion that the summer period is normally very adverse to *Aphytis* (table 20, August parasitization, p. 609; also figs. 16, 17, 18, pp. 594, 596, 597).

Table 16 shows the influence of high temperatures and low humidities on the success of Persian *Aphytis* in parasitizing *Hemiberlesia lataniae* (Signoret) on potato tubers in cabinets in the laboratory. These data support the evidence obtained under field conditions. With a humidity of 18 per cent and a temperature of 90° F, no progeny of *Aphytis* were obtained, but when a comparable high temperature (88° F) was used in combination with a much more favorable relative humidity (61 per cent), 67 progeny were obtained from 200 adults. Even this was very unsatisfactory, however, as replacement of the parent stock was not accomplished.

TABLE 16
INFLUENCE OF CONSTANT TEMPERATURE AND
RELATIVE HUMIDITY ON PRODUCTION OF PROGENY
OF PERSIAN *APHYTIS* ON *HEMIBERLESIA LATANIAE*
(SIGNORET) ON POTATO TUBERS IN CONTROLLED
CABINETS*

Number of <i>Aphytis</i> stock	Temperature	Relative humidity	Number of progeny
	°F.	per cent	
200.....	90	18	0
200.....	74	63	302
200.....	88	61	67

* Each group of *Aphytis* was exposed to a surplus of host scales on two potato tubers. The *Aphytis* were released free in the cabinets, which had an interior working space of 28" x 28" x 28". A very light air movement was achieved by use of a low-speed fan pulling air through a muslin-covered vent.

When both relative humidity and the temperature were favorable (74° F and 63 per cent relative humidity), 200 adults produced 302 progeny. Thus, 88° F was more adverse than 74° F when both were used with a comparable relative humidity. The vapor pressure deficit at 88° F and 61 per cent relative humidity is 13.1 mm., while at 74° F and 63 per cent relative humidity

it is only 8.0 mm. Therefore it is not possible to conclude that the difference is due simply to the higher temperature used because the difference in moisture deficiency of the air was perhaps sufficient to account for the difference in progeny obtained.

INSECTARY PRODUCTION

Soon after the first field releases of Persian *Aphytis* had been made in 1951 it became apparent that this parasite held much promise as an effective enemy of *Parlatoria oleae*. An extensive colonization program was initiated to establish the species throughout the scale-infested areas of California and several large test areas were set up for evaluation of the parasites' effectiveness in the field. Work was begun in the insectary, where techniques were developed for producing the large numbers of parasites necessary to implement the program. The Persian *Aphytis* proved very amenable to insectary manipulation and from January to September 15, 1955, over 16 million parasites were provided for the field release program, with a gratifying economy of man-hours and materials.

Equipment and Facilities

The scale infesting rack. The infesting rack (fig. 8) is a unit made to support trays of potatoes, one above another, during the infesting operation. The rack is made of light steel piping with outside diameter of $\frac{3}{4}$ inch, with junctions brazed or welded together. Each of the four corner posts is $38\frac{1}{2}$ inches high. The pipes, serving as shelves, are attached to the corner posts at $3\frac{3}{4}$ inch intervals, beginning about 10 inches from the bottom. As may be observed from figure 8, the construction of the rack permits the trays to be put in or taken out on either side or end. This adds materially to the convenience of the unit.

The two tray-supporting pipes forming the sides of the rack are $13\frac{1}{2}$ inches apart over the $26\frac{1}{2}$ inch mid-section, but they are spread apart at either end to a distance of $19\frac{1}{2}$ inches at the point of attachment to the posts. The cross elements are attached to these sides at positions 9 inches from each end. The bend in the side pipes begins about 8 inches from each end. The over-all length of the rack is 44 inches.

The screen trays used in the rack are 40 inches long and $16\frac{1}{4}$ inches wide. They are made of $\frac{1}{2}$ -inch mesh hardware cloth fastened to a metal frame with a reinforcing brace from side to side at the middle.

The parasitization unit. This unit (fig. 9) consists of a box, or tray, with sides of $\frac{3}{4}$ -inch pine boards and a bottom of 3-ply $\frac{1}{4}$ -inch plywood. The inside measurements of the box are: length 25 inches, width $16\frac{1}{2}$ inches, and depth $3\frac{1}{2}$ inches. Holes one inch in diameter, one in each side of the box, are located midway from the ends and one inch from the top edge. A narrow groove or slot, $\frac{1}{2}$ inch deep and between $\frac{1}{32}$ and $\frac{1}{16}$ inch wide, is made in the center of the top edge of the unit, extending continuously around the box. A sheet of light, bleached muslin 3 inches wider and longer than the unit is used as a cover. The cloth is fitted and held taut and secure by pushing the cloth into the slot by means of an instrument such as a dull putty knife with rounded corners. Corks are used to stopper the holes in each end.

Fig. 8. Rack for infesting potatoes with *Hemiberlesia lataniac*.

Fig. 9. Parasitization unit.

The production-collection unit. This unit (fig. 10) has no attached top or bottom but consists of four walls 12 inches high. The two side walls are $27\frac{1}{2}$ inches long and the two ends $18\frac{1}{2}$ inches. It is constructed of $\frac{1}{2}$ inch plywood painted with white enamel. An opening 7 by $18\frac{1}{2}$ inches is cut in each side about $2\frac{1}{2}$ inches from the base. The apertures are covered with nylon or cotton organdy which is glued to the inside surface of the wall. Two plywood boards $19\frac{1}{2}$ inches long and 8 inches wide serve as covers for these apertures. Each is gripped and held tightly against the side of the box with a spring screen-door catch located below the board position.

Sponge rubber gasket strips are glued around the top and bottom edges of the walls. Each end has a 1-inch hole located 1 inch from the top and midway between the sides. A cork is provided for each hole. Two half-inch dowel rods are fitted lengthwise inside the box and solidly fastened at each end by being inserted into holes drilled into the end boards one inch from the bottom and 3 inches from each side. These two rods support the element that carries eight small hardware-cloth screens.

The screen-holding element consists of two parallel end boards, $10\frac{1}{2}$ inches high and 16 inches long, made of $\frac{1}{2}$ inch plywood. The boards are connected by twelve $\frac{3}{8}$ -inch dowel rods, each $25\frac{1}{4}$ inches long. The ends of the rods fit tightly in the holes in each board. Three rods are fitted $\frac{3}{4}$ inch from the bottom, one midway between the ends of the boards and the other $1\frac{1}{2}$ inches from each end. Three more rods are fixed in the same manner and glued into position each 3 inches higher. These then form 4 dowel-rod "shelves" for supporting the screens within the unit. Notches are cut $\frac{1}{2}$ inch deep into the bottom edge of each end board to fit over the two dowel rods of the box so as to prevent the element from slipping from side to side. Hand grips are attached to each end to facilitate the lifting of the element from the unit when it is loaded with material.

Fig. 10. The production-collection unit.

The small screens are of $\frac{1}{2}$ inch hardware cloth, 17 inches long and $13\frac{1}{2}$ inches wide. Each corner is notched so as to permit the edges of both sides and ends to be turned up forming one-inch walls all around. The screens' final dimensions are $11\frac{1}{2}$ inches wide and 15 inches long. Screens fit side by side, two on each of the dowel-rod "shelves" of the element. Eight screens form a capacity load.

Fig. 11. Parasite cleaning unit.

When in operation, the four-walled unit rests upon a section of $\frac{3}{4}$ inch plywood $21\frac{1}{2}$ inches wide and $30\frac{1}{2}$ inches long upon which is laid a sheet of heavy brown wrapping paper of the same size. A similar section of plywood, but without the paper, serves as the top of the unit and is held firmly in place with weights or clamps so as to effect an insect-tight closure. Sponge rubber strips may be glued to the cover so as to match those on the edges of the unit as shown in the illustration.

The cleaning unit. The cleaning unit (fig. 11) consists of a plastic specimen box $1\frac{3}{4}$ inches square and $\frac{3}{4}$ inch high, including the snug-fitting slip-on lid. Four thumb tacks are glued to the base of the box, one at each corner. Three outlet holes $\frac{3}{16}$ inch in diameter are located in each side, $\frac{1}{4}$ inch from the base. The outside of the box is painted with black enamel.

Culture Methods and Production

The insect host. Latania scale, *Hemiberlesia lataniae*, was used as the insect host for culture purposes although it has never been recorded as a host of *A. maculicornis* in nature. The natural host *Parlatoria oleae* is particularly difficult to mass produce in the insectary and its use for this purpose is avoided whenever possible.

The attributes that make *H. lataniae* especially desirable are: (1) the young migratory scale crawlers settle and readily establish themselves on

potato tubers used as host material; (2) the species is uniparental and thus the total population is composed of productive females; (3) the fecundity is very high; (4) egg laying continues over a period of a month to six weeks; and (5) the mature females, being relatively large, yield uniformly large parasites.

The stages in the life cycle of this adapted host at 79° F and 65 per cent relative humidity are completed as follows: white cap to yellow stage, 14 days; yellow to brown stage, 10 days; brown stage to last stage, 13 days. Egg laying begins about 15 days later, the eggs hatching in less than 24 hours.

The plant host. Potato tubers, particularly the Russet or Burbank varieties, were used as the host for the scale. These varieties were chosen chiefly for keeping quality, although the scale develops somewhat better on smooth-skinned potatoes such as the White Rose variety. The Russet type is also the one most available in the potato-producing regions of Oregon, Washington and Idaho where the crop is free of the potato tuber worm, *Gnorimoschema operculella* Zell. Contamination of cultures by such pests is to be avoided at all costs in such a large-scale production program.

Only smaller, egg-sized tubers, screened and selected out of A-1 quality grade, were used. Smooth tubers having a light surface texture and free of protuberances and mechanical injuries are most desirable. The best keeping potatoes appear to be those grown with a minimum of irrigation and harvested when fully mature after the vines have been frost-killed. Potatoes such as these have been held in cold storage as long as one year with relatively little loss due to decomposition or shrinkage.

If good, tuber-worm free, White Rose potatoes are available from the northern regions, they are preferable to Russet or Burbank varieties if they can be used after only a 2 to 3 month period in cold-storage. If obtained from the warmer regions of California, they need to be fumigated with methyl bromide to avoid hazardous tuber worm infestations in the insectary.

Infesting the tubers. Infesting the potatoes with scales was accomplished by utilizing the "drop" of young scales from heavily-producing mother scales on potatoes placed above them. Usually, a battery of five large trays of potatoes covered with producing scales was formed in the five upper positions of the infesting rack, with one or two trays of potatoes to be infested being placed beneath them on two of the three lower positions. The scales on the producing potatoes of each tray were the same age but the ages of scales, from tray to tray, was maintained in chronological sequence, each about 9 to 10 days apart. Every 9 or 10 days the oldest tray was removed and one just coming into production was put in its place.

The two trays immediately beneath the production units (battery) were rotated each day. When the top one was removed to the maturing area, the lower one was then put in its place. A new tray was then placed beneath. This tray caught the young scales which fell from the tray above. The bottom trays were usually used for parasite production. Trays placed in the lowest position were left for a 9 to 10 day period (or less if adequately infested sooner) and such trays were generally used as "mother stock" to fill in the battery at the appropriate time.

It is advisable to locate the infesting racks in a dimly-lit room having a dif-

fused light source which gives enough light to promote scale movement but not enough to strongly attract the crawlers away from potatoes being infested. Air currents strong enough to carry the light-bodied, falling crawlers away from the potatoes below are also to be avoided.

When a single infesting rack is adequate for the program, a light wooden frame covered on the sides and top with brown wrapping paper may be constructed so as to be lowered over the rack to rest on the floor. This cover would provide the diffused light and calm air conditions necessary within the unit,

Fig. 12. Insectary host scale, *Hemiberlesia lataniae*, on a potato tuber.

and the room could then be used for other purposes with normal light and ventilation.

The ideal infestation for *Aphytis* production is one where the full grown scales are close together but not overlapping (fig. 12). Each scale is thus more vulnerable to the parasite from any approach and is not masked or obstructed by the coverings of neighboring scales. The potatoes destined for parent stock should be heavily infested on all sides.

As the scale production season approaches, it is desirable to build up the scale population from the low inter-seasonal maintenance level to full production volume as rapidly as possible. The settling of scale crawlers may be accelerated and their proper dispersion pattern enhanced by covering each potato to be infested with a piece of wet cheese cloth large enough to extend down and almost around the tubers. The wet cheese cloth will adhere closely to the potato after drying, if wrapped on tightly. Crawlers tend to crawl into the mesh of the cloths and settle on the potatoes, thus making for an even

distribution and a maximum settling economy of young. Through the use of this technique, two trays of potatoes have been infested for parasite production in 24 hours. The cloths should not be removed for at least 24 hours in order to give the crawlers time to become well established.

The trays of infested potatoes should be placed in racks and held there until the scales reach the proper age for use, either as mother scales or parasite hosts.

Fig. 13. Parasitization unit being placed in darkened holding unit.

The infesting room and holding room should be held at a temperature of 78–80° F and a relative humidity of 60–65 per cent.

Parasitizing the scales. When the scales are well into their last “spinning” stage—about 38 to 40 days old at 79° F—they are ready to be exposed to *Aphytis*. The potatoes are then transferred from the larger trays to the smaller hardware cloth trays and placed in the parasitization unit, two trays to each unit. Strips of brown waxed paper $\frac{3}{4}$ inch wide (to which have been applied small honey droplets) are inserted edgewise between alternate rows of potatoes, and between and around the insides of the unit but outside the screens. The potatoes should not be packed solidly.

The cover cloth is tucked into a groove along one side of the unit and laid back to one side. Two thousand parasites are anesthetized and measured into a vial and then distributed fairly evenly over the potatoes. The cloth cover is drawn across and quickly fixed in place before the parasites revive and become active. The unit is placed in a wooden rack (fig. 13) which is exposed to light of about equal intensity on each side. The rack is draped with brown wrap-

PLATES

Plate I. *a*, *Aphytis maculicornis* egg on mature female host, *Parlatoria oleae*, showing scale covering removed; *b*, Young *Aphytis maculicornis* larva on mature female host, *Parlatoria oleae*, with scale covering removed; *c*, Mature *Aphytis maculicornis* larva on female host, *Parlatoria oleae*; *d*, Two scale coverings of mature female *Parlatoria oleae* detached and showing mature pupae of *Aphytis maculicornis*; *e*, Scale covering of mature female *Parlatoria oleae* in normal position on olive leaf, showing exit hole of *Aphytis maculicornis*; *f*, Scale covering of mature male *Parlatoria oleae* in normal position on olive leaf, showing exit hole of *Aphytis maculicornis*—compare size and shape with female scale. (Photography by F. E. Skinner.)

Plate II. *a*, Female scale of *Parlatoria oleae* showing leaf discoloration; *b*, An olive tree heavily infested with *Parlatoria oleae*; *c*, Tree to left treated with DDT to inhibit action of *Aphytis maculicornis*, and showing lack of vigor, defoliation, and dieback resulting from heavy *P. oleae* densities. Trees to right had no treatments with DDT, and *Aphytis* kept the scale under good control, with tree growth and condition excellent; *d*, Intermediate shot of typical branch from trees to left, Plate II *c*; *e*, DDT-treated, parasite-free tree, showing nature of damage by *P. oleae*; *f*, Untreated, parasite-present trees to right, Plate II *c*, showing clean condition. (Photography by F. E. Skinner.)

ping paper to diffuse and render the light non-directional and dim. It was found advantageous to darken the cloth cover of the parasitization unit around the periphery by laying cardboard strips about $1\frac{1}{2}$ inches wide around the edge. This deters the parasites from thrusting themselves between the cloth and box edge where many otherwise would become trapped.

In about five days the peak of parasite egg laying is past. To maintain the parasite activity at a continuous level 2,000 more *Aphytis* are then introduced to the unit. These are anesthetized and placed in a glass tube 6 inches long and 1 inch in diameter, open at both ends. From this they are gently blown into the unit through the aperture in the side. Five days later, another 2,000 parasites are added, making a total of 6,000 *Aphytis* per unit.

The adults developing from the first eggs deposited will begin to emerge on the 17th day, so on the 16th day the unit is dismantled and the parent parasites still alive are anesthetized. The trays are then removed and placed in the production-collection unit. No attempt is made to recover and use these remaining parasites.

