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SUMMARY

A resting stage without encystment has been found in *Cyclops strenuus strenuus* Fischer from localities in southern Norway, the stage of dormancy being the IVth copepodid stage. The resting period is primarily confined to the summer season, but dormancy may regularly be prolonged for at least 10 months. Environmental factors probably play an important part in the regulation of the resting period. Rapid changes in physical and chemical factors combined with low temperatures are likely to be factors that may initiate revival from dormancy.

Except for the lack of a recognizable cyst the annual cycle of *C. s. strenuus* shows a striking similarity to that of the American *Cyclops bicuspidatus thomasi* Forbes.

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SOME EFFECTS OF METEOROLOGICAL FACTORS ON ALL STAGES OF *APHYTIS LINGNANENSIS*,¹ A PARASITE OF THE CALIFORNIA RED SCALE^{2, 3}

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INTRODUCTION

As times passes it becomes more evident in biological control work that density-independent (usually abiotic) factors may indirectly play as important a role in successful control as density-

dependent (usually biotic) factors. True, in areas more or less optimum for a given pest, only biotic factors may act in such a manner as to bring about control at a low average population density; however, abiotic factors in these areas may not be optimum so far as the natural enemies are concerned, and, hence, control of the pest may be neutralized. Most of the work describing population interactions between hosts and natural enemies developed by biomathematicians has ignored abiotic variations in the environment. It is obvious to the field entomologist that in many, if not most, cases such variation is at times extreme enough to effect seriously either the pest, the natural enemies, or both. When such variations occur at regular intervals (for instance as winters do), then otherwise efficient natural enemies may not be left with an uninterrupted period of sufficient length within which to obtain and maintain control of their host. Clausen (1952) in one of the first general discussions of this problem states, "In temperate regions, enforced hibernation during the winter often brings several complications

¹This newly described species, formerly known as *Aphytis* "A", was imported from China and Formosa. Specimens are on file in the collection of the Department of Biological Control, University of California, Riverside. *Aphytis chrysomphali* (Mercet), a closely related species long established in southern California, made up a small proportion of the field counts. In general, the conclusions made herein with respect to *A. lingnanensis* apply to *A. chrysomphali* as well.

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that may entirely prevent establishment and effectiveness. The introduced species may not be able to withstand the low temperatures, though these are not detrimental to the host. . . . We must consequently recognize, in biological control work, that any pronounced departures in climatic conditions from one which is constantly favorable throughout the year in temperature, rainfall, and humidity is certain to reduce the frequency of success."

The present paper deals with evidence acquired over a six-year period on a parasite which intrinsically is capable of controlling its host at low population levels but in certain areas is prevented from doing so by adverse weather conditions, principally low winter temperatures. Remarkably similar results, differing only in degree, have recently been reported by Lord and MacPhee (1953) in an excellent paper dealing with the ecology of *Lepidosaphes ulmi* (L.) and its parasite *Aphytis mytilaspidis* (LeB.). They showed that natural control of the oyster-shell scale by *Aphytis mytilaspidis* usually occurs in the mild-wintered Annapolis Valley of Nova Scotia but that the severe winters (-20°F . or lower) of central New Brunswick limit the success of the parasite.

In a paper concerning developments toward biological control of the California red scale, *Aonidiella aurantii* (Mask.), by *Aphytis chrysomphali* and *Aphytis* "A," DeBach *et al.* (1950) stated that "there are indications that the California red scale in certain areas . . . may not be so amenable to natural control by *Aphytis* as elsewhere." Additional information gathered up to 1954 emphasized the truth of this statement and has permitted, in part at least, analysis of the factors responsible.

From the field data acquired, it has been consistently evident that *Aphytis* populations in certain areas of southern California are depleted out of all proportion to the California red-scale population during the winter and in some areas at other times of the year. Laboratory studies have shown that low temperatures are the principal cause of mortality. During the remainder of the year in southern California, *Aphytis* populations tend to increase although high temperature-low humidity-induced mortality may occur in summer and fall.