Under field conditions there is seldom more than one egg deposited on a scale. When the parasite population is high two eggs are sometimes found, but very rarely does more than a single larva develop to maturity. When superparasitism occurs the scale usually is killed by the young larvae before they can develop to maturity. Two larvae may develop to maturity if the eggs are laid at nearly the same time and on opposite sides of the host. In the insectary, superparasitism with a consequent host mortality and reduction of parasite production, may occur when the host material is exposed to an excessive parasite population. Host feeding, such as occurs with *Aphytis chrysomphali* (DeBach and White, 1960) has not been observed with *A. maculicornis*.

The sex ratio of *A. maculicornis* in the insectary when adequate mating time has been allowed is nearly 50:50, but slightly favoring the females. In the second generation arising within the production-collection unit males tend to predominate, however, since the newly emerged, virgin females laying only male eggs may oviposit several times before encountering a male parasite.

Operating the production-collecting unit. The production-collection unit holds eight small screen trays, from four parasitization units. Every day for a total of 34 days (two developmental periods of 17 days each) emerging *Aphytis* are anesthetized and removed from the unit. During the 24 hours between daily collection periods, the parasites will have emerged, mated, and deposited considerable numbers of eggs on scales previously unparasitized. Thus a second generation is automatically produced within the unit.

To collect parasites, the cover boards are placed over the ventilation openings on either side of the unit, the cork is removed from one end, and an ether/carbon-dioxide mixture injection hose is inserted. The gas is allowed to flow for $1\frac{1}{2}$ minutes at about $3\frac{1}{2}$ lbs. pressure. The hose is then withdrawn, the stopper returned, and the cover removed from the unit after it is sharply jarred. Some of the parasites usually have fallen or come to rest on the potatoes and may be removed by blowing gently over the potatoes; this causes the parasites to fall through to the paper on which the unit rests. The

entire unit is then lifted from the paper (fig. 14) and placed in position on a similar paper alongside, where the unit will remain until collection time the following day.

Fig. 14. Manipulation of the production-collection unit. Anesthetized *Aphytis* on paper at left, and unit being moved to next paper.

The paper on which the anesthetized parasites have fallen is quickly picked up by two opposite edges which are brought together to form a rounded trough into which the inert parasites slide when the paper is tapped sharply. The paper trough is then tipped so that the parasites will slide downward and into the plastic cleaning unit. The cleaning unit is then capped and placed in a one-gallon glass battery jar. The latter is then covered tightly with a bleached muslin cloth, held snugly in place with 2 or 3 rubber bands. In about 20 minutes all of the parasites will have revived and almost all will have emerged from the cleaning unit leaving the debris, etc. behind. The parasites are then briefly anesthetized, permitting the cleaning unit to be removed. The gas, being heavier than air, is poured from the jar, and the jar is then recapped and placed in a refrigerator at 55–60° F, or in a cool, dark, humid (50 per cent R.H.) place until time for shipment to field locations.

Each jar is supplied with a sheet of waxed paper about $2\frac{1}{2} \times 4$ inches in size and covered with honey droplets as food for the parasites while being held in storage. The honey should not be allowed to be depleted as the parasites die quickly without food. The honey sheets are prepared as described by Finney (1949).

The parasites may be measured out volumetrically in a unit such as de-

scribed by DeBach and White (1960), or in the calibrated stem of a very small glass funnel cut to a length of about 3 inches. The parasites should be held under continuous carbon dioxide/ether anesthetization for not more than 10 minutes. Five minutes is a safer working limit, however.

The parasites are transported to the field in half-pint paper food cartons (fig. 15), each of which contains a bit of excelsior to provide extra "roosting"

Fig. 15. Method of shipping *Aphytis* for field colonization.

area when large numbers of parasites are allotted to a unit. It is not necessary to provide food when the destination is less than 36 hours away if the parasites have been well fed just prior to shipping. For longer trips, a strip of waxed paper with honey droplets should be attached with tabs of masking tape to the inside wall of each unit.

The volume of parasite production necessary to implement the establishment of *Aphytis* throughout the scale-infested areas of California, and to supply parasites for release in the various study plots, was achieved through the use of the equipment and methods described above. The practicability of a more ambitious program—such as annual release of insectary-reared parasites to commercially supplement those already in the field—would depend almost entirely upon how economically parasites could be produced. To reduce costs to a minimum, mass-handling techniques would need further development. Additionally, equipment would have to be obtained to utilize all insectary floor space with maximum efficiency.

POPULATION DYNAMICS OF HOST AND PARASITE

Methods

In December, 1955, a study of the population dynamics of the host *P. oleae*, and Persian *Aphytis* in two olive groves was initiated in order to appraise

the potentialities and shortcomings of the parasite and to suggest methods of augmenting the biological control experienced. Another study, initiated at the Whitney grove near Exeter in 1957, was ended prematurely when the grower removed the trees.

These studies, begun in 1955 at the Duncan grove at Herndon and the Bell grove at Hills Valley, Fresno County, were completed in 1960. Counts of populations of scales and parasites on branchlets were made at monthly intervals from December, 1955, through December, 1960. The sampling method used was consistently adhered to even though a different means of sampling would sometimes have been more helpful in answering certain questions.

Two sample trees were used at each of the two groves. Branchlets were taken from the northeasterly, the southwesterly and the inside, or trunk positions, as distinct subsamples within each tree. During the 5-year course of this study some modification in sample size was made, since the number of branchlets taken when scale densities were high proved inadequate when densities dropped to low levels. Because of the frequency of cutting samples, and the adverse affect of too much thinning both on normal tree growth and the microenvironment of the insects, it was not possible at low densities, to increase sample size enough to obtain a satisfactory population estimate. Increasing the number of trees would have been helpful at that time, but previous data would not have contained such added trees. Except for some shortcomings which will be referred to, the data present a fair general picture of the dynamics of the host and the parasite at these representative locations, and of the degree of control exerted by *Aphytis* season to season and year to year. When combined with other data presented in this study, the results described below make possible a reliable appraisal of the potentials and limitations of both the host and its parasite under similar San Joaquin Valley conditions.

Usually, 12 or 24 branchlets were taken from both the northeasterly and southwesterly sides of each tree, and 6 or 12 branchlets from the inside or trunk positions. Unluckily, all the foliage at the inside positions at the Duncan grove was inadvertently removed in the grower's pruning operation shortly after the study was started, and that subsample category was lost.

Scales and parasites present were counted on four young leaves, four medium-age leaves and on four of the oldest leaves on each branchlet; counts were also taken on the internodes below each pair of leaves. Thus, no fixed length of branchlet was taken, but a fixed number of leaves and internodes formed the sample unit, and this unit contained leaves and internodes of different ages, making up sub-classes of data. Within each position on the tree branchlets were taken at random, although malformed or damaged branchlets, or those having only young leaves or old leaves only, were not taken.

Preliminary sampling of scales at the Bell location in December, 1955, under a moderate density of scales gave some leads as to sample size as follows: for 6 branchlets, $\bar{x}$, 6.2 and $s_{\bar{x}}$, 2.3, 35 per cent; for 12 branchlets, $\bar{x}$, 5.6 and $s_{\bar{x}}$, 1.5, 25 per cent; for 24 branchlets, $\bar{x}$, 6.6 and $s_{\bar{x}}$, 1.4, 21 per cent.

Samplings from 24 branchlets would have given better results but it was not considered possible to cut that many branchlets from any given position within the tree with the necessary frequency to show population trends in time, without damage to the microenvironment. Hence, we settled on 12

branchlets, but increased this to 24 when the densities fell very low. At the Bell grove, the excessive tree vigor and growth proved adequate to sustain, for limited duration, such a pruning program without adverse effects.

All stages of scales were recorded separately. Hatched egg shells were also counted in order to obtain a better measure of the total egg production. During the period of deposition of eggs of the fall brood, counts were made twice a month rather than monthly. Parasites were observed by turning each scale covering of the susceptible host stages, and the parasite eggs, larvae and pupae were recorded. The data as to whether in exposed or protected positions were also recorded separately.

Figures 16, 17, 18 and table 17, present in the most useful form the data obtained from these observations. Data for each host stage, for example, were plotted individually on graph paper, and from the resultant presentation the period of overwhelming predominance of each stage in the life cycle was evident.

Figures 16, 17, 18 and table 17, show the total populations of the broods at the specific times in the life cycle. For example, the bar for mature females for the February-March period includes not only the mature females (which greatly predominate over all other stages) but also the small number of immature third stage females (retarded ones). The bar representing the brood at time of overwhelming preponderance of young settled stages (first and second stages) also includes any early-maturing males or immature third-stage females present at that time.

The scale and parasite densities in these figures are presented as numbers per branchlet. Table 18 shows the production of eggs per female scale, as differentially affected by parasite activity during the spring and summer periods.

Population Dynamics in the Bell Grove

Persian *Aphytis* were first released in the Bell grove at Hills Valley, Fresno County, on January 31, 1955, and releases in the 72-tree experimental block were continued throughout that spring and summer. Olive scale infestation in this grove was newer than at many places near Fresno, and heavily infested trees were still confined to border rows and scattered positions elsewhere. Nevertheless, in 1954 the crop was unmarketable except for oil.

Figure 16 shows *Aphytis* occurrence in this grove in terms of percentage of parasitization, and also as densities per branchlet.

A substantial though not heavy density of scales existed in this plot at the initiation of the population studies in 1955, although at other areas in this grove in 1954 R. L. Doult found that 85 per cent of the fruits were commercial culls due to scale. Persian *Aphytis* had been present in the orchard for approximately one year when our studies started, but less than that in this particular plot area. Some reduction of scales had already resulted, undoubtedly, but it is obvious from figure 16 that the parasite had not yet achieved its maximal effect.

Starting with the third-stage female scales of the February-March period, it is seen that the density was 6.55 mature and parasite-susceptible female

Fig. 16. Population dynamics of *Parlatoria oleae* and Persian *Aphytis* in the Bell Grove.

TABLE 17

P. OLEAE AND *APHYTIS* DENSITIES AT THREE LOCATIONS FOR THE PERIOD 1956-1960,* EXPRESSED AS AVERAGE NUMBER OF SCALES PER TWIG, PER CENT PARASITIZATION, AND AVERAGE NUMBER OF *APHYTIS* PER TWIG—THE STAGES OF THE SCALES BEING AS SHOWN IN

FIGURES 16, 17, AND 18.

Sample date: first week of each month, except second August sample (third week)

Year	Month	Predom. scale stage	Location								
			Bell (Hills Valley)			Duncan—Herndon			Whitney—Exeter		
			<i>P. oleae</i> per twig	<i>A. maculicornis</i>		<i>P. oleae</i> per twig	<i>A. maculicornis</i>		<i>P. oleae</i> per twig	<i>A. maculicornis</i>	
				per cent	per twig		per cent	per twig		per cent	per twig
1956	Feb.-Mar....	M ₃	6.55	3.5	0.33	1.55	4.6	0.06			
	April.....	M ₃	4.70	11.5	1.19	1.06	7.9	0.08			
	May.....	Egg	13.72	54.7	1.44	3.44	33.9	0.53			
	June.....	1 and 2	3.13	6.2	0.01	0.68	14.3	0.03			
	July.....	I ₃	1.57	1.1	0.01	0.45	0.0	0.0			
	August.....	M ₃	0.51	4.9	0.04	0.15	0.0	0.0			
	August.....	Egg	28.67			4.21					
	September..	1 and 2	4.83	8.3	0.01	3.03	0.0	0.0			
	October.....	I ₃	1.88	7.1	0.06	4.70	0.0	0.0			
	December... M ₃		0.90	1.5	0.01	1.25	0.0	0.0			
1957	Feb.-Mar....	M ₃	0.61	6.9	0.04	1.35	0.0	0.0			
	April.....	M ₃	0.43	53.1	0.24	1.06	0.0	0.0			
	May.....	Egg	0.57	50.0	0.21	6.98	40.9	0.19			
	June.....	1 and 2	0.25	57.1	0.03	2.59	63.6	0.07			
	July.....	I ₃	0.06	28.6	0.02	1.00	0.0	0.0			
	August.....	M ₃	0.03	0.0	0.0	0.79	0.0	0.0			
	August.....	Egg	1.12	0.0	0.0	22.68	0.0	0.0			
	September..	1 and 2	1.10	0.0	0.0	13.13	0.0	0.0			
	October.....	I ₃	0.51	0.0	0.0	7.32	0.0	0.0	73.70	0.0	0.0
	December... M ₃		0.15	5.5	0.01	6.42	0.2	0.01	44.25	0.0	0.02
1958	Feb.-Mar....	M ₃	0.29	13.6	0.03	5.67	0.2	0.01	37.27	0.4	0.11
	April.....	M ₃	0.13	12.5	0.02	3.26	0.3	0.01	21.08	1.4	0.31
	May.....	Egg	0.18	80.0	0.03	39.87	37.2	1.16	219.03	28.1	4.11
	June.....	1 and 2	0.05	0.0	0.0	8.02	92.8	0.19	142.36	100.0	0.22
	July.....	I ₃	0.09	0.0	0.0	4.45	3.1	0.11	47.92	5.3	2.11
	August.....	M ₃	0.08	0.0	0.0	1.98	0.0	0.0	12.42	5.6	0.72
	August.....	Egg	1.90	0.0	0.0	25.08	2.4	0.04	204.44	24.1	2.89
	September..	1 and 2	0.15	14.3	0.01	14.51	0.0	0.0	75.75	44.3	1.08
	October.....	I ₃	0.25	4.3	0.01	18.22	0.4	0.02	77.72	3.6	1.92
	December... M ₃		0.12	0.0	0.0	13.62	3.5	0.48	60.36	7.7	4.64
1959	Feb.-Mar....	M ₃	0.15	8.3	0.01	8.08	6.3	0.51	46.72	17.6	8.21
	April.....	M ₃	0.12	80.0	0.10	3.68	90.9	3.35	17.33	89.1	15.44
	May.....	Egg	0.12	0.0	0.0	1.58	100.0	0.17	12.44	84.8	1.08
	June.....	1 and 2	0.04	0.0	0.0	0.92	0.0	0.0	6.33	40.0	0.17
	July.....	I ₃	0.08	0.0	0.0	0.27	0.0	0.0	2.66	0.0	0.0
	August.....	M ₃	0.12	0.0	0.0	0.46	0.0	0.0	0.92	0.0	0.0
	August.....	Egg	3.67	0.0	0.0	9.25	0.0	0.0	†		
	September..	1 and 2	1.82	0.0	0.0	0.06†	0.0	0.0			
	October.....	I ₃	0.34	0.0	0.0	0.40	0.0	0.0			
	December... M ₃		0.30	2.9	0.01	0.31	0.0	0.0			
1960	Feb.-Mar....	M ₃	0.83	6.0	0.03	0.06	0.0	0.01			
	April.....	M ₃	0.26	81.3	0.22	0.08	75.0	0.04			
	May.....	Egg	0.33	50.0	0.02	0.0	50.0	0.02			
	June.....	1 and 2	0.0	0.0	0.0	0.0	0.0	0.0			
	July.....	I ₃	0.04	0.0	0.0	0.29	0.0	0.0			
	August.....	M ₃	0.15	0.0	0.0	0.35	0.0	0.0			
	August.....	Egg	2.67	0.0	0.0	5.39	0.0	0.0			
	September..	1 and 2	0.10	0.0	0.0	0.15	0.0	0.0			
	October.....	I ₃	0.23	0.0	0.0	0.56	0.0	0.0			
	December... M ₃		0.27	3.1	0.01	0.38	0.0	0.0			

* Except Whitney location.

† Reduction due partially to oil treatment—August 1959.

‡ Discontinued—trees removed.

Fig. 17. Population dynamics of *Parlatoria oleae* and Persian *Aphytis* in the Duncan grove.

Fig. 18. Population dynamics of *Parlatoria oleae* and Persian *Aphytis* in the Whitney grove.

scales per branchlet or twig, and the parasitization at the same time was low, as is common for the winter months, at 5.2 per cent for January, 3.4 per cent for February, and 0.8 per cent for March (an emergence effect), based on immature parasites on susceptible host stages. Parasitization rose to 11.5 per cent by April 1 as the mature female scale population declined to 4.70 per branchlet. Parasitization then rose more rapidly from early April to early May (and probably still more so in mid-May), a result which is not reflected here in further decrease of the mature female scale population, but which caused a corresponding reduction in the eggs produced because of destruction

TABLE 18
EGG PRODUCTION PER MATURE FEMALE *P. OLEAE* DURING SPRING WHEN
APHYTIS ARE ACTIVE, AND DURING SUMMER WHEN
APHYTIS ARE NEARLY ABSENT*

Year	Bell Grove		Duncan Grove		Whitney Grove	
	Spring	Summer	Spring	Summer	Spring	Summer
1956.....	2.1	56.2	2.2	28.1	...	
1957.....	0.9	37.3	5.2	28.7	...	
1958.....	0.6	23.8	7.0	12.7	5.9	16.5
1959.....	0.8	29.4	0.2	20.1	0.3	13.2
1960.....	0.4	17.8	0.0	15.4	...	

* Egg production based on peak abundance of mature females just prior to ovulation.

of females prior to egg deposition. The parasitization on May 1 was 54.7 per cent. Combined parasitization during late March, April and continuing into May, was so effective that even though many immature third-stage female scales were maturing during that period, and should otherwise have produced an abundance of eggs, the ratio of eggs produced per female present at peak abundance in February and March was low at 2.1 eggs per female (table 18).

A very low ratio of eggs produced per successfully overwintered female is characteristic for the spring brood where *Aphytis* activity is intense, but egg production where *Aphytis* is absent at this time appears to be similar to that of the females of the next generation, which, under Central Valley conditions, are attacked only slightly by *Aphytis*.

The 13.7 eggs per branchlet produced a successful hatch, as *Hemisarcophyes* were not active and the eggs beneath the scales were protected from weather stresses. Our methods did not permit an estimate of the crawler population, although the populations of first and second settled stages (as compared with the egg populations) give a picture of the numerical loss from the egg stage to the young settled stages. The populations of these two latter stages should, possibly, be regarded collectively because in some instances the population samples showed higher numbers in the second stage than in the first stage from which they developed. This apparent anomaly is probably due to the very short time-span of the first stage, as well as to the fact that between two respective monthly counts a considerable number of eggs hatched and the scales developed through the first stage to the second. The first stage population is therefore inadequately measured and so the data for the first and second stages are plotted collectively.

During this spring period in 1956 there was a substantial loss in the scale population which was entirely unassociated with *Aphytis* activity, the eggs, the crawlers and the first and second stages of scales being unattacked by Persian *Aphytis*. The population per branchlet declined from 13.7 eggs to 3.1 young settled stages in June, to 1.6 immature third stages (including males) in July, and to 0.5 fully mature females in August. It must be remembered, however, that the male population was also included in the 1.6 figure for July, whereas the 0.5 figure for August is for females only. Thus, the figures indicate additional mortality of females during the interval.

An important point is revealed by considering the ratios of egg production per mature female during the summer period when *Aphytis* were not effective compared with that of the spring period just discussed when *Aphytis* were effective (table 18). Spring egg production in this grove was at the replacement level of 2 per female (assuming equal numbers of each sex and no premature mortality) only in 1956, before *Aphytis* had become fully effective. For the next four years, egg production for this generation was less than half that required for replacement of parent stock even if 100 per cent hatch and no subsequent premature mortality occurred. This has been true for the spring brood throughout the period of study, in spite of the fact that population densities of hosts were so low during these four years that even the highly preferred fruits each year were as free of scales as those from groves treated effectively with parathion. This emphasizes the high searching efficiency of Persian *Aphytis* at very low host densities—if meteorological conditions are suitable.

Table 18 shows that summer egg production in this grove varied from a high of 56.2 to a low of 17.8 per female; thus in sharp contrast to that of the spring period. Figure 16 shows us that parasites were very active in this grove by April 1 every year, and that by approximately May 1 the activity had increased so greatly that many female scales were dead (or rendered unproductive) from one to two months prior to the normal time of peak egg production, and most of those which did live long enough to produce eggs were killed by parasites after only a small portion of the potential quota of eggs had been laid. Since these observations were based upon dissections, the intergrading relation during a period of intense parasite activity was apparent.

It is important to remember that the fall brood of male crawlers develops to a stage susceptible to *Aphytis* as early as late September, and that some of the female scales are susceptible in late October and November. As a limitation to host increase, however, we need only consider parasitization of females. The scale overwinters mainly as susceptible, nearly mature females, and this same population of females remains susceptible to repeated attacks by *Aphytis* from October to late May of the following year. Since *Aphytis* has a short developmental period (15 days at 80° F, and less at warmer temperatures) during warm periods of the fall and in spring, it develops several generations on the same overwintering brood of female hosts. The parasitization of *P. oleae* by *Aphytis* as shown in figure 16 (and in other references) depicts what may be called *instantaneous* parasitization only, since each parasite must be present on a host at the instant of examination

in order for it to be recorded. The data were not based upon emergence holes observed in the scale covering and thus do not reveal the accumulated generation mortality of scales due to the action of successive generations of *Aphytis*.

It was not possible to use evidence of parasitization based on exit holes because we were sampling representative populations on old leaves and old woody segments, as well as on new ones. Thus, it would not be possible to relate any such exit holes to any specific brood or year—and we needed data relating to current events only. We could not use new growth only, because the general purpose was to use a sample representative of both old and new tissues.

If *Aphytis* were intensively active the entire period, and if they commonly survived the summer period in good numbers, this accumulative aspect could be so great that parasitization at any one time might be only 30 per cent, and yet a high degree of control would be exerted. To be effective, total parasitization need not necessarily approach 98 per cent, as there are many other causes of mortality. This is a point often overlooked in analyses of such relationships. In this case, however, *Aphytis* is scarce at the end of each summer and increases in numbers with each subsequent generation. Therefore, parasitization during October, November, and early December is seldom greater than 10 to 15 per cent and is often much lower. Late December and January are too cold for much activity; very few *Aphytis* eggs are deposited and very few of the pupae emerge during the coldest months, but instead, remain quiescent until warmer weather in February and early March. Reproduction of *Aphytis* then proceeds at a very rapid rate (fig. 7, p. 577), and two to four generations may result before egg deposition on the overwintering brood of hosts ceases in early June.

It is possible to use a rule-of-thumb assumption that two generations of *Aphytis* develop during the fall, and that during February, April and May, three additional generations occur. Applying this rough correction to the Bell grove data, we find that the accumulated total generation mortality from parasitization of the overwintering brood is much higher than the maximum shown in figure 16 for this brood at any given time, although the instantaneous parasitization itself rose to as high as 80 per cent on several occasions. The accumulated parasitization based on the rule-of-thumb assumption mentioned would be above 95 per cent in some instances.⁷ This is an exceptional performance in view of the fact that densities of hosts were very low.

Figure 16 shows, however, that total parasitization of the summer egg-laying females and preclusion of egg deposition by *Aphytis* was very low even at this favorable location. This undoubtedly accounts for a major part if not all of the difference in spring and summer egg production. Peak abundance of mature females during the summer period coincided with initiation of egg deposition.

It is pertinent, finally, to inquire if there may be an inherently higher fecundity of females of the summer brood. Only a trace of unparasitized females were present at the Bell grove during the spring period, but a sum-

⁷ In other groves, in fact, the instantaneous parasitization alone has been as high as 98 or 99 per cent at times.

mary from the detailed data for the Duncan grove, using only the egg production by *unparasitized* females of the spring brood at a time when they had completed laying most of their eggs, shows that the average fecundity was 22 to 23 eggs per female during both the spring and summer periods. Thus, there was no difference inherent to the seasons of the year.

We now consider the dynamics of the host and its mortality resulting from causes other than *Aphytis*. Although Bacon (unpublished notes), Stafford (personal discussions), and the authors have on occasions found the predatory mite *Hemisarcoptes malus* to be a potent mortality factor for male scales and also for gravid females and eggs at high densities, and while such general predators as *Chrysopa* spp., *Cybocephalus* spp., *Chilocorus* spp., and the parasite *Aspidiotiphagus citrinus* may cause some mortality, the total mortality resulting from action of these species in the orchards studied in detail was negligible.

Extensive biannual studies in many olive groves and many additional miscellaneous observations indicate strongly that, as an arboreal environment, olives in California are rather barren faunistically. *P. oleae*, and to a much lesser degree black scale, *Saissetia oleae* (Bern.), and oleander scale, *Aspidiotus hederae* (Vallot), are the only phytophagous insects which are at all common; the vagrant mite, *Oxypleurites mazwelli* Keif., which sometimes attacks young tip foliage, may also be mentioned here. Occasionally, migrant thrips cause trouble. There is no known pathogenic microorganism which causes disease in *P. oleae*.

Olive scale on olive has no significant competitor in orchards under good management (including proper pruning) in the main areas of commercial plantings in Madera, Fresno and Tulare counties. That is, other phytophagous species are seldom plentiful enough to compete directly with olive scale or to make the simple food-chain relationships complex. Inter-specific competition in such orchards is not a pertinent factor in the population dynamics of *P. oleae*. This may not be true, however, around dooryards, in relatively humid situations, or in other general areas. Black scale in such situations may significantly compete with olive scale. Thus, it seems that mortality of *P. oleae* in this grove, as well as in the Duncan grove, was associated with two main factors: (1) meteorological conditions and (2) action of *Aphytis*.

It is not possible to entirely disassociate the nutritional and water requirement factor from the meteorological factor. Lack of adequate irrigation has been observed to cause near-annihilation of *P. oleae* infestations in some groves, but whether this is caused by the scale's inability to obtain sufficient water or proper nutritive elements is not known. If the former is the case, the amount of water needed might vary with the desiccating power of the air. In general, however, the trees in the two groves presently considered appeared nutritionally suitable to the scales at all times. The Bell grove was always well irrigated, but this was not true of the Duncan grove.

Soil moisture in both groves was abundant during the spring period of scale egg production. If shortage of soil moisture contributed somewhat to mortality at the Duncan grove it was only during summer—at which time *Aphytis* was only a minor cause of mortality of scales.

Inadequate nutrition is sometimes a potent cause of mortality of scales, but this apparently occurs only when scales exist at heavy densities at given leaf or twig positions, for example. This is often observed in populations of overwintered females which have started from a high density of young settled stages on twig segments which, as the brood matures during the fall, winter and spring, no longer support the maturing females adequately. This is simply a question of very localized food shortage, and is density-dependent in nature even though there may be a superabundance of food at other positions on the same branch, twig or leaf. Nutrition may commonly be a limiting factor at times in such highly localized spots, even though in general it is not at all limiting for the population on the tree as a whole.

The densities of scales in these two study groves, and in groves generally where *Aphytis* is active, are too low for nutrition to serve as a very general mortality factor. However, this does not mean that it is totally unimportant as a factor causing some variation in mortality or in fecundity.

Winter rains and cold seemed much less harmful to scales than the summer periods of high temperatures and low humidities, particularly as the latter affect the young scales.

During late fall, winter, and spring female scales did not die in appreciable numbers except from *Aphytis* attack. The main loss in *apparent* population density during this period (when densities were high enough to be meaningful) is in reality not mortality, but *emergence* of males; there was no significant reduction in living females beyond what is accounted for by low parasitization by *Aphytis*.

For the Bell grove, the peak of the overwintered female population was usually about one-half as high as the preceding population of both males and females as shown for October (although in one instance the data show the opposite). In February and March, 1960, the female population was twice as high as that recorded for the combined male and female population of the previous October.⁸ The high egg count of August, 1959, when considered along with subsequent counts, suggests that the estimate of the true population in both the young settled stages (September) and the immature third stage (October) were unrealistically low—and that the count for mature females in February and March was probably unrealistically high. Due to variability in the distribution of the population (colonial in nature), and the sampling error involved, month-to-month figures on population densities of given stages are not very reliable when densities are very low.

It seems apparent that reductions in density from the relatively high egg populations of each brood were, up to the immature third stage, associated almost exclusively with behavioral reactions of crawlers in dropping off, and with meteorological factors. The desiccating power of the air could possibly be a critical factor, and would be influenced by high temperatures, low humidities and air movement. The loss from crawlers dropping off may also be assumed to bear some relationship to meteorological conditions. The decline in density from the egg stage to the young settled stages included trivial losses in hatch, losses in the crawler stage, and losses in the first and second settled stages. A majority of the loss is in the crawler stage (tables

⁸ Each month's figures are based on an independent sample of branchlets.

1, 17, pp. 554, 595), but mortality in the first settled stage may also be high. The fact that crawler success was twice as high in the fall period as in the spring period appears to be connected with the higher humidities associated with dews and with their persistence in fall mornings. In tests made under field conditions, total settling success by crawlers was only 7 to 23 per cent, the crawler mortality varying from 77 per cent in the fall to 93 per cent in the spring. While the artificiality of these tests contributed in some degree to the mortality (for example, transfers were made only in midday although crawlers normally are hatching and settling during more favorable hours as well), the data obtained do confirm in general the field data indicating that mortality in the crawler stage is high.

TABLE 19
MORTALITY OF CRAWLERS AND EARLY SETTLED STAGES, BASED ON
EGG POPULATIONS AT THE DUNCAN GROVE, COMPARING SPRING
AND FALL BROODS (POPULATIONS ON 36 BRANCHLETS)

Year	Season	Eggs	Number of survivors in second stage	Mortality
				<i>per cent</i>
1956	Spring.....	124	25	80*
	Fall.....	152	109	28*
1957	Spring.....	251	93	63†
	Fall.....	817	473	42†
1958	Spring.....	1,436	289	80*
	Fall.....	903	522	42*
Mean	Spring.....	...	...	74*
	Fall.....	...	...	37*

* Highly significant.

† Significance at the 0.10-0.05 level.

In the Duncan grove, where densities remained high enough for estimates of populations to be more reliable, indicated crawler mortality was consistently higher in the spring brood than in the fall brood (table 19). At the Bell grove, where densities were very low due to excellent biological control, the figures were not entirely consistent although the average for the entire 5-year period suggests a difference, the spring crawler mortality being 74 per cent, and the fall mortality, 57 per cent.

The conclusion from these data that *Aphytis* action is the only density-dependent factor of importance and is responsible for excellent control of *P. oleae* under the pattern of weather experienced is also supported by a direct comparison of *P. oleae* populations under *Aphytis*-free and *Aphytis*-present conditions. In these tests (p. 619) *P. oleae* quickly and consistently built up to very high densities on the *Aphytis*-free trees—that is, to an average level of 90.7 third-stage females per branchlet. This is 900 times the level on the trees where *Aphytis* were not inhibited. This control by *Aphytis* occurred in spite of the fact that one generation of the host each year suffered only a very low mortality from *Aphytis*. However, the degree of control is, as a whole, a function of *Aphytis* action and the meteorological and cultural conditions prevailing in the grove.

If the rate of increase in scales were much greater than it is in summer, that is, if the mortality in the young stages due to climatic factors were much less, the parasite would not be able to increase fast enough each spring to achieve the observed degree of control. This is why the degree of control achieved varies from year to year and from locality to locality. Yet, within the meteorological framework which is obviously otherwise favorable for the attainment of almost uniformly devastating maximal densities, the parasite effects a control which is outstanding, even though variable in degree, in time, or in place.

The tests using *Aphytis*-free check trees thus provide a manipulated field condition in which *Aphytis* action is removed. Here it is important to note that the unaltered natural situation furnishes a comparable example of a nearly *Aphytis*-free condition which involves no application of a chemical and which applies to one of the two generations of scales each year. Similarly, there is a conspicuous increase in scales which survive pressures in the nearly mature stage under both conditions and for the intervals in which *Aphytis* activity is subdued.

Another important factor in the grove is the pruning and cultural system used. Under heavy yearly pruning, and favored by an excellent soil and irrigation program, the trees produced an abundance of new leaders (limbs) three to eight feet in length each year. Since the crawlers must move onto this new growth by crawling from older wood sources, concentration of scales on the fruits (the commercially critical issue), where the general density of scales is low anyway, does not occur. Pruning itself tends to retard increase in densities of scales, but the populations on the DDT-treated trees under the same pruning program, show that pruning alone serves very little in the control of this scale (table 23, p. 621).