Southern California topography is exceedingly varied and this results in a diversity of environmental conditions within short distances. Mountains and hills serve as barriers to the movement of air currents coming from the ocean as well

as from the desert. Areas which are cut off from the coast tend to be hotter in summer and colder in winter than those along the coast. Figure 1, which shows mountain barrier areas in black, illustrates how climatic zones in the citrus areas are affected by such barriers as well as by their distance from the ocean. The zones indicated in Figure 1 are approximate, but they furnish a fair idea of the citrus areas mentioned in this paper by the designations of coastal, intermediate, or interior. Within each of these zones small local areas may have a microclimate characteristic of one of the other zones.

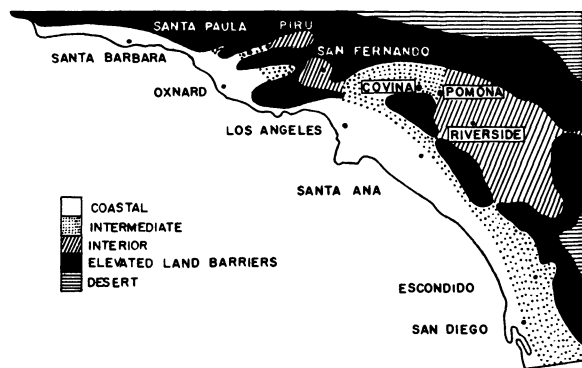


FIG. 1. General climatic zones in southern California citrus areas.

FIELD STUDIES

"[Many insects] accustomed to warm surroundings. . . . soon die even at temperatures well above freezing-point. The cause of death is not understood. It is often attributed to the accumulation of toxic products which at normal temperatures would be eliminated. . . . This type of effect by cold is sometimes termed the 'quantity factor' because it must act for some time before it causes death."—Wigglesworth, 1939, p. 364.

In the early spring of 1949 field observations and counts showed that a high proportion of *Aphytis* pupae were dead. Since that time detailed semi-monthly or monthly counts on live and dead pupae have been made at various stations in southern California. Inasmuch as pupal counts are the most accurate for field-collected material, they, exclusively, will be used in this paper for purposes of presentation. All stages, however, are affected adversely, as will be shown later by laboratory data. These data were all derived from population samples made in completely untreated citrus groves, so effects from insecticides were never involved. *A. lingnanensis* was colonized in large numbers in all test plots and usually became dominant over the original *A. chrysomphali* pop-

ulations within one year. However, *A. chrysomphali* constitutes a small proportion of the field counts. Counts were made by bringing in California red-scale-infested citrus fruits from the field, dissecting under the stereoscopic binocular microscope, and recording live and dead stages of *Aphytis* as well as of the scales.

Differences in mortality between areas. Inasmuch as previous studies on natural control of California red scale by *A. lingnanensis* and *chrysomphali* have indicated that these parasites are more successful in coastal areas than in interior areas, a comparison of the relative pupal mortality in representative groves for the two areas has been made. These data are presented in Table I and represent monthly averages acquired during a four-year period.

TABLE I. Average per cent dead *Aphytis* pupae per month for the period 1950-1953 in a coastal and two interior area groves

	Grove location		
	1. Coastal: warmest winter, mildest summer. Santa Barbara	2. Interior: warm winter, severest summer. Riverside	3. Interior: cooler winter, mild summer. Claremont
January . . .	14	40	25
February . . .	22	52	61
March	56	51	80
April	44	46	84
May	27	27	62
June	28	42	68
July	15	47	26
August	21	24	15
September . .	24	44	26
October	25	18	14
November . . .	34	27	20
December . . .	31	42	25

It is evident from Table I that pupal mortality was considerably greater at the interior stations than at the coastal station, especially from January to June. This winter mortality will be discussed first, followed by a section on differences during the remainder of the year. Weather data were compiled from the records of the Santa Barbara Botanical Garden (coastal area No. 1), the University of California Citrus Experiment Station at Riverside (interior area No. 2), and from the United States Weather Bureau at Pomona for the Claremont region (interior area No. 3).