Population Dynamics in the Duncan Grove

The Duncan grove, Herndon, Fresno County, was the first test plot where Persian *Aphytis* was released (Doutt, 1954), releases being made from February 28, 1952, to May 7, 1952. Prior to release of this parasite, *P. oleae* had built up such a heavily-encrusted infestation that the trees were unkempt, lacked vigor and had an abundance of dead and dying branches (plate 2b, p. 548). Doutt recorded the density of mature female scales at 1.66 per leaf prior to release of *Aphytis*, and the fruit crop was consistently heavily damaged and unmarketable. Within a period of five months after release of *Aphytis* the infestation dropped to a density of 0.06 per leaf and after seventeen months to 0.018 per leaf; infestations on the twigs decreased correspondingly. Thus, at the initiation of the monthly sampling program presently considered, the scale population had for three years been under substantial ecological control.

While the Bell grove represents most favorable conditions for biological control of *P. oleae*, the Duncan grove is representative of an intermediate condition in which *Aphytis* gives less adequate control on a continuing basis—though in the Duncan grove it must be noted that part of the reason was the application of insecticides in adjacent fields.

Figure 17 (p. 596) shows parasitization in the Duncan grove expressed as a percentage, with actual density of parasites presented on a branchlet basis. This dual presentation shows that high parasitization by *Aphytis* may be achieved when *Aphytis* are either scarce or abundant; as an example, in April, 1960, there was high parasitization even though both parasites and hosts were scarce.

Control by *Aphytis* in this grove was fairly good in 1956, adequate in 1957 (partially as a carry-over effect from 1956), and inadequate in 1958 during the spring. The unusual survival of parasites during the summer of 1958 reversed the trend, and in the spring of 1959 overwintered female scales were so heavily attacked that egg production was only 0.2 per female (table 18, p. 598). The control continued to be very good in 1960, although the only grower-caused disturbance in the program may have affected results for this year: the trees were treated with 2 per cent oil for control of black scale in late August, 1959, and consequently it is not certain that parasites by themselves would have adequately reduced the scale in the spring of 1960. However, three facts suggest that *Aphytis* would have continued adequate control even if oil treatment had not been made: (1) the abundance of the parasite in January, 1960; (2) its rapid increase to a level of almost 80 per cent instantaneous parasitization; and (3) a nearly complete accumulated parasite preclusion of host egg deposition.

Figure 17 shows that in those spring periods when *Aphytis* gave adequate control there was an early increase of *Aphytis*; as a result, a large portion of the overwintered female scales were killed before they had laid any eggs, while many others were killed after only a few eggs were deposited. For example, in 1956 there was an early presence of *Aphytis* at a good relative abundance and by May 1 instantaneous parasitization of mature females had reached nearly 80 per cent, the ratio of eggs produced per female (table 18) being only 2.2, whereas the females of the next generation, being almost entirely free of *Aphytis* attack, deposited 28.1 eggs per female.

During the spring there was a very substantial loss between the egg stage and the young settled stages, with some moderate further diminution between the second stage and the immature third stage due mainly to weather hazards. At this early period in the study our sampling method for the summer brood was very inadequate and the peak egg population was missed because counts were taken only once during the critical month; later, two counts were taken each August. Using known production records per female from other data, and estimating the number of eggs the known number of females present in July should have produced, we made a correction of the egg population which is far more realistic than the uncorrected figure based on the inadequate sample. Using this corrected figure (though still definitely too low), it is seen that the indicated mortality of crawlers and young settled stages in August and September of 1956 was unusually low at this location, although the relatively smaller number of mature females present in December suggests that the sample gave us a somewhat unrealistically high immature third-stage population.

Regardless of the utility of this "correction" procedure, *Aphytis* was not present in the samples during the winter months and had not been sampled in 1956 after July (due to severity of heat and low humidities, plus probable

insecticidal air-borne "drifts" from cotton, figs and grapes). However, *Aphytis* increased rapidly from April 1 to May 1, 1957, achieving a parasitization of 43 per cent (no accumulation effect up to that time), and of 67 per cent on June 1 (fig. 17). The June 1 parasitization was only partially effective, and the parasitization up to mid-May was by itself inadequate to preclude egg deposition; 5.2 eggs were produced per female—too many for good control when it is recalled that the next brood is free of parasite attack, even though this egg deposition was only about one-sixth that of the following brood. Nevertheless, commercial control of the scale by *Aphytis* was achieved in 1957 (table 21, p. 620).

The high egg production in August, 1957, and the limited severity of the autumn weather on the ensuing young stages of scales, produced a high density of scales that could be brought under control by *Aphytis* only if the latter were abundant and active very early in 1958. Again, the parasite was nearly annihilated in July, 1957; it did not reappear in the samples until December, and then at very low numbers and at a very low percentage of parasitization. Winter cold did not permit increase, and *Aphytis* were still very scarce until April 1. With an abundance of hosts and milder spring temperatures, parasitization then rose rapidly, but this increase was too late to preclude fairly successful scale egg deposition. The highest density of parasites was on May 1 although parasitization was only 37 per cent at that time; by June 1 the number of suitable hosts had declined, because of previous parasite activity and death after deposition of eggs, and consequently a lower density of parasites in June accounted for a much higher percentage parasitization (fig. 17).

As already noted, the excellent survival of *Aphytis* during the summer of 1958—a survival phenomenal to the extent that it occurred consistently throughout the Central Valley area—"set the stage" for good control of the rather high scale densities (still very moderate in terms of pre-*Aphytis* densities) present in the spring of 1959. Parasites were active in the fall months, increased to a substantial parasitization of the immature third-stage scales in December, January, February and March, and almost completely precluded egg deposition in the spring, the number of eggs being 0.2 per female scale (table 18).

There are two probable reasons why the number of eggs produced per female in August was low in 1958 as contrasted to August production during other years. The density of scales had been moderately high during the preceding brood and the number of mature females present were several times as high as during any other August. The greater density of females, occurring in a clustered distribution, could conceivably have lowered the average production of eggs to about one-half that of the other summer periods. Data from the Whitney grove, where densities of females were high, also suggest this explanation. It is also probable that some of the mature females were killed by *Chilocorus bipustulatus* (L.) which was active in the grove that spring and summer and which, though feeding on black scale more effectively, also fed on *P. oleae* to a significant extent. This is the only instance when *C. bipustulatus* became a factor of any significance in any orchards studied.

Table 19 gives the mortality of crawlers and early settled stages at the Duncan grove for the years 1956–1958, inclusive. Similar figures for the Bell grove were not presented because the densities of scales there were so low that adequate comparisons of the crawler and early-settled-stage mortalities for the spring and fall broods was not possible. Also, the 1959 and 1960 data for the Duncan grove were not usable for two reasons: (1) treatment of the grove with oil for control of black scale had an effect on the fall brood but not on the spring brood in 1959, and (2) because the 1960 sample for the spring brood contained no scales, there was no basis for comparison of the mortalities in the two broods that year. Table 19 shows that early-stage mortality of the spring broods was 80 per cent in 1956, 63 per cent in 1957 and 80 per cent in 1958, whereas the contrasting mortalities in the fall broods were 28 per cent, 42 per cent and 42 per cent for 1956, 1957 and 1958, respectively. Thus, the mean mortality for the spring brood was 74 per cent and for the fall brood 37 per cent, there being a highly significant difference in the means.

Concluding the discussion of the population dynamics in the Duncan grove, it can be said that fair commercial control was achieved every year except in 1958. Even though *Aphytis* activity was only partially satisfactory in 1957, scale density had been reduced so much in 1956 that it did not build back to a damaging level until the fall of 1958—and in the spring of 1959 the parasite again effectively reduced the scale. Cotton, grapes and figs were grown near the grove, and drift of the insecticides used on these crops appears to have been a factor reducing the effectiveness of *Aphytis*, as there generally are fewer scales on olives in parks and city streets in the general area (page 629).

Population Dynamics in the Whitney Grove

The Whitney grove had had an unusually heavy infestation of *P. oleae* for at least three years prior to initiation of studies there, and it was chosen because of this history of persistence of scales in spite of the presence of *Aphytis*. The olives were partially shaded by walnuts, a point to which we shall have reference later.

The detailed monthly population studies were begun in October, 1957, and discontinued in July, 1959, when the trees were removed in order to plant the ground to another crop. While the record is thus not of sufficient duration for general significance, a few points are worth noting. For example, table 18 shows that during 1958 (when spring activity of *Aphytis* reached a high level only in late May and June) the egg production per female *P. oleae* was rather high at 5.9; but in 1959, when *Aphytis* had been active during the previous fall and had thus increased earlier and to higher levels in the early spring period, production of eggs was only 0.3 per female. Production for the corresponding summer periods, when *Aphytis* were rare, was 16.5 for 1958, and 13.2 for 1959—in each case much higher than the spring figures.

It is interesting to note that densities of scales at this location were very high during this limited study period in spite of the fact that egg produc-

tion per female during the unparasitized brood generally was considerably less than in the Bell grove where densities of scales were lower, and somewhat less than at the Duncan grove where densities were intermediate. However, the data for 1956 presented in table 8 (p. 562) indicate that mortality in the young stages at this grove (from causes other than *Aphytis*) is less than that which occurs at the Bell grove.

If we may extrapolate from these data for 1956 (not necessarily valid) it would seem that total premature mortality of the fall brood when parasites are inactive is somewhat higher in the Bell grove than in the Whitney grove. If this is true, the main reason why densities have continued rather high at the Whitney grove while they declined to very low levels at the Bell grove must be associated with some effect of meteorological conditions and cultural practices and/or *Aphytis* activity. The limited comparative data available indicate a *higher* fecundity of the scale at the Bell grove; possibly this is due in part to limited local-area nutritive deficiencies at the Whitney grove, because of the higher scale densities, and (perhaps more important) because of lower tree vigor. This condition may partially or entirely offset the indications of a differential mortality due to meteorological causes. Thus, *Aphytis* activity, cultural practices (physical removal of the scales by pruning), and the forcing of long new leaders yearly offer the most likely answer to the problem.

In regard to *Aphytis* action, parasitization of 4.1 per cent in the spring of 1957 (table 20), was, for March 5, too low to be meaningful at such an early date. In many groves it has been common for instantaneous parasitization to increase from a negligible 3 to 5 per cent in early March to as high as 80 to 95 per cent (good control) by mid-April. During the spring periods of 1957 and 1958 there was no adequate parasitization by *Aphytis* in this grove, and the monthly records of poor survival during the respective preceding summers indicate why the spring parasitization was low.

In general, the data discussed suggest why *Aphytis* has been less effective and the scale maintained at high densities even though *Aphytis* had been present several years. The Whitney grove, even though located in a favorable Tulare County citrus growing area, has a seasonal sequence of *Aphytis* activity similar to that in the more northerly locations of Willows and Orland in Glenn and Colusa counties. In these latter locations, high *Aphytis* activity has not occurred until May or even June. This suggests the possibility that the shading of the olive trees at the Whitney grove may have cooled the spring microenvironment enough to affect *Aphytis*, or that the mere absence of sunlight may have acted on the movements of the parasite to the extent that its rate of increase was retarded and peak parasitization delayed. The shading effect may also be involved in the lower mortality of young scales, and cooler spring conditions may retard *Aphytis* much more than it does *P. oleae*. The latter would still have its normal two generations each year, with probably little or no reduction in fecundity. On the other hand, the favorable summer of 1958 caused an exceptional spring abundance of *Aphytis* in 1959 at all locations, and the Whitney grove was no exception.

We also feel that the rather neglected condition and lack of a pruning program at the Whitney grove (in contrast to the heavy yearly pruning

TABLE 20
AVERAGE DENSITIES OF *P. OLEAE* AND PARASITIZATION BY PERSIAN
APHYTIS DURING APRIL OR MAY (INCLUDING A FEW FOR MARCH),
AND DURING AUGUST, AT ELEVEN OLIVE GROVES IN TULARE,
FRESNO, MADERA, AND GLENN COUNTIES, CALIFORNIA

Location	Population data	1957		1958		1959		1960	
		Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Whitney (Exeter)	M ₃ ♀ ♀ per branchlet	45.9	21.2	48.6	18.6	21.8			...
	Per cent parasitized	4.1	0.0+	7.4	10.6	89.1	...		...
	Unparasitized M ₃ ♀ ♀	44.1	21.1	45.0	16.7	2.4	...		...
Kirkpatrick (Lindsay)	M ₃ ♀ ♀ per branchlet	0.9	0.0+	0.0†	0.0+	0.3	1.2	1.9	0.9
	Per cent parasitized	1.9	0.0	0.0	0.0	6.3	0.0	69.8	0.0
	Unparasitized M ₃ ♀ ♀	0.8	0.0+	0.0+	0.0+	0.3	1.2	0.6	0.9
Long (Seville)	M ₃ ♀ ♀ per branchlet	Not	0.2	2.5	1.6	9.0	0.0	0.0	0.0†
	Per cent parasitized	under	0.0	51.9	12.5	93.7	0.0		0.0
	Unparasitized M ₃ ♀ ♀	study	0.2	1.2	1.4	0.6	0.0	0.0	0.0+
Bell (Hills Valley)	M ₃ ♀ ♀ per branchlet	0.4	0.0+	0.2	0.1†	0.1	0.4	0.2	0.1
	Per cent parasitized	44.2	0.0	29.6	5.0	100.0	0.0	81.9	0.0
	Unparasitized M ₃ ♀ ♀	0.2	0.0+	0.1+§	0.1†	0.0	0.4	0.0+	0.1
Long (Ivanhoe)	M ₃ ♀ ♀ per branchlet	Not		0.0	0.0	0.1—	0.0	0.0	0.0
	Per cent parasitized	under				66.7	...		...
	Unparasitized M ₃ ♀ ♀	study		0.0	0.0	0.0	0.0	0.0	0.0
Duncan (Herndon)	M ₃ ♀ ♀ per branchlet	1.6	0.7	1.2	3.8	3.2	0.7	0.0+	1.5
	Per cent parasitized	6.1	0.0	4.3	2.6	90.2	0.0	100.0	0.0
	Unparasitized M ₃ ♀ ♀	1.5	0.7	1.1	3.7	0.3	0.7	0.0	1.5
Bell (Clovis)	M ₃ ♀ ♀ per branchlet	0.4	0.3	2.5	0.3	0.2—	0.5	1.9	2.5
	Per cent parasitized	0.0	0.0	71.0	26.3	100.0	0.0	57.4	1.4
	Unparasitized M ₃ ♀ ♀	0.4	0.3	0.7	0.2	0.0	0.5	0.8	2.4
Oberti (Madera)	M ₃ ♀ ♀ per branchlet	30.9	6.3	19.8	11.6	3.4	0.4	0.6	0.5
	Per cent parasitized	6.1	0.0	5.6	26.7	79.4	0.0	89.7	0.0
	Unparasitized M ₃ ♀ ♀	29.1	6.3	18.7	8.5	0.7	0.4	0.1—	0.5
Oberti-Sheeler (Madera)	M ₃ ♀ ♀ per branchlet	0.3	0.1+	1.6	1.4	3.8	0.5†	0.1	0.0
	Per cent parasitized	0.0	0.0	43.6	7.1	92.4	3.3	57.1	...
	Unparasitized M ₃ ♀ ♀	0.3	0.1+	0.9	1.3	0.3	0.5	0.1—	0.0
436 N. Colusa St. (Willows)	M ₃ ♀ ♀ per branchlet	0.9	0.9	5.9	Sampl-	1.3	0.9	0.3	0.2
	Per cent parasitized	36.2	0.0	49.1	ing	48.7	3.6	20.0†	0.0
	Unparasitized M ₃ ♀ ♀	0.6	0.9	3.0	missed	0.0+	0.9	0.2	0.2
727 A Street (Orland)	M ₃ ♀ ♀ per branchlet	0.0	0.1—	0.1+	Sampl-	0.2	0.6	0.6	1.0
	Per cent parasitized		0.0	50.0¶	ing	50.0	0.0	81.0	1.6
	Unparasitized M ₃ ♀ ♀	0.0	0.1—	0.1—	missed	0.0+	0.6	0.1	0.9

* Densities on each date and at each grove are based on populations on 60 twigs and 720 leaves taken equally from 5 trees except for the Bell (Hills Valley) grove where 144 twigs and 1,728 leaves were taken from 12 trees.

† Treated for scale by mistake in June, 1959, just after nearly all scales had been killed by *Aphytis* (most effective year).

‡ Low, possibly because of mosquito treatments.