Winter mortality. An average of 80 per cent or more dead pupae was obtained during the months of March and April at the interior station (No. 3) having the most severe winter climate, whereas the only mortality at the coastal station (No. 1) above 50 per cent was in March when

56 per cent was recorded. The warmer interior station (No. 2), which is in a so-called frostless area, was intermediate. In general, the per cent dead pupae peaked for the year during March and April and then decreased. There seemed to be a tendency for pupal mortality to increase slightly from May to June, but no logical reason for this is apparent. The weather at that time of year should be close to optimum.

It might appear from the data in Table I that the most severe conditions occur in March or April because recorded mortality was the greatest in these months. Usually, however, January and February are the most severe winter months in southern California, and it is assumed that March and April mortalities reflect, in large part, previous adverse conditions which had a cumulative effect through eggs, larvae, and pupae. Other data, not herein reported, indicate that the observed increases in mortality are not due merely to accumulations of dead pupae. Successive counts usually show no indication that scales dead or parasitized the previous month remain on the tree to the extent of appreciably influencing the next count. Preliminary data now available indicate that *Aphytis* eggs subjected to sub-lethal low temperatures, then moved to optimum temperatures, may hatch and develop to the pupal stage only to succumb before emergence. Should occasional adverse periods occur in the field which are sub-lethal, it is evident that the cumulative effect could very well result in the type of mortality data presented in Table I. Particularly would this be true when it is realized that winter slows development, and that eggs deposited during January, assuming all lived, would not be expected to develop to adults until sometime in March. Thus, sub-lethal adverse temperatures acting against *Aphytis* eggs in January and February and against *Aphytis* larvae in February or March could very well produce cumulative effects resulting in peak pupal mortalities during March and April. Definitely lethal conditions could, of course, occur at any given time during the winter and cause considerable mortality to all stages at that time.

Differences in winter mortality between years. Since data from several groves are available for several successive years, it has been possible to analyze for differences in pupal mortality between years. For this purpose average monthly mortalities were derived for the same three groves for the winters of 1951-1952 and 1952-1953. These two winters represent, respectively, the most severe and the least severe, as far as pupal mortality is concerned, of the four winters for which

detailed data are available. The data, which are graphed in Figure 2, show very striking differences in mortality between the two winters. Mortalities were similar in November, but by April of the 1951-1952 winter there was a peak of 97 per cent pupal mortality whereas only 45 per cent mortality was attained at the peak of the 1952-1953 winter. The most interesting and significant fact about these data is that the winter of 1951-1952, which resulted in extremely high pupal mortalities, was not an unusually severe freeze winter from the standpoint of its effect on citrus. This fact has caused considerable difficulty in analysis of the specific winter factors involved in *Aphytis* pupal mortality since the most obvious lead, extreme low temperatures, was not enough to explain the high mortality during this particular winter. The following discussion seeks to clarify this situation.

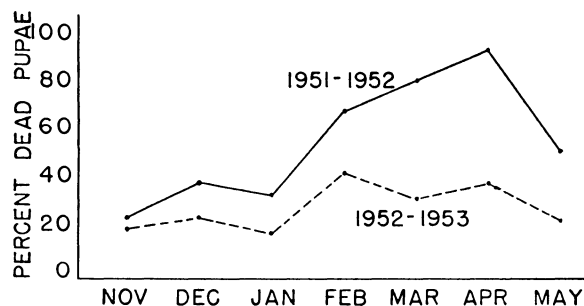


FIG. 2. Winter mortality of *Aphytis* pupae in different years.

Winter climatic factors and mortality. Several meteorological factors can be postulated as possible causes of winter mortality of *Aphytis* because of their departure from magnitudes expressed in other seasons. Average temperatures, evaporation and sunlight duration and intensity are lower, and rainfall is higher during winter months in southern California. Effects from all but temperature can be minimized for the following reasons. A lower rate of evaporation is known from laboratory studies to be beneficial, so except for occasional "north wind" periods, winter humidities are favorable. North winds create very dry conditions for from one to three days which may have an appreciable effect on adult *Aphytis*, without apparent damage to immature stages. Reduced sunlight duration and intensity should have no detrimental effect since the immature stages of *Aphytis* develop well in the laboratory in the virtual absence of light. Increased rainfall is probably not a factor because (1) rainfall is usually greater in coastal areas where it has been shown that mortality is less, and (2) one of the groves under

study was irrigated by overhead sprinklers approximately once each week during the summer season, which corresponded with the period of lowest mortality. This leaves low winter temperature as the major possibility. In general, low winter temperatures give a fair correlation with observed *Aphytis* mortality. The data in Table II taken in three groves for a total of ten winter observations represent mean monthly minimum temperatures for December through March and an average of monthly per cent dead *Aphytis* pupae for the period of January through April.

TABLE II. Mean monthly minimum winter temperatures and per cent dead *Aphytis*

Grove location	Winter*	Mean monthly min. temp. °F. December through March	Average monthly per cent dead pupae Jan. through April
No. 1 Coastal: mild location. Santa Barbara...	1949-1950	44.8	37
	1950-1951	46.4	36
	1952-1953	45.8	20
No. 2 Interior: fairly mild location. Riverside.....	1949-1950	45.0	44
	1950-1951	46.2	36
	1951-1952	46.0	69
	1952-1953	47.2	29
No. 3 Interior: colder location. Claremont.....	1950-1951	44.6	63
	1951-1952	41.4	70
	1952-1953	43.2	56

*Insufficient mortality data were obtained for No. 1, 1951-1952 and No. 3, 1949-1950.

These averages show a negative correlation between mean monthly minimum temperatures and per cent dead *Aphytis* pupae of 0.6358. This would indicate that minimum temperatures alone do not tell the whole story.

The poorest fit among these observations was for the winter of 1951-1952 in grove No. 2 where a rather high mean monthly minimum (*i.e.*, warmer than average) of 46.0°F. was associated with a high monthly average of 69 per cent dead *Aphytis* pupae. These figures were thought to be substantially accurate, and, finally, at least a partial explanation for the deviation was found. The winter months (December through March) of 1951-1952 had an appreciably lower mean monthly maximum temperature than the three other winters studied, especially in the area of grove No. 2 where the greatest deviation occurred. In this area the mean monthly maximum temperatures were from 4.4 to 6.5°F. lower for 1951-1952 than

for 1949-1950, 1950-1951, or 1952-1953. It would appear likely, therefore, that an interaction between low temperatures and high temperatures during winter results in the observed mortalities. Regarding this point Harries and Douglass (1948) in their fine ecological work with *Eutettix tenellus* (Baker) state, "The effect of cold periods during the winter . . . appears to depend to an important extent on the daily maximum temperatures, since the intensity of subfreezing temperatures . . . have little effect when relaxed by the diurnal temperature fluctuations." With this in mind, plus the laboratory knowledge that the developmental zero of *Aphytis* is around 60°F., and with the assumption that appreciable mortality results only below 50°F., several summations were made involving both high and low winter temperatures. The simplest of these was based on daily maximum-minimum temperatures. For each day the number of degrees above 60°F. was recorded in a plus column and the number of degrees below 50°F. in a minus column. These columns can be summed for any given period, and the difference between plus and minus will indicate the relative severity of that period. When this was done for grove No. 2 and compared with the data of Table II, the following was forthcoming:

Winter	Mean monthly min. temp. °F. December through March	Aver. monthly percent dead pupae January through April	Difference between summation of degrees above 60 °F. and below 50 °F. December through March
1949-1950..	45.0	44	+202
1950-1951..	46.2	36	+668
1951-1952..	46.0	69	-149
1952-1953..	47.2	29	+724

It will be recalled that the mean monthly minimum temperatures for the 1951-1952 winter failed to explain the high average mortality of 69 per cent which occurred. It appears clear from column 4, above, that a consideration of high temperatures helps considerably. The severity of the winter based on mortality (column 3) is in close agreement with the severity of the winter as determined by summation of high and low temperatures (column 4). Apparently the time above 60°F. is as important to *Aphytis* survival as time below 50°F. is to mortality. This is a much too simple method, however, when used as described, because critical causes of mortality may be masked. For instance, three severe weeks in a row are undoubtedly much more harmful to *Aphytis* than three equally severe weeks scattered through the

winter between favorable periods. Also, this method does not give as good an agreement between the three groves of Table II as did the minimum temperatures only. These studies are being pursued in an attempt to develop a method for precise evaluation of average differences between areas as well as of relative severity of winters as they occur.

Summer and fall mortality. Reference to Table I for the data from July to December shows that there is much less difference in pupal mortality between areas during summer and fall. The coastal area grove No. 1 and the interior area grove No. 3 (which has a cooler summer than No. 2) averaged the least mortality and were very similar in observed mortality. This may be accounted for by the fact that although grove No. 3 is in a hotter, drier area than grove No. 1, grove No. 3 is irrigated by overhead sprinklers about once per week during the hot part of the year, and the ground is covered by a heavy mulch which remains moist constantly and probably tends to modify the grove climate considerably. Grove No. 2 is in the hottest part of the interior citrus area; it is isolated from other groves, and the trees are small so there is little modification of general summer climatic conditions. This is reflected by greater average mortalities during the hot dry months from July to September. In all areas mortalities from October through December are generally the lowest of the year, and differences in pupal mortality, if any, among areas are slight.

LABORATORY STUDIES

The field data preceding, using pupal mortality as an index, serve to indicate areas in southern California and periods of the year most adverse to *Aphytis lingnanensis* and *chrysomphali*. These data leave much to be explained; hence, laboratory information was acquired regarding the effect of temperature and humidity on all stages of *A. lingnanensis*.

Laboratory test units consisted of small tightly sealed battery jars which contained various concentrations of H₂SO₄ as the humidity controlling agent. Constant temperatures were achieved by placing the test units in well-regulated constant temperature cabinets. The host for *Aphytis* in all tests was the California red scale cultured on mature green lemons taken from one grove. For purposes of reducing moisture loss from the fruit, as well as delimiting the area of infestation, approximately 70 per cent of the surfaces of the lemons was covered with paraffin wax.

Constant low temperatures and mortality.

Tests were run at temperatures of 30°, 40°, 50°, and 60°F. constant for periods of ½, 1, 2, 4, and 8 days, using eggs, larvae, pupae, and adults of *Aphytis*. Relative humidity was held constant at 60 per cent. Each stage was exposed only during that stage alone for the time indicated and then held under optimum conditions (approximately 80°F. and 60 per cent R.H.) until sufficient time had elapsed for complete development or death to occur. Partial results from these tests are condensed into Table III, using only the 30°F. temperature in order to afford a simpler illustration of the relative mortality in time and between different developmental stages. Nine hundred and forty-one individuals were used in the 30°F. test.

TABLE III. *Per cent mortality* of different stages of Aphytis subjected to 30°F. constant and 60 per cent R.H. for various times*

Duration of exposure time: Days	Per cent dead			
	Eggs	Larvae	Pupae	Adults
1.....	41	82	10	100
2.....	83	100	Insufficient data	100
4.....	100	100	66	100
8.....	100	100	No data	100

*The mortality count of immature stages was made after removal of organisms from test conditions to 80 °F. and 60% R. H. and allowing sufficient time for development to the next stage. Direct mortality of adults was determined at intervals of 1, 2, 4, and 8 days after subjection to the test conditions. Virtually all individuals of a given stage develop to the next stage when held at 80 °F. and 60% R. H.