§ Sample taken April 2; however, parasitization by May (accumulated) was over 90 per cent and control continued good.

|| Only 0.29 per cent on April 17. Figure given is for May 20, too late for effective control.

¶ Only 16.7 per cent on April 17. Figure given is for May 20, too late for effective control.

and excellent care at the Bell grove) played a significant part in the differences of control attained. During 1957 a test was conducted to see if heavy pruning and use of an oil treatment to reduce the scale population to a less encrusted condition—which offers protection against *Aphytis*—would augment biological control afterwards. A temporary reduction of scales was noted after using this procedure, but the *Aphytis* were unable to prevent a resurgence of the scales during the subsequent year. Because of the poor condition of the trees, however, long new leaders did not develop, and hence the possible good result from continued pruning under more favorable circumstances was not disproved. The Whitney grove thus presents an unanswered problem, and one which is not explained by the climate of the area in general.

DEGREE OF COMMERCIAL CONTROL BY *APHYTIS*

Methods

In evaluating the effectiveness of Persian *Aphytis* in the commercial control of *P. oleae*, our principal approaches have been (1) the employment of population counts of scales and the degree of parasitism at two significant periods each year, that is, one for each brood of the scale; (2) counts of scales on fruits (including the level of commercially unacceptable fruits); and (3) the use of DDT-treated, *Aphytis*-free trees as controls to show what the infestation would be if *Aphytis* were not active. The geographic scope of these particular control studies was broader than the detailed population dynamics studies discussed previously. Data are available for thirteen groves in four counties, but some of the studies were conducted for short periods of time only because of: (1) lack of time, (2) the lesser importance of olives in some areas, (3) the representativeness (or otherwise) of the plots in terms of the industry as a whole, and (4) the owners' withdrawal of the groves from the program.

In order to obtain information embracing additional ecological and agricultural areas, two general surveys covering all the areas where olive scale is an important pest were also conducted in 1956 and 1960. However, notes dealing with conditions prior to the introduction of *Aphytis* are available from surveys made by W. W. Wiard and by various county agricultural commissioners and farm advisors, and from studies by R. L. Douth and K. S. Hagen of the Department of Biological Control, University of California, covering 1951–1953.

We shall first discuss the results of the specific population analyses for the groves under the regular program of bi-annual sampling. Following this, we shall review the results of the surveys, adding such generalities as seem indicated.

Biannual Population Analyses

Table 20 presents the main body of data for eleven groves under biological control studies from 1957 through 1960. Data are also available for the Duncan (Herndon), Kearney Park (Fresno) and Graydon (Earlimart) groves

for a few additional years (Doutt, 1954). The Kearney Park location consisted of scattered trees in a shaded park and these trees were removed in 1955. The Graydon grove at Earlimart was a small one surrounded by alfalfa on two sides, by cotton on a third, and grapes on the fourth side. During 1956 and 1957, treatments of these crops with various insecticides caused such obvious drift effects in interfering with *Aphytis* that densities of *P. oleae* were correlated with distance from the adjacent crops; scale densities were strikingly highest immediately adjacent to the grapes and cotton. Parathion treatments for spotted alfalfa aphid were initiated on the two alfalfa sides, and this caused an untenable condition for the grower, with the result that the grove was dropped from the biological control program. The grove had up to that time improved very markedly (particularly at interior positions) from a previously severe infestation.

Table 17 and figures 16 and 17 show results for the years prior to 1957 for the Duncan and Bell-Hills Valley groves (see pages 593-607 for discussion of these results).

Table 20 illustrates several general facts about the groves in the study years. The counts in the spring of 1957 (except for the Orland and Willows locations) were taken too early in the season to serve as suitable measures of the effectiveness of the parasite for that host brood. Monthly samples from several of the same locations showed much higher parasitization five to six weeks later, and this is characteristic. Survival of parasites during the hot dry summers is indicated by the data for the fall periods as percentage parasitization; this should be considered in connection with actual densities of hosts.

The summer of 1957 was especially severe and zero parasitization was encountered at the fall sample date in every study area except the Whitney location, where very large numbers of scales were examined and 0.0+ per cent parasitization was encountered. This accounts for the fact that, in general, the parasitization obtained in the spring period of 1958 was belated and low. The summer of 1958 was especially favorable, however, and the parasitization was unusually high for that season at all locations where densities of hosts were high enough for the sample to be meaningful. As a result, the parasitization in the spring of 1959 was the highest recorded, and very good control by *Aphytis* was achieved that year at all locations studied. The summers of 1959 and 1960 were again normal and poor survival of *Aphytis* obtained. Despite this, the parasite was generally able to maintain good control in 1960, and this was due in part to the hold-over effect from the high degree of control achieved in 1959 and to a mild winter and spring, with consequent faster recovery of *Aphytis*.

There is some indication that as time passes there is occurring a natural selection of a stock which responds somewhat more satisfactorily under cool fall and spring conditions; observations suggest an earlier increase in parasite abundance in the spring now (1961) than was true in 1953 (Doutt, 1954). However, this observation is entirely inconclusive.

Kirkpatrick grove, Lindsay. This grove offers an interesting example of quick and excellent biological control. Had there not existed one unusual corner tree, the answer as to whether this control was due to parasites would

not have been immediately ascertainable. While the use of the DDT-treated "check" trees would have later answered the question (table 23, p. 621), in the absence of those tests and in the absence of the particular corner tree, the general data from this grove would hardly suggest *Aphytis* as the answer to continued low densities of scales. However, the exterior corner tree of the 36-tree corner plot was so situated that it usually had been missed in the otherwise thorough parathion treatments given the grove each year. This tree, having no *Aphytis*, had maintained a heavily-encrusted scale condition. The record for the tree (1 of the 5 trees in the sample) showed a high scale density when the regular insecticidal program was stopped and *Aphytis* were introduced in the spring of 1957. During the first spring, *Aphytis* was very effective although the sample for parasitization taken in early March (table 20) was too early to indicate this. The great abundance of exit holes later in the season (when none had been present before) showed *Aphytis* to be the cause of the sudden and otherwise highly unlikely severe reduction of the scale population. Scale densities remained low in all the trees during the fall of 1957 and throughout 1958 and in fact near-zero densities were recorded (samples of 720 leaves and corresponding twig segments); no parasites were found in the very few scales encountered. As a result of near-absence of parasites (and scales as hosts) on most of these trees during the summers of 1957 and 1958, *Aphytis* were not very active at the time of sampling in the spring of 1959, although they were abundant at every other location under study. The 0.3 mature female scales per branchlet for the spring of 1959 constituted a several-fold increase, and this increase continued to the fall of 1959. However, the parasitization in the spring of 1960 was sufficient, at such low host densities, to depress the scales to a satisfactory level again (table 20).

While events on the high-density corner tree almost immediately showed the controlling effect of *Aphytis*, our records from early March to early April of 1957, 1958, and 1959 do not indicate enough parasitization to account for the *continued* control. In every case where data are available from early March to late May, *Aphytis* increases in a more or less geometric fashion (fig. 7, p. 577). Hence, it is probable that substantial parasitization of the spring females in relation to such low host densities did occur subsequent to the dates on which the records were taken. In this instance we have supporting evidence in the form of *Aphytis*-free check trees (table 23). The increase in scales on the *Aphytis*-free trees was very great, densities in 1960 being 676 times the initial densities while densities in the *Aphytis*-present trees were only twice the original figure (even though still commercially important). In fact, this increase was temporarily nearly arrested in the spring of 1959. Under the environmental conditions obtaining, *Aphytis* accounted for the period of good commercial control.

Table 21 (p. 620) shows that there were essentially no commercially scaly fruits in the biological control trees, the highest level being in 1960, at 1.0 per cent. The level of cull fruits in the DDT-treated, *Aphytis*-free check trees (table 22, p. 620), was 93 per cent, however. The slow increase in scaly fruits was due to the exceptionally scale-free condition at the initiation of the study. In every instance studied there is an outstanding contrast be-

tween the *Aphytis*-free and *Aphytis*-present conditions. Most of the trees remained clean, but a few of them immediately adjacent to the two treated with DDT also developed somewhat higher densities of scale (drift effect), and this also happened at other groves where the trees were plantedly fairly close together.

Long grove, Ivanhoe. This grove was chosen because, unlike the Whitney grove, *P. oleae* appeared to be *entirely* absent in 1957. We wished to learn if *Aphytis* could be the key factor, within the environmental conditions prevailing and the cultural practices employed, of this apparent absence. The question is only equivocally answered by the data, however, because of the July, 1959, application of oil for treatment of black scale, and because DDT-treated *Aphytis*-free check trees were not employed in this grove.

Two samplings in 1958 showed no living scales and consequently no parasites were counted although an old scale covering with an exit-hole of *Aphytis* was encountered. By spring, 1959, the population had noticeably increased although the density was still less than 0.1 mature female per branchlet. We feel that if *Aphytis* can maintain itself and so readily find and parasitize *P. oleae* when the scales are so rare on a tree, then it can in fact account for extremely low levels of scale abundance if conditions are favorable for it. Other evidence substantiating this belief is, for example, the proven effectiveness of *Aphytis* (by use of *Aphytis*-free comparison trees) at very low scale densities at the Bell and Kirkpatrick groves where, in the case of the latter, the records of parasitism, like those in this instance, are otherwise seemingly inadequate to explain the degree of control. The recorded parasitization in this instance seems high enough if it adequately represents the true population mean. It seems that if the oil treatment had not been applied, and if *Aphytis*-free comparison trees had been used, we could probably have demonstrated a key role of *Aphytis* in maintaining such extremely low densities of *P. oleae*.

The scale densities in this grove have remained too low to require determination of the level of commercial cullage of fruits due to scale.

Long grove, Seville. This young 60-acre olive grove was not treated for olive scale for three years prior to initiation of biological control studies there. *Aphytis* had arrived in the grove on their own and apparently were giving commercially acceptable control. Subsequent to the initiation of these studies there was a gradual increase of scales up to the spring of 1959 (comparing fall to fall, or spring to spring figures). This may be in part accounted for by increase in density of the foliage and branches, spread of scales from the early foci of infestation and the fact that cotton was grown on three sides of the grove during 1957 and 1958.

The scale infestation in the fall of 1958 was heavy enough to suggest a possible commercially injurious density by the fall of 1959 (table 20). However, the unusually favorable survival of *Aphytis* in the summer of 1958, combined with the consequent early increase in activity in the spring of 1959 and disappearance of the cotton problem, resulted in an instantaneous parasitization of 93.7 per cent and an accumulated parasitization approaching 100 per cent. Undoubtedly, parasitization of many of the remaining scales occurred subsequent to the date of the sample, April 14. Both the scales and

the parasites in 1960 were at such extremely low levels that sample size was inadequate to turn up either; hence the zero figures in table 20.

The perfection of this control was, unfortunately, confused by the treatment of the trees for black scale with oil in June, 1959. This treatment was unnecessary for olive scale because *Aphytis* had decimated the scale population prior to the date of oil application. Table 23 data presents evidence from the DDT-treated *Aphytis*-free trees which tells the story of control of *P. oleae* by *Aphytis*; in the fall of 1960 the *Aphytis*-free trees had infestation 993 times as great as the *Aphytis*-present trees.

Tables 21 and 22 present the record of commercially marked fruits from this grove for the years 1958 to 1960, inclusive. Table 21 shows that an unacceptably high level of scaly fruits occurred in 1958, although the fruits were clean in 1957 judging by study samples. However, the grower picked early in 1958, as is his custom regardless of scale infestation, and he reported a much lower commercial cullage (2 to 4 per cent for the most part) than our counts indicated. The observations just noted in regard to the complete control of the scale in this grove by *Aphytis* in the spring of 1959, and the application of oil in June of that year, apply here also. The level of commercially marked fruits in 1959 could hardly have been greater than 1 to 2 per cent even if the oil had not been applied.

Continued good control by *Aphytis* in 1960 is shown by the per-branchlet density of female scales of 0.03, and the commercially marked fruits at 0.0 per cent. In contrast, the DDT-treated trees were comparable in marked fruits at initiation of the test in 1958, the test was interfered with in 1959, and a great increase of the scale population occurred up to 1960, resulting in a level of 79.0 per cent marked fruits.

Bell grove, Hills Valley. This grove, which was discussed in detail on pages 593-604, has been a most favorable one for *Aphytis* control of *P. oleae*—a control which, as we have seen, may depend upon many interrelated factors. Here, the location and the cultural practices appear to give *Aphytis* the margin of advantage necessary to overcome many factors which can work against control. *Aphytis* seems to reach very low levels in this grove also during the summer period, but usually the lowest level is of short duration. In spite of a high number of eggs produced per female scale, the parasite has invariably increased sufficiently early in the spring to maintain excellent commercial control (tables 20, 21 and 22).

Figure 16 (p. 594) indicates that olive scales were so few in numbers in late 1960 that although sample size had been doubled the results only inadequately picture the relative changes in density from stage to stage and brood to brood. The comparison of the *Aphytis*-free and *Aphytis*-present condition verifies in an even more striking way the conclusions arrived at through other approaches.

The records for culled fruits for this grove extend from 1955 to 1960, inclusive, but only in 1955 was the fruit crop sufficiently scaly to represent a definite economic loss. At that time biological control had not progressed far enough to be satisfactory. Our counts showed that 23.7 per cent of the fruits were commercially marked, although the grower's commercial cullage due to scale that year was only about 4 per cent. Analysis of packing house

practices at that time indicated a wide divergence of standards on marked fruit, and also showed that the standard we had adopted was as strict as that employed by any of the commercial packers in the area, and stricter than most.

During 1956, biological control gave fully adequate protection in this grove. Fruits from the biological control block and those from the large parathion-treated area were nearly identical in degree of culled fruits, the scaly fruits coming from the tops of the trees mainly in the parathion-treated area and from rather random positions in the biological control trees. Again, the packing house culled much less scaly fruit than our recorded 3.6 per cent. It seems that when the scale causes no more than 3 or 4 per cent culls, the graders have so many more fruits to cull because of bruises and other damages that they shift most of their attention away from scale damage. Consequently they do not cull many fruits having scales which they might otherwise classify as unsatisfactory.

During 1957 and 1958 the fruits were remarkably free from scale damage—in 1959 only 1.4 per cent were marked, and in 1960 only 0.3 per cent (table 21). Table 22 shows the increase in commercially scaly fruits from 1958 to 1960, inclusive, in the comparable DDT-treated, *Aphytis*-free trees. It is apparent that the fruit crop in 1960 would have been unmarketable at 85 per cent cullage without *Aphytis* control; with such control the grower obtained very clean fruits from this 80-acre grove.

No insecticide applications have been made in the biological control block since 1955 when a program of spot treatment was advised. At that time, a scattering of trees was treated with oil in order to reduce the possibility of commercial loss in the biological control block during the interval of transition to adequate biological control. It had been intended that the spot-treatment procedure would be continued if needed, but this proved unnecessary and in 1958 the entire planting of 80 acres was shifted to the biological control program. The program has been maintained since that time, with consequent substantial savings to the grower.

Duncan grove, Herndon. This grove was discussed in detail in the previous section; additional basic data for the grove are presented in table 20 (p. 609).

Aphytis control of olive scale was fairly successful here but not as invariably so as at the Hills Valley grove. The proven effectiveness of *Aphytis* extends back to 1952 and 1953 (Doutt, 1954), and the record of commercially marked fruits begun in 1955 shows that the fruits have been relatively commercially clean during most of the period the grove has been under biological control. The major exception was in 1958, when 27.4 per cent of the fruits were marked; that year cotton was grown adjacent to the grove. The year 1958 was also the culmination of a period of increase in scales sufficient to have definitely upset the biological control had it not been a very favorable year for survival of *Aphytis* generally (but less so in this grove than in any other place studied). Control became more effective in 1958, although not fully adequate. In any event, the grove's location, when combined with the poor management and lack of a suitable pruning program, makes it marginal for biological control by *Aphytis*, particularly during certain years. The grove is surrounded by crops which are often treated with various insecticides.

ticides from the air, and the drift from these, it is felt, is a potent factor in the poor survival of *Aphytis* during the summer periods.

Very excellent control of fruit marking was obtained in 1960, only 0.4 per cent of the crop being marked. However, it should not be inferred that control would have been this satisfactory had not an oil treatment for black scale been applied during July of 1959. Because of its timing, the treatment was not highly effective against olive scale, but it undoubtedly reduced densities somewhat. However, oil-treated trees which were adjacent to the DDT-treated trees, and which received drift of DDT, built up substantial densities of scales in spite of the oil treatment; in the rest of the oil-treated orchard where *Aphytis* was uninhibited, the densities remained low (0.4 per cent cull fruits).

It will be helpful here to compare the scale populations on the two DDT-treated, parasite-free trees in this grove in 1960 with the corresponding populations on the *Aphytis*-present trees (tables 21, 22, p. 620), and to compare these figures with the densities of scales in the grove in 1952, prior to introduction of the parasite. For the latter, Doutt (1954) recorded the density of mature females at 1.66 per leaf on February 28, 1952. The density of mature females per leaf at the comparable seasonal period in 1960 on the DDT-treated (experimentally reestablished parasite-free condition) was 5.0 per leaf (not presented in table 23), whereas at the same time in 1960 the other trees under *Aphytis* control had very negligible densities—in fact, the sample of 720 leaves had only 1 scale present. Furthermore, by August, 1960, the comparable density per leaf in the DDT-treated trees was 14.0. By the autumn of 1960 the DDT-treated, *Aphytis*-free comparison trees produced a living scale infestation about eight times as great as that present in 1952 when the orchard was heavily encrusted with living and dead scales and the trees were suffering from die-back. The density in 1952 was the end result of several years of heavy infestations, and this may well be the reason why densities of live scales were only 1.66 per leaf then, as compared with 5.0 per leaf for the same seasonal period in 1960, and 14.0 in the fall of 1960. The trees which were treated with DDT from 1957 to 1960 had been free of high scale densities from 1953 to 1957 (because of *Aphytis* action) and presumably had regained enough vigor and nutritional condition to sustain an increase in density of scales, from 1957 to 1960, to a level higher than could be maintained on a long-continuing basis. In fact, the density on the DDT-treated trees in August, 1960, was so high that this experimental and demonstration test had to be discontinued to prevent severe injury to the trees.

Oberti grove, Madera. Prior to 1957, the biological control section of this grove had been under an ineffective oil-treatment program. Infestation was especially high on the corner trees and those next to buildings where the spraying operation did not give good coverage. The orchard was well managed and the trees were vigorous, although scaly. The density of females on the first sample in the spring of 1957 was 30.9 per branchlet (table 20). Parasites had just been introduced and activity the first year was inadequate. In the spring of 1958 *Aphytis* were still very scarce in proportion to the high numbers of scales (and somewhat less so that year at other places

also). In fact, losses of fruits because of scales increased from 1957 to 1958.

The good survival of *Aphytis* in the summer of 1958 presaged the reduction of this heavy infestation through intense *Aphytis* action in the spring of 1959. In fact, the control did reach commercial satisfaction, at only 4.4 per cent marked fruits. The summer survival of *Aphytis* at this location was the highest of any grove in 1959, and as a result the very high degree of control held in 1960, with only 1.0 per cent marked fruits.⁹ Although *Aphytis* were not encountered in the August, 1959, sample, other samples taken in November showed 25 per cent parasitization—a level which is more than sufficient to trigger subsequent spring effectiveness. Thus, this heavily infested grove which appeared at first not to respond to *Aphytis* had come under very good biological control, and this control was still holding in 1961.

Bell grove, Clovis. The Bell grove at Clovis was under the same management practices as the Bell grove at Hills Valley. However, the Clovis grove is in a more centrally located part of the San Joaquin Valley, while the Hills Valley grove is nestled close to the foothills of the Sierra Nevada and thus has somewhat ameliorated climatic conditions. In addition, the soil at the Hills Valley location is much more sandy and the trees are spaced about 40 feet apart, as contrasted to 20 feet apart in the Clovis grove. These factors affect the consequences of pruning operations relative to dynamics of the scale.

The Clovis grove was shifted from a program of effective parathion treatment to biological control in 1956. The spring sample in 1957 was taken too early to properly indicate parasite significance, but the host densities shown at that period are useful for later comparisons (table 20). There was a definite increase in scales during 1957 and by spring, 1958, there were 2.5 female scales per branchlet—but by this time *Aphytis* had increased its activity and the subsequent fall scale brood density was only 0.3 per branchlet.

The generally high level of *Aphytis* survival in the summer of 1958, and the 26.3 per cent parasitization, as shown by the fall sample, set the stage at all locations for effective control during the spring of 1959. Thus, the scale was held at a very satisfactory level through the fall of 1959. Although scale densities increased during the fall brood that year, and the subsequent females of the spring brood of 1960 were again more abundant than desired, commercial control was not yet threatened. The parasitization in the spring of 1960 was lower in the sample area than desired. Later analyses indicated, however, that the area from which the samples had been taken, being nearly adjacent to a cotton-field, had been disturbed by insecticide treatments. The rest of the 40-acre grove has remained under fully satisfactory control by *Aphytis*.

Counts of commercially marked fruits in this grove were taken from 1957 to 1960, inclusively. Since the scale had been under satisfactory control with insecticides, the objective was simply to maintain control with *Aphytis*, and no reduction was expected. The best measure of the success of this objective is obtained by comparing the commercially marked fruits from the *Aphytis*-

⁹ During the summer of 1960 for the first time, the more recently introduced internal parasite, *Coccophagoides* sp., was parasitizing a substantial percentage of the scales, thus supplementing the activity of *Aphytis*.

free trees with fruits from the *Aphytis*-present trees (see data of tables 21, 22). From 1958 to 1960, inclusive, the period of the DDT treatments, the percentage of marked fruits on the *Aphytis*-free trees steadily increased (8.5 per cent in 1958, 74.5 per cent in 1959, and 100.0 per cent in 1960) while the fruits from the *Aphytis*-present biological control trees remained relatively free of scales. The sequence of densities of the mature female scales under the two conditions for this period stand in similar contrast (table 23, p. 621). The effectiveness of *Aphytis* is thus clearly demonstrable.

Oberti-Sheeler grove, Madera. This grove had been under effective oil treatment prior to initiation of the biological control program, and the density of female scales was only 0.3 per branchlet. Although there was a ten-fold increase in densities up to the spring of 1958, at which time parasitization was both low and delayed in timing, the increase was not yet sufficient to cause a high percentage of fruit marking (table 21), the density being 1.6 females per branchlet (table 20).

Scale densities had reached a disturbing level by the spring of 1959, but the exceedingly high and early parasite activity that spring, which was due to high hold-over in the summer of 1958, resulted in fully adequate reduction of the population (the oil treatment applied by ranch employees in June, 1959, was an error and was not by direction of the grower). During the time that the control test was in operation the number of scales on the DDT-treated, parasite-free trees increased many-fold over that in the *Aphytis*-present block.

North Colusa Street, Willows, and "A" Street, Orland. Single rows of street and dooryard trees constituted these experimental areas. The objective here was to determine the effectiveness of *Aphytis* in this area, so as to obtain information on Glenn county for possible use later relative to the olive area near Corning, Tehama County, where the scale had not then been found.

During the period of this study *Aphytis* has been variably effective. During 1957 and 1958, spring parasitization at the Willows location was late and too low for successful economic control (table 20). Sampling was missed in the fall of 1958, but from the spring of 1957 to the spring of 1959 the scale density had declined from an injurious level of 5.9 females per branchlet to 1.3, at which time instantaneous parasitization was only 48.7 per cent. The parasitization in late May was 93 per cent, however, although high parasitization at this date is too late for effectiveness because too many host eggs have been deposited. The results were somewhat similar at Orland, although the scales at that location have remained fairly scarce, probably due to the fact that the trees receive little or no water during the summer. Even under these conditions scale infestations were not as heavy after the introduction of *Aphytis*. It is probable, therefore, that moderate *Aphytis* activity, combined with climatic and cultural conditions which are unfavorable to the host, gives marginal control in most years and adequate control in some years. Heat from the burning of grass refuse beneath the trees during the past two summers has killed much of the scale and *Aphytis* populations and thus has been a disturbing factor. The records of commercially marked fruits also show an intermediate, inadequate degree of control.

We can only speculate as to the reason for the lower activity of *Aphytis* at the proper time in spring in this area as contrasted to its activity in the San Joaquin Valley. The most likely explanation would seem to be a differential effect of the climates on the scale host and *Aphytis*: the scale's life cycle is delayed by about three weeks at the Willows and Orland locations, and *Aphytis* becomes abundant and develops great activity about five to six weeks later than it does in the more southerly locations. In both areas, *Aphytis* overwinters in small numbers as a result of depletion during the hot, dry summer. There is a definite accumulation of *Aphytis* in the pupal stages during the winter period, and it is suggested that the climatic conditions necessary for emergence from these pupae and for resumption of breeding on a broad basis are sufficiently delayed in the Willows-Orland area to account (in part at least) for the observed differences in parasite effectiveness.

Detailed biological studies based on data taken at least twice each month during the period in question could answer this question in a general way; these data would need to be correlated with accurate on-the-spot meteorological data in the trees.

It seems plausible that the scale, which always has two generations a year, is handicapped very little if at all by the shorter season in this more northern area, whereas the number of generations of *Aphytis* may be definitely reduced.

Another explanation of differences in commercial marking of fruits could lie in the strong indication that at the more northerly locations the same densities of scales cause a more severe discoloration of the fruits. This would give a higher commercial cullage even if densities per branchlet were relatively low.

There are other possible explanations of the poor showing of *Aphytis* at these two locations. Area-wide aerosol insecticide applications for mosquito and fly control have been practiced to some extent in Willows, and we have strong observational evidence that this practice prevents successful action by *Aphytis*. Also, for the past two years the heavy cover of dry weeds, grass, and additional piled refuse beneath the olive trees at the Orland location has been destroyed by burning. This could have nearly annihilated the *Aphytis*, which are in any event under stress for survival during the summer period. The severity of such burning on the scale applies also, but perhaps to a lesser extent than is true with *Aphytis*.

DDT-Treated (*Aphytis*-Free) Check-Method Studies

Use of DDT-treated, *Aphytis*-free control trees (as used by DeBach, 1955) in association with each of seven representative biological control groves was initiated in the fall of 1957 as a means of appraising the degree of control by Persian *Aphytis*. In such situations the parasite was held at a low non-functional level by use of DDT, although the DDT treatment did not maintain continuously a completely parasite-free condition, as the surrounding trees had an abundance of *Aphytis* which continued to move into them. One plot was later lost, leaving six; these were in Madera, Fresno, and Tulare

counties (tables 21, 22, 23). Two trees were used in each grove and were treated once in the fall and twice or more in the winter and early spring (depending upon reappearance of *Aphytis*); timing was such as to avoid treating the scale crawler populations. Treatments were continued through

TABLE 21

PERCENTAGE OF COMMERCIALY MARKED OLIVES IN TEN OLIVE GROVE BLOCKS UNDER BIOLOGICAL CONTROL BY *APHYTIS* IN TULARE, FRESNO, MADERA, AND GLENN COUNTIES
(See table 22 for direct comparison with *Aphytis*-absent condition for the pertinent groves.)

Location	Number of fruits examined	1955	1956	1957	1958	1959	1960
Whitney (Exeter).....	500*		...	92.0	91.6	10.0*	...
Kirkpatrick (Lindsay)....	500		...	0.8	0.0	†	1.0
Long (Seville).....	500		...	0.8	11.0	0.6‡	0.0
Bell (Hills Valley).....	1,200	23.7	3.6	0.02	0.02	1.4	0.3
Duncan (Herndon).....	500	3.8	5.4	4.4	27.4	7.4§	0.4
Bell (Clovis).....	500		...	1.0	2.0	2.6	2.0
Oberti (Madera).....	500		...	22.2	60.2	4.4	1.0
Oberti-Sheeler (Madera)....	500		...	1.0	17.8	0.2‡	...
N. Colusa St. (Willows)...	500		...	49.1	41.4	12.0	26.7
"A" Street (Orland).....	500		...	9.4	10.8	9.4	33.4

* 100 fruits (1 tree only available) in 1959.

† Fruits picked prior to sample date, previously observed to be no greater than 2 per cent.

‡ Interference by oil treatment in 1959 but previous parasitization in the spring had assured a high level of control.

§ Oil treatment for black scale made, but due to timing and early spring effectiveness of *Aphytis* the effect on the olive scale was not great.

|| Grass fires scorched many limbs in the trees, probably severe on *P. oleae* but more so on *Aphytis*.

TABLE 22

PERCENTAGE OF COMMERCIALY MARKED OLIVES IN SIX OLIVE GROVES, ON TREES KEPT *APHYTIS*-FREE FOR THREE YEARS BY DDT, IN FRESNO, MADERA, AND TULARE COUNTIES
(See table 21 for direct comparison with *Aphytis*-present condition for the pertinent groves.)

Location	County	Number of fruits examined	1958	1959	1960
Kirkpatrick (Lindsay).....	Tulare	200	0.5	*	93.0
Long (Seville).....	Tulare	200	12.0	†	79.0
Bell (Hills Valley).....	Fresno	200	6.0	42.0	85.2
Duncan (Herndon).....	Fresno	200	52.0	93.5	98.0
Bell (Clovis).....	Fresno	200	8.5	74.5	100.0
Oberti (Madera).....	Madera	200	83.5	92.0	98.5

* Fruit picked by grower prior to sample date; scale previously observed to be markedly increasing.

† Interference by oil treatment, scale previously observed to be markedly increasing.

the spring of 1960, but were not required during the summer periods because summer weather prevents a build-up of *Aphytis*.

DDT was applied as a spray at the rate of 2 lbs. of 50 per cent wettable powder per 100 gallons of water for the 1958 treatments. Starting in January, 1959, applications were made at the rate of 4 lbs. of powder per 100 gallons of water. Approximately 15-25 gallons of material were applied per tree, depending on tree size. Thorough coverage was the only criterion. Limbs, trunks and foliage were covered well.

TABLE 23

AVERAGE NUMBER OF LIVE, MATURE FEMALE SCALES (ALL OR MOST OF THE POPULATION) PER BRANCHLET ON DDT-TREATED, *APHYTIS*-FREE TREES, CONTRASTED WITH DENSITIES IN SURROUNDING BIOLOGICAL CONTROL BLOCK OF TREES

Location	1958		1959				1960				Net change as per cent of densities in fall of 1958		1960 ratio of densities, DDT: <i>Aphytis</i>
	Fall		Spring		Fall		Spring		Fall		DDT trees	<i>Aphytis</i> trees	
	DDT trees	<i>Aphytis</i> trees	DDT trees	<i>Aphytis</i> trees	DDT trees	<i>Aphytis</i> trees	DDT trees	<i>Aphytis</i> trees	DDT trees	<i>Aphytis</i> trees			
Kirkpatrick (Lindsay)	0.0+	0.0+	0.3	0.3	5.5	1.2	25.5	1.9	67.6	0.9	+676:1	+ 2:1	75:1
Long (Seville)	2.0*	1.6	4.2	9.0	2.7	0.0	12.6	0.0	29.8	0.03	+15:1	- 5:1	983:1
Bell (Hills Valley)	0.8	1.3	10.6	0.1	12.1	0.4	25.6	0.2	90.7	0.1	+113:1	-10:1	907:1
Bell (Clovis)	1.2	3.0	12.4	0.2-	43.9	0.5	55.6	1.9	287.8	2.5	+ 85:1	- 3:1	140:1
Duncan (Herndon)	2.0	3.8	38.1	3.2	134.0	0.7	60.4	0.0+	169.8	1.5	+240:1	1:1	113:1
Oberti (Madera)	16.9	11.6	23.9	3.4	43.5	0.4	120.3	0.6	204.2	0.5	+ 12:1	-23:1	408:1

* Treated with oil through error of grower in June, 1958, killing many scales. The treatment was incorporated with a hormone spray and was unnecessary for olive scale control as the very high parasitization had decimated the scale population during April and May, prior to oil application. The DDT treatments in these trees were begun one scale generation later than in the other groves (original test trees proved inaccessible in winter).

At the beginning of this study, the trees selected for DDT treatment had densities of scales roughly equivalent to those of the surrounding trees of the biological control blocks. The first post-treatment samples were taken in the summer of 1958 and were continued on a bi-annual basis through the spring and fall of 1960, at which time the study was discontinued. Some of the trees were severely affected.