From these data it is evident that the adult stage was most susceptible to low temperatures, the pupal stage was least susceptible, and the egg and larval stages were intermediate. Larvae appeared to be somewhat more susceptible than eggs at 30°F.; however, additional data indicate that eggs may be more susceptible than larvae at somewhat higher temperatures (50° to 60°F.) with long (8 day) exposure periods. Table III does not emphasize enough the sensitivity of adult *Aphytis* to low temperatures; actually 90 per cent died after a ½-day exposure to 30°F. As would be expected, mortality increased with time of exposure, so that after four days at 30°F. all stages, except pupae, showed complete mortality.

In order to make a better illustration of the relationship between various temperatures, times of exposure, and mortality, the complete data acquired for the egg stage are given in Table IV. Fifteen hundred and forty-six eggs were used in this test.

TABLE IV. *Relation of various times of exposure and constant temperatures to mortality* of eggs of Aphytis*

Duration of exposure time: Days	Temp. °F.			
	30	40	50	60
½.....	0	0	0	0
1.....	41	6	0	1
2.....	83	5	8	2
4.....	100	10	5	3
8.....	100	100	40	23

*The mortality count was made after removal of eggs from test conditions to 80° F. and 60% R. H. and allowance of sufficient time for development to the larval stage. Virtually all eggs develop to larvae when held at 80° F. and 60% R. H. constant.

From these data one can approximate through interpolation the effect on egg mortality of any combination of constant temperature between 30° and 60°F. and exposure time of from ½ to 8 days. At 30°F. mortality increases rapidly with exposure times above ½ day, reaching 83 per cent dead at 2 days and 100 per cent dead at 4 days. Obviously there is a vast difference between exposure to 30°F. and 40°F. except for the longest period of 8 days. Four days of exposure to 40°F. resulted in only 10 per cent mortality. On the other hand, 8 days of exposure to the rather mild, low temperatures of 50° and 60°F. caused substantial mortalities of 40 and 23 per cent, respectively. Such exposures are not extremely unusual in southern California citrus areas; hence, it is evident that considerable mortality may result from prolonged cool spells without the necessity of freezing temperatures occurring.

Constant low temperatures and the rate of development. The foregoing tests furnished additional data which indicate that not only does mortality of immature stages result from exposure to low temperatures but that survivors when returned to optimum conditions do not develop so rapidly as would normally be expected. The following example of this "carry-over" effect, derived from exposure of eggs to low temperatures, illustrates this point. *Aphytis* eggs were subjected to various low temperatures of from 30°F. to 60°F. for 2 days and then removed to optimum conditions (80°F.) and held for 10 days. At the end of this holding period all should have been in the pupal stage; however, various retarded stages of development were exhibited. An average per cent of expected development was calculated from these figures based on known rates of development of normal individuals not previously subjected to low temperatures. The results are as follows:

Exposure temp. °F. (2-day period)	Per cent of expected development completed at 80 °F. 10 days after exposure
30.....	50
40.....	75
50.....	87
60.....	88

The significance of these data lies in the fact that immature stages may be slowed not only in development during actual exposure to cold but subsequent to it even though conditions following such exposure are optimum for growth. Under winter conditions, therefore, the chances of enough eventual exposure to cause mortality are greatly increased.