Table 23 shows the population figures for the *Aphytis*-free trees and for the *Aphytis*-present trees. Tables 21 and 22 give the comparable percentage of culled fruits from the two conditions for each grove. The contrasts are striking, and show the high degree of control.

Aphytis had been present for various periods in these groves when the comparison trees were first treated with DDT. This in part explains the variations in densities between the groves at the first count-date following initiation of the tests—that is, the counts for the fall of 1958 (table 23). The densities in *Aphytis*-free and *Aphytis*-present trees after the first spring period were relatively comparable in all the groves, however, and only in the Oberti grove were densities high. This grove had only recently been taken off an ineffective treatment program and the block of trees turned over to biological control and use of *Aphytis*.

By the spring of 1959 there was a comparatively substantial increase in densities of scales in the *Aphytis*-free trees, including the Kirkpatrick grove where densities had been so very low at the initiation of the tests (because of previous parathion treatment) that even after this increase densities were still very low. In the *Aphytis*-present trees there was no increase in densities of scales except in the Long grove—a grove which was particularly conducive to scale increase that year. The increase in this grove was somewhat greater in the *Aphytis* trees than in the *Aphytis*-free trees, and was no doubt due to simple tree variation which was seen to be reversed by the action of *Aphytis* in 1959 and 1960 (see page 613). In the other instances at this early date (spring, 1959) *Aphytis* demonstrated an ability to hold the previously low densities at their former levels or, in the case of the Oberti grove, to reduce the density to one-third its original level.

If the progress is followed further, brood by brood, a mounting contrast between the *Aphytis*-free and *Aphytis*-present conditions can be seen; by the spring and fall of 1960 the contrast had become enormous. In all six groves *Aphytis* had held the densities to commercially acceptable levels—lower than at the initiation of the tests, in most instances. In the DDT-treated, *Aphytis*-free trees, however, the scales had increased to the point of heavily-overlapping encrustations, with increases in density from 12 to 676 times that at the initiation of the tests. A comparison of the 1960 parasite-free and parasite-present densities shows that the maximum contrast was 993:1 and the minimum 75:1. Such data, more unmistakably than that which can be obtained by any other presently known means, reveal the capacity of *Aphytis* for controlling *P. oleae* even in climatic environments which are very hazardous to the parasite during the summer period.

The contrast in densities of scales per branchlet is more striking than the records of culled fruits would indicate, although there is also striking contrast in the latter, as seen in tables 21, 22. The reason for this is the

marked preference of crawlers for fruits during the fall period and the fact that a few scales on a fruit, concentrated there even in low-density trees, may cull the fruit just as readily as may many scales.

Plate 2, *c* to *f* (p. 548), shows the general contrast in growth and vigor and in scaliness of fruits and leaves between the *Aphytis*-free and *Aphytis*-present trees at the Clovis grove. It is seen that leaf-drop and die-back had already started in the DDT-treated trees, while the trees in the *Aphytis* block remain dense in foliage and in vigorous shoot growth. Regrettably, pictures cannot reveal the full extent of the contrast which is so readily discernable to the observer.

Influence of Insecticidal Drift on *Aphytis*

General observations for several years prior to the presently-reported tests had suggested that drift of insecticides from adjacent areas being treated may be a reason for reduced effectiveness or complete failure of control of olive scale by *Aphytis*. For example, in the Graydon olive grove at Earlimart, which was under experimental control by *Aphytis*, it was observed (and substantiated by population counts) that the scales on olives were progressively more abundant toward an adjacent grape vineyard from a position about six rows in from the vineyard. The vineyard had been treated with insecticides by airplane. In the years following the general establishment of Persian *Aphytis*, those olive trees having heavily encrusted infestations of *P. oleae* have been almost entirely border trees or small plantings which are surrounded by agricultural crops receiving insecticidal applications, often by airplane dusting. Some examples of unusually persisting heavy infestations of scales were in the few cities or towns which were using aerosol fogging applications for mosquito control.

DeBach and Bartlett (1951), Bartlett (1958), and others have reported the detrimental effects of many insecticides on various natural enemies. DeBach and Bartlett's work demonstrates that many of the very small Hymenopterous parasites, such as *Aphytis* spp., are very susceptible to such materials.

To gain some idea of the influence of drift of DDT from adjacent airplane dusting operations on effectiveness of Persian *Aphytis*, several tests were made in 1957. Experience with applications of DDT and parathion by ground spraying equipment on trees in the groves under our regular study program furnish evidence concerning such contrasting methods of application. It became apparent that ground spraying operations (at least those using DDT and parathion) do not directly affect Persian *Aphytis* which are more than three or four orchard rows way. Ground-rig spraying with DDT was used as the means of establishing *Aphytis*-free trees for comparison with the adjacent trees where *Aphytis* activity was not impaired.

The first test on effects of airplane dusting was conducted to determine the specific mortality caused by drift of DDT at the time of the application. The second test was to determine the residual toxicity of the material deposited on adjacent olive leaves. Tables 24 and 25 give the results.

During the tests, results of which are presented in table 24, there was almost no wind at the time (early morning). *Aphytis* were exposed in one-

half pint ice-cream cartons with tops and bottoms covered with fine organdy cloth, and the organdy probably excluded a part of the drift. Newly-emerged adult *Aphytis* were used in each unit, and three units were used for each test. The test is indicative only of possible adverse effects on *Aphytis* under conditions more favorable for drift. The absence of wind and the partial exclusion of drift by the organdy were factors contributing to the low effect

TABLE 24
MORTALITY OF PERSIAN *APHYTIS* EXPOSED TO DDT
DRIFT FROM AIRPLANE DUSTING OF COTTON

Distance from treated area	Number of <i>Aphytis</i> exposed	48-hour mortality per cent
Adjacent, 8 feet.....	217	96.8
Line of slight drift, 100 feet.....	249	51.0
Line of slight drift, 300 feet.....	234	30.4
Control, in automobile.....	246	28.5

in this test. Nevertheless, about 50 per cent mortality was experienced 100 feet away from the application, as compared with only 28.5 per cent for the control (which was kept inside a closed automobile), and with 96.8 per cent mortality 8 feet from the edge of the treated area.

TABLE 25
MORTALITY OF PERSIAN *APHYTIS* WHEN EXPOSED
FOR FOUR DAYS TO DDT RESIDUE ON LEAVES
OF OLIVES ADJACENT TO COTTON DUSTED
BY AIRPLANE

Age of residue, in days, at beginning of exposure	Number of <i>Aphytis</i>	Per cent mortality	
		Clean olive leaves	Olive leaves having DDT residue
5.....	300	13.5	76.6
11.....	300	9.9	96.1
31.....	300	39.4	63.4
39.....	300	21.3	14.5

The insects used for the test on 31-day-old residue (table 25) were obviously senile or weak (nearly 40 per cent died in the control) and thus no conclusion is possible regarding that age-class of residue. The difference in results of the two groups suggests a toxicity lingering up to 31 days, but toxicity up to 11 days was definite. It is obvious from these tests that *Aphytis* in small groves or in border trees receiving insecticide drift at frequent intervals from several sides, or from extensive area-treatments on windy days, could be annihilated or reduced to ineffective low levels—considering also the severe stress they face each summer from the climatic pattern. *Aphytis* may withstand the latter alone, but it cannot succeed under both these adverse factors.

General Surveys on Control by *Aphytis*

At the time of the general colonization of *Aphytis* in 1953, *P. oleae* infestations where releases were made were classed as light, medium, or heavy density by W. W. Wiard and others associated in this distribution program. During this year some 300 separate colonizations were made, and others were made in later years.

In the fall of 1956 the senior author and Mr. Wiard revisited thirty of the above locations, particularly those situated in cities or towns where agricultural insecticide operations were likely to be of less impact on *Aphytis*. In the fall of 1960 the authors again visited the sites covered in 1956, as well as a number of others which had been rated in 1953 as to infestation by *P. oleae*.

At the time of these two surveys, samples of olive fruits were rated as to infestation by *P. oleae*. The activity of *Aphytis* subsequent to the time of the colonizations appears to be the only broadly valid explanation of the differences in infestations in 1953 and in 1960, although other explanations may apply to reductions in specific cases. In addition to the data from the specific surveys, a great many unrecorded observations by the authors, as well as by various county agricultural officials and the farmers and homeowners themselves, attest to the striking reduction (comparing 1960 conditions with 1952) in the pest status of this scale insect throughout the San Joaquin Valley.

Of the 30 infestations surveyed in 1956, olive fruits were available from 23. Thirteen of the 23 had had heavy to very heavy *P. oleae* infestations in 1953. The remaining 10 locations had had medium infestations. The 1956 ratings were: 10 of the 23 were under fair control; 9 of the 23 experienced reductions in density but were not under control; 4 of the 23 showed no detectable reductions.

Of the four locations where no reduction in densities was apparent, two were adjacent to cotton fields which subsequently became part of housing development areas, after which the cotton was no longer grown; both of these locations then showed evidence of increased *Aphytis* activity and good control of the scale. A third location was in a backyard area having a severe black scale infestation and ant activity in 1956. The fourth location consisted of olives interplanted with walnuts, but in this case insecticidal treatment did not seem to be involved (see p. 607).

Table 26 presents the records on culled olive fruits from the locations covered in the 1956 and 1960 surveys. If we regard 45 to 50 per cent culls as meaning little or no control by *Aphytis*, we see that in 1960 only 6 locations among the 35 visited in the San Joaquin Valley area exceeded that level. These are the Kahl location, Le Grand Road, Madera—66.7 per cent; a Kearney Park location—48.0 per cent; the Seldon property in Lindsay—45–50 per cent; the Whitney location near Exeter—80.0 per cent; the Cunningham ranch at Bakersfield—92.0 per cent and a location in the vicinity of Banducci Corner, near Bakersfield—96.0 per cent. The Kearney Park trees were adjacent to cotton and also shaded by adjacent eucalyptus trees; the Kahl location in Madera and the two locations near Bakersfield

were adjacent to cotton plantings. The single tree at the Seldon property in Lindsay was in a dry back lot and was located next to a barbecue pit where fires are built—a situation too severe for *Aphytis*, if not for *P. oleae*. This last statement is supported by the fact that a heavy scale infestation on privet at the same location, but in the well watered front lawn area, has been brought under good control.

The Whitney location near Exeter presents the chief problem, however. Here, densities on the single remaining tree returned to a high level in 1960 from a period of temporary control in 1959, and we have no explanation as to why *Aphytis* has responded so poorly. Detailed records show conclusively that *Aphytis* at this location is more retarded in spring activity than is typical of the area (p. 607).

In comparing the 1960 general status of infestations with that of 1956, it appears that the few places where no control was experienced in 1960 are similar to those where no control was experienced in 1956, with respect to apparent reasons for the lack of control—adjacency to cotton being the predominant reason for failure. However, in general there were many more locations, relatively speaking, which had only an intermediate degree of control, and as a result there were fewer with complete control in 1956 (in contrast to the improved status in 1960).

Of the infestations having an intermediate status in 1960, some were in locations where drift of insecticides was a probable cause of reduced *Aphytis* activity, while others were in dry, vegetatively barren locations, the olive trees being either single trees or a single row of trees. This suggests that *Aphytis* may be favored in a group planting of well-watered trees over poorly-watered trees, or over isolated trees in a dry, summer-scorched area where drift or movement of *Aphytis* away from the trees could be a factor.

One point regarding these surveys is certain: there was a very marked improvement in the degree of control in general, comparing 1956 with 1953, and 1960 with 1956. Fully satisfactory commercial control was evident at a great many of the locations, and the reasons for failure at other places were apparent in most instances.

In addition to the places included in table 26 the survey in 1960 was extended to Kings county, but the results are not tabulated because no comparable figures for 1956 are available. Seven infestations of *P. oleae*, originally medium to very heavy in density, were visited in this county. Six of the locations involved olives, in part, and all except one were under a considerable degree of control by *Aphytis*. Three were close to cotton fields and had somewhat unsatisfactory percentages of cull fruits, although only one fell in a high cullage category.

Data were also obtained at a number of locations in Glenn and Butte counties in the Sacramento Valley. The control on olives by *Aphytis* was less striking in these locations. This seems due partly to retarded spring reproduction by *Aphytis* and partly to a different severity of discoloration of the fruits by scales of the same density and age-class (contrasting the status in the northern Sacramento Valley with that in the southern San Joaquin Valley).

No quantitative data regarding densities on miscellaneous host plants

in backyard and park areas were obtained, but in general the scale was already under fairly good control on these hosts as early as 1956, and this was even more generally true in 1960. Apricot, plum, peach, Toyon, rose, apple, ash, lilac, cotoneaster, oleander, privet and many other hosts were observed. Privet (and occasionally Oregon grape, or *Mahonia*, and ash) was the only host plant on which scales persisted to any degree at all and many plantings of privet were relatively clean both in 1956 and in 1960. It is worth noting that the habit of growth and the pruning method used for privet are such as would be least conducive to control by *Aphytis*. New vigorous leader growth (which creates a dilution effect) is automatically pruned back and the segments containing the old overlapping scale coverings—that is, more old, short, spur growth—is retained. The resulting denseness of foliage is also conducive to scale increase.

The status of *P. oleae* on most ornamental shrubs and backyard shade and fruit trees at present is very satisfactory. It seems safe to say that the total value of Persian *Aphytis* in protecting such plants is far greater than that which would result if all the olive groves were to come under complete control by this method. This latter would be a boon to the olive grower and one he would recognize and surely welcome, yet the landscaping benefits to the homeowner and to public properties have already been accomplished, although they have been generally unnoticed by any except specialists familiar with this program.

POSSIBLE CONSERVATION AND AUGMENTATION OF CONTROL BY *APHYTIS*

General Possibilities

The activities of Persian *Aphytis* cause a very marked reduction of *P. oleae* infestations in certain years and sometimes entirely adequate commercial control, but only in instances does the parasite give adequate control year after year. Present research, therefore, is directed toward discovering methods for utilizing *Aphytis* to better commercial advantage. Several possibilities are presently indicated, and among the more promising are the following:

1. Augmentation of the action of *Aphytis* by manipulating the environment, or by adding stocks of *Aphytis* when their numbers have been drastically reduced.
2. Supplementing the activity of the parasite by use of limited insecticide programs designed to add to the control achieved by *Aphytis* without impairing the parasite's effectiveness.
3. Improvement of grower-management practices, such as employment of more extensive and more regular (annual) pruning, or use of a system of irrigation which might conserve the parasite population at times critical for it.
4. Introduction of other natural enemies of *P. oleae*. Three additional species appear to be established but only one has shown any success as yet; their introduction and status will form the subject of a later paper.

TABLE 26
SURVEY OF CULL FRUITS OF OLIVES IN 1956 AND 1960, SHOWING
PROGRESS OF GENERAL CONTROL BY *APHYTIS*

County	Location	1956		1960		Remarks, and status of scale prior to release of <i>Aphytis</i>
		Number of fruits	Culls <i>per cent</i>	Number of fruits	Culls <i>per cent</i>	
Stanislaus	Griffith at Hughson	50	4.0	100	26.0	Recent years receiving airplane spray treatments used for adjacent almonds—a program not in use in 1956. Decline in control.
Stanislaus	Griswold and McHenry Aves., Modesto	No data obtained		100	1.0	Good control.
Stanislaus	1306 Rouse St., Modesto	No data prior to releases		100	1.0	Good control. <i>Aphytis</i> released 1957.
Stanislaus	Scenic Ave., Modesto, $\frac{1}{2}$ mi. W. Agric. Bldg.	No data		100	0.0	Few <i>P. oleae</i> present. Good control.
Stanislaus	Franklin and Walnut, Modesto	No data		100	19.0	Degree of infestation unexplainable. Dry, abandoned lot.
Merced	Fluetch, 22nd St., Merced	100	30.0	250	2.5	Susceptible variety as to discoloration. Good control.
Merced	E. 21st St., Merced	50	24.0	Olive not present.		Other host plants under good control.
Merced	Fullerton, Le Grand	No data		100	1.0	Good control.
Merced	Turner, Le Grande	No data		100	0.0	Good control.
Merced	Canal Farm Inn Los Banos	50	34.0	100	26.0	Reason for poor control unknown.
Merced	523 Washington St., Los Banos	50	46.0	50	0.0	Good control, but same scale density as at Hwy. 33 and West Avenue.
Merced	Cunha orchard, Gustine	42	16.0	50	4.0	Good control.
Merced	Hwy. 33 and West Avenue, Gustine	50	96.0	100	13.0	Susceptible variety as to discoloration; better control as to density.
Merced	G. Murray, Gustine	25	12.0	100	0.0	Good control.
Madera	120 Cypress, Madera	50	84.0	Trees removed		In 1957 and 1958 <i>Aphytis</i> gave good control.
Madera	805 $\frac{1}{2}$ Austin St., Madera	50	30.0	100	0.0	Good control. Area-wide fly control stopped.
Madera	Montgomery, 3 mi. S. Madera	50	0.0	200	14.5	Black scale unusually heavy in 1956, trees almost dying—not supporting olive scale. Single row of olive trees. Control not fully adequate, adjacent to mosquito control operations.
Madera	De Caesare, Madera	100	5.0	100	0.0	Good control.
Madera	Riggs Nursery, Madera	50	10.0	100	1.0	Good control. Originally medium infestation.
Madera	913-15 W. 4th St., Madera	Not visited		100	1.0	Good control. Originally heavy infestation.
Madera	318 N. "B" St., Madera	Not visited		100	0.0	Good control. Originally heavy infestation.