This brings out a point which needs emphasis. All the laboratory data heretofore recorded apply to exposure to low temperatures during one stage only in the development of the individual. In the field, of course, this does not usually happen in winter time. From December through March most, if not all, developmental stages of an individual *Aphytis* will be subjected to low temperatures. It is evident, therefore, that field mortality can easily be much greater for any given temperature than would be indicated from laboratory studies concerning exposure during one stage only. Certain earlier laboratory tests further demonstrate this point. Each immature stage of *Aphytis* was subjected constantly to 57°F. from that stage on until a pre-emergence pupal count was made of survivors that developed that far. Those which died before becoming mature pupae were not considered in this analysis. Of those which began as eggs, 98 per cent died as mature pupae. Those which began as young larvae showed 70 per cent mortality as mature pupae, and those which began as mature larvae or young pupae showed 62 and 60 per cent mortality, respectively, as mature pupae. In addition, as already mentioned, preliminary field data now being accumulated indicate that there may be a real cumulative effect from cold exposure, in that eggs subjected to low temperatures may develop normally, but more slowly, to the pupal stage only to succumb during emergence of the adult. Most laboratory data tabulated herein were based upon counts of mature pupae; hence, this possible additional mortality was not obtained.

During the final preparation of this paper, the first indication of a third and probably very important effect of low temperatures on *Aphytis* was discovered. In addition to causing mortality

and producing "carry-over" effects on the rate of development, low temperatures also sterilize adult *Aphytis*. When a group of mated female *Aphytis* was subjected to 30°F. for six hours and the survivors (about 50 per cent) allowed to oviposit, the progeny were virtually all males (1779 males; 1 female), whereas normally about 80 to 90 per cent females are produced in the insectary using the same host. This means that the sperm in the spermathecae of the mated females were nearly all killed by subjection to 30°F. for 6 hours. A test involving 25 males which were subjected to 30°F. for 6 hours and then mated to 24- to 36-hour old virgin females, reared at a constant 80°, yielded 97 per cent male offspring. The obvious interpretation is that the males were likewise rendered sterile by this exposure, since production of female progeny in *A. lingnanensis* is nearly always contingent upon fertilization. Other sterility effects which operate through immature stages may occur. Such effects are discussed by Flanders (1938) and DeBach (1943). From the standpoint of adverse effects on natural control, sterility of *Aphytis* adults resulting from subjection to 30°F. for 6 hours assumes great importance, because such exposures occur rather commonly during the winter in southern California. Obviously if such exposures result in the production of practically all male progeny, populations of *Aphytis* would decline rapidly.

Alternating temperatures and mortality. Thus far it has appeared from the laboratory data that low temperatures (30° to 50°F.) are always detrimental to *Aphytis*, the ultimate effect depending only upon duration and intensity. It may be recalled from the discussion of the field data, however, that periods of high temperatures following low temperatures appeared to alleviate the adverse effects. Accordingly, laboratory tests were run to explore this hypothesis.

A constant relative humidity of 60 per cent was used in all tests. For these tests host material containing newly laid eggs of *Aphytis* was placed in a constant temperature of 40°F. for 12 hours, then removed to a constant temperature of 80°F. for 12 hours, then repeated until the life cycle was completed. Three hundred and five individuals were used in this test. Oddly enough, as it might seem, all but 7 per cent of the original eggs completed development to the adult stage. At least 3 per cent mortality during the complete life cycle is expected under optimum conditions; hence, very little mortality occurred. The developmental period was slightly more than doubled as would be expected, but the actual time spent at 80°F. (16.5 days) was only

slightly more than in the checks. Checks run at 80°F. constant showed complete development from egg to adult in 15 days.

The most striking part about these results was that individuals could be subjected to an average total of 16.5 days at 40°F. during their life cycle and still develop through to adulthood. It will be recalled from Table IV that eggs subjected to 40°F. constant were all dead by 8 days. In fact eggs do not hatch up to 55°F. constant, and at 60° constant other tests indicate little development past young larvae. Those few which survived had an average life cycle of 54 days. This latter temperature (60°F. constant) gives the same average as the 40°F. for 12 hours, alternating with 80°F. for 12 hours, yet the life cycle is much longer at the constant cool temperature. Survival was also lower. Obviously, therefore, high temperatures following short exposures to low temperatures greatly reduce, and perhaps even neutralize, the adverse effects from low temperatures which would otherwise occur. It appears that the alleviating effect of the high temperatures must depend upon the length of time previously exposed to low temperatures, for it is highly probable that 40°F. for 12 hours, followed by 80°F. for 12 hours, will be less severe than 40°F. for 24 hours followed by 80°F. for 24 hours.