County	Location	1956		1960		Remarks, and status of scale prior to release of <i>Aphytis</i>
		Number of fruits	Culls <i>per cent</i>	Number of fruits	Culls <i>per cent</i>	
Madera	610 Ninth St., Madera	Not visited		200	2.0	Good control. Originally heavy infestation.
Madera	Ave. 15 and Rd. 28, Madera	Not visited		150	0.0	Good control. No pre- <i>Aphytis</i> rating.
Madera	Kahl, Le Grand Rd., Madera	Not visited		150	66.7	No control. Single row olives with cotton on both sides.
Fresno	2982 E. Olive St., Fresno	50	40.0	130	0.0	Good control.
Fresno	1004 W. Clinton, Fresno	50	16.0	100	0.0	Good control.
Fresno	2 mi. S. Clovis on Clovis Ave.	100	35.0	100	1.0	In 1956, cotton planted adjacent; in 1960, is part of housing development.
Fresno	Kearney Park, west side	Not visited		200	1.5	Originally heavy infestation, 90-100 per cent culls. Good control at this open area and away from cotton.
Fresno*	Kearney Park, east side	Not visited		50	48.0	Area shaded by palms and eucalyptus, and also across road from cotton. No control. Originally heavy infestation.
Tulare	Seldon, Lindsay	Not visited		75	(45-50)	Dry back lot. Single tree, next to barbecue pit. Privet in front lawn (watered) now under good control.
Tulare	300 block, Honolulu St.	Not visited		100	4.0	Satisfactory control.
Tulare	Greer, Lindsay	Not visited		150	2.0	<i>Aphytis</i> released in 1957. Good control, but spots are intermediate.
Tulare	Rocky Hill location	Visited and heavy scale present		No fruits, but scale fairly abundant		Abandoned single row of trees on dry hillside. Too severe for <i>Aphytis</i> but scale does survive.
Tulare	Houghton, Lindsay	Not visited		Intermediate scale densities		<i>Aphytis</i> released only in 1959, previously treated. Control not yet effected.
Tulare†	Whitney, Exeter	100	85.0	100	80.0	Control at this location only in 1959. See previous sections.
Tulare	Cook ranch, Exeter	50	0.0	Not visited		Heavy infestation originally. Good control in 1956.
Kern	5300 Niles Rd., Bakersfield	10 (no more available)	0.0	90	0.0	Heavy infestation originally. Good control.
Kern	Cunningham ranch Bakersfield	50	100.0	100	92.0	Single row of trees between cotton fields. No control.
Kern	½ mi. N. E. Banducci Corner, Bakersfield	Not visited		100	4.0	Adjacent to citrus. Satisfactory control.
Kern	2 blocks south of previous location, Bakersfield.	Not visited		100	96.0	Cotton on three sides. No control.

* See also data for Clovis and Hills Valley in other sections.

† See also data for Long, Kirkpatrick, Whitney locations in other sections.

While Schtschepitilnikowa (personal communication) has reported marked increase in parasitization of San Jose scale in Russia by a related parasite, *Aphytis proclia* (Walker) (Syn. *A. diaspidis* (Howard) ; see Mercet, 1932), through the employment of a cover crop of *Phacelia* which furnishes nectar for the parasite and thus greatly prolongs its egg deposition period, such a procedure seems less promising with Persian *Aphytis*. The Persian *Aphytis* under most favorable conditions in the laboratory deposits most of its eggs rather quickly and extending adult life would not necessarily add greatly to fecundity. Furthermore, field tests in which strips of waxed paper covered with thousands of droplets of honey were dispersed throughout a tree did not permit survival of adult *Aphytis* for twenty-four hours in a hot, dry environment, such as is often encountered in the San Joaquin Valley, whereas addition of humidity did. Consequently, no tests employing nectar-producing cover crops have been conducted.

The employment of heavier and annual pruning of the trees could have a very beneficial result insofar as older wood having heavier scale concentrations would be replaced by new, clean leaders extending several feet from the old sources of scales. This gives a maximum of wood bearing fruits at positions rather hazardously distant from the major sources of crawlers. When parent scale densities are limited by *Aphytis* to generally low levels, as often happens, this practice could make the difference between inadequate and fully adequate commercial control without the use of insecticides. Up to now no specific tests have yet been conducted on this question although tests are advisable. However, Hartmann, Optiz and Hoffman (1960) have shown that pruning should be kept to a minimum to insure maximum yield in olives. This would preclude maximal utilization of this means of augmenting control of scales by *Aphytis*.

It is conceivable that increasing the general humidity by growing a cover crop, and/or by use of alternating spot-method sprinkler irrigation so that some spots in all areas are continuously receiving water during the hottest periods of the day in July and August, might increase the carry-over of *Aphytis* through the adverse summer period. This would suppose a movement of *Aphytis* from tree to tree toward the more humid trees. While no tests have been conducted along this line, we are presently employing an automatic humidifier when the humidity falls below 50 per cent in two trees in one grove in order to see if the effectiveness of *Aphytis* will be increased. This test should answer the question as to whether the scale or the parasite will be favored most, and will also furnish additional evidence of the role of humidity in *Aphytis* success or failure.

Presently, in an orchard treated yearly with oil and in which *Aphytis* remains well established in spite of the oil treatments, we are keeping two comparison trees treated frequently with 4 per cent DDT spray in order to curtail effective action of *Aphytis*. The object is to learn if the oil spray alone is responsible for achieving the high degree of control obtained, or if it is only the combination of oil and activity of *Aphytis* that is responsible. The test has not been under way long enough to answer the question but the particular oil used seems to give good control alone. Tests are also contemplated in which oil treatments will be employed only on a strip-treat-

ment basis similar to that successfully employed by DeBach (1958*b*) in the integrated biological and chemical control of purple scale, *Lepidosaphes beckii* (Newm.), by *Aphytis lepidosaphes* Comp. on citrus. On olives such a procedure might prove to be necessary during certain years only, while *Aphytis* alone would be adequate at other times.

Fall Releases of *Aphytis*

The method of integrated insecticide usage may prove commercially useful, but because of the fact that some growers are reluctant to go back to any form of oil treatments, we feel it more feasible at present to fully

TABLE 27

NUMBERS OF *P. OLEAE*, PERSIAN *APHYTIS* AND PERCENTAGE OF PARASITIZATION IN SUPPLEMENTING FALL RELEASE BLOCKS AND CONTROL BLOCKS OF OLIVE TREES*

Location	Sample dates	Release block			Control block		
		Mature ♀ scales	<i>Aphytis</i>	Parasit- ization	Mature ♀ scales	<i>Aphytis</i>	Parasit- ization
				<i>per cent</i>			<i>per cent</i>
Wilkerson (Lindsay)	11-3-59.....	2,042	4	0.2	491	0	0.0
	2-1-60.....	455	15	3.3	1,365	4	0.3
	4-20-60.....	906	339	37.4	593	5	0.8
Long (Seville)	11-3-59.....	33	1	3.3	77	0	0.0
	2-2-60.....	37	9	24.3	65	0	0.0
	4-19-60.....	1	1	100.0	52	33	63.4
Bell (Hills Valley)	11-3-59.....	21	3	14.3	22	0	0.0
	2-3-60.....	36	9	25.0	12	0	0.0
	4-19-60.....	6	5	83.3	8	7	87.5
Bell (Clovis)	11-9-59.....	32	1	3.1	61	2	3.3
	2-3-60.....	70	18	25.7	83	0	0.0
	4-19-60.....	26	21	80.7	69	53	76.8
Duncan (Herndon)	11-2-59.....	135	15	11.1	15	0	0.0
	2-4-60.....	65	8	12.3	41	0	0.0
	4-20-60.....	11	10	90.9	4	4	100.0

* Four trees were used as the sample unit in each block and 12 leaves from each of 12 twigs from each tree constituted sample size.

explore the possibilities of using supplementary fall releases of *Aphytis* without employment of any chemical treatments. With this objective in mind, we conducted tests with fall releases of *Aphytis* in 1959, and continued them on an increased basis in 1960. The results from the fall releases of 1959 were very encouraging, but the winter was so mild and the early spring so favorable that year that the *Aphytis* present at lower densities where supplementary releases were not made increased very rapidly and finally almost equalled the densities in the blocks where supplementary fall releases were made. Table 27 shows the sharp contrast between the *Aphytis* in the release blocks and in the control blocks, up to early February.

Six biological control orchards were selected for this study. Each plot, consisting of 36 trees (a block of six rows in each direction), received *Aphytis* liberations from insectary-produced material during the months of October, November, and early December, 1959. Each tree received 1,000 *Aphytis* at approximately 10 to 14-day intervals until a total of five to six thousand had been released per tree (7,000 at the Wilkerson Grove).

Samples from the release plots were taken from the four centrally located trees. Samples from four control trees outside the release area were taken concurrently. It is obvious that natural movements of parasites from release areas to non-release areas (although areas were six to eight rows apart) may, within several months, tend to destroy the experimental design intended. Hence, samples of parasitization made shortly after intense parasite activity is initiated in February or early March of the following year give a better estimate of the value of releases than do samples taken at later times. Table 27 shows the progress of parasitization by *Aphytis* from late fall through the peak of *Aphytis* activity in mid-April, 1960.

The data given in table 27 suggest that the most critical time for evaluation of this procedure (in 1960) probably would have been in early March, rather than early February or the latter half of April. Unfortunately, samples were not taken at that time. The sample in November was too early for major significance, although parasites were found in the control sample only at the Bell (Clovis) location, whereas parasites were encountered in *every* release block sample. From February 1 to 4, parasitization in the release block samples was generally markedly higher: there was an increase from 0.2 to 3.3 at the Wilkerson grove; from 3.3 to 24.3 at the Long grove; from 14.3 to 25.0 at the Bell (Hills Valley) grove; from 3.1 to 25.7 at the Bell (Clovis) grove; and from 11.1 to 12.3 at the Duncan grove. Only a slight increase for the same period was recorded for the control sample at the Wilkerson grove, while no parasites were encountered in any of the samples from the other groves. This is clear evidence of initially beneficial results from the fall releases of *Aphytis*.

April 19 and 20 data are too late for critical evaluation purposes but these data are of interest with reference to the Wilkerson grove, where, on February 1, the parasitization was still low at 3.3 per cent in the release block and only 0.3 per cent in the control block. On April 20 the parasitization in the release block had risen to 37.4 per cent, while the control block sample was still only 0.8 per cent. Thus, in spite of apparently adverse conditions, the release of additional *Aphytis* caused a sharp, though belated, increase in parasitization.

It is obvious that parasitization in the release blocks and control blocks had somewhat equalized by late April, but it is pertinent that the critical time for evaluation of the effective economic parasitization by this parasite is three to four weeks earlier. Therefore, the achievement of a high level of parasitization earlier in the season when a fall release program is used could mean the difference between adequate commercial control by *Aphytis* and the employment of an insecticide program.

Records obtained over a period of several years and based on densities of scales and parasitization (particularly in late March), as well as records

of commercial damage to fruits, will be needed to fully evaluate this approach—a program which has given promising results to date. The cost of such a program could conceivably prove less than the cost of standard insecticide operations, and the hazards associated with insecticides and the possibilities of creating other pest problems would be avoided. However, if *Aphytis* continues to improve in its effectiveness, a fall release program may not be needed. Again, the general establishment of *Coccophagoides* in olive groves may make such releases unnecessary. A program to accomplish this establishment is now underway.

SUMMARY

The Aphelinid parasite *Aphytis maculicornis* (Masi), which attacks olive scale, *Parlatoria oleae* (Colvée), was collected by A. M. Boyce in Iran and Iraq and shipped to R. L. Doutt of the Department of Biological Control of the University of California in 1951. This stock, subsequently termed Persian *Aphytis*, was colonized by Doutt in California in early 1952. Immediately promising parasitization results were obtained in experimental groves (Doutt 1954).

From 1952 to 1960, more than 27 million parasites were colonized in 24 counties of California. Continuing studies showed that the degree of control required for full commercial satisfaction is stringent because of the concentration of scale crawlers on the fruits during the early fall period. Partly for this reason, partly because the summer period is too hot and dry and therefore marginal for survival of adult *Aphytis*, and partly because of disturbances from drift of insecticides, commercial control is not consistently satisfactory; it is variable by years, locations, and cultural conditions in olive groves. Adverse meteorological conditions are more severe on the parasite than on the scale, although the latter is adversely affected also. Because of this adversity, *Aphytis* is entirely unsuccessful on the summer females. The degree of weather severity on the scale determines in part the extent of its population increase during the summer generation of relaxed parasite pressure, and the degree of severity on the parasite determines the latter's capacity to build back to sufficiently high levels early enough each spring to give commercial control. All these factors are interrelated. Mortality of young scales (exclusive of natural enemy action) was higher in the spring brood than in the fall brood for the years studied. The humidity pattern at the time of crawler activity and young settled-stage development is more favorable during the fall brood than during the spring brood.

Intensive population dynamics studies in three groves, and biannual population analyses in eleven groves—mainly in the San Joaquin Valley—showed conclusively that Persian *Aphytis* gives a high degree of commercial control of the scale in many groves. The sharp decline in the heavy infestations of olive scale immediately subsequent to introduction of this parasite in 1952–1953 was a general phenomenon on all of the scale's many host plants. Detailed studies showed that not only did the level of infestation of olive scales bear correlation with parasite activity during the preceding spring of the respective season, but also that this was expressed in part as an action

of the parasite in reducing the realized egg production of the overwintered brood of females to a level below that required for replacement. On the other hand, the summer females maintained a high level of egg production and the absence of *Aphytis* pressure was the only significant explanation of the differences, for *unparasitized* females of the overwintered brood also had an equal fecundity with their summer-brood counterparts. Further, the assignment to *Aphytis* of the key role in control of olive scale within the existing meteorological framework of the environment was established by comparison studies using DDT-treated, *Aphytis*-free trees side by side with *Aphytis*-present trees. In less than three years' time the populations of olive scales on the DDT-treated, *Aphytis*-free trees built up to levels varying from 75 times to 993 times the levels in the respective *Aphytis*-present trees.

Lastly, the very high degree of control of *P. oleae* on a great variety of hosts around dooryards, city streets, and parks is certainly the result of *Aphytis* action. The savings to homeowners and to landscaping values in general is a tremendous accomplishment, although almost unnoticed except by officials and technical staffs familiar with this program. The savings to the olive industry is just beginning to be realized. Greater potential savings are presently precluded in part because of drift of insecticides from adjacent crop lands which are treated by airplane applications. Potentially, the vast deciduous fruit industry in California may have benefited likewise. However, the present program of treating such crops for other pests precludes any claim we might make for biological control of *P. oleae* as a pest of these crops, for under the treatments used olive scale is not of significant occurrence. The total value of this program will surely run into millions of dollars in only a few years. Even where no insecticides are used at all the situation is vastly different today from that of only eight years ago, before the general establishment of *Aphytis*, when this scale created a deplorable condition of heavily-encrusted limbs, twigs and leaves, and a sickly unkempt condition in many of our most useful plants.

This work illustrates the views of Huffaker (in press) concerning the inter-relatedness of the density-independent conditioning forces of environment and the density-dependent governing role of certain natural enemies as agents of control.

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