TABLE V. *Effects of different combinations of constant humidity and temperature on adult Aphytis as measured by time in days to 50 per cent mortality*

Temp. °F.	Relative humidity—per cent		
	20%	50%	80%
	Days to 50 per cent mortality		
50.....	3	7	9
60.....	5	11	22
70.....	7	11	18
80.....	2	6	7
90.....	1	4	7
Average.....	3.6	7.8	12.6

EFFECT OF HUMIDITY AND TEMPERATURE INTERACTION ON MORTALITY

The previous discussions concerning the effects of low temperature on *Aphytis* purposely have neglected humidity effects because low temperatures occur in southern California during that part of the year exhibiting the highest relative humidities, which are those most favorable to *Aphytis*. In addition, we have been dealing principally with immature stages of *Aphytis*, which under the protective scale covering of their host usually are in a highly humid microenvironment. Adult

Aphytis, however, are more likely to be influenced by adverse humidity conditions.

Tests on adult *Aphytis* were conducted at three relative humidities, low (20 per cent R.H.), medium (50 per cent R.H.), and high (80 per cent R.H.) and at five temperatures ranging from 50° to 90°F. Results are presented in Table V. Nine hundred individuals were used in this test.

From these data it is clear that *Aphytis* adults are very seriously affected by low humidities. At 20 per cent R.H. they live on the average less than one-third as long as at 80 per cent R.H. The extreme effect, however, is seen at the high temperatures combined with low humidity. At 80° and 90°F. and 20 per cent R.H., adult *Aphytis* lived only one-tenth to one-twentieth as long as at 60° to 70°F. and 80 per cent R.H. It is also evident from Table V that adult longevity is adversely affected by high temperatures (*i.e.*, above 70°F.) regardless of humidity. It is known, also, that immature stages show considerable mortality at 90°F. and that they show some increase in mortality at low humidities. These data then help explain the higher pupal mortality observed in grove No. 2 (Table I) during the hot dry months of July and September.

During the period from about October to March, strong north winds of from one to three days' duration occasionally blow from the Mojave Desert through mountain passes and into the southern California citrus areas. During these winds, which are most severe in the interior valley citrus areas, the temperature is usually well above normal for that period of the year, and the relative humidity may remain below 10 per cent for 24 hours or more and below 20 per cent for 48 hours or more. Such conditions would approach those in Table V where at 20 per cent R.H. and 80° or 90°F. *Aphytis* adults lived only 1 or 2 days. Counts of adult parasites made before and after a strong "north" wind showed little reduction after 24 hours but nearly complete disappearance of the parasites after 3 days. The protected immature stages are probably not affected nearly so adversely as are the adults. These winds, then, have a considerable effect on *Aphytis* adults, much less on immature states, and relatively little on the California red scale, which is completely protected by the scale covering and has a constant supply of moisture from the plant as well. The effect of these winds will be to produce sharp oscillations in *Aphytis* populations but not steady declines.

DISCUSSION

The preceding data have shown that considerable mortality to both immature and adult stages

of *Aphytis* may result from the effect of various meteorological factors. Principal among these are low winter temperatures, high summer temperatures, and low humidities. The question may be asked, however, whether the observed mortalities actually seriously lower *Aphytis* populations to the extent that biological control is negated. Such a question is apropos inasmuch as many students of population dynamics have postulated that climate can have no controlling effect on animal populations. However, all the field evidence in the present case indicates that the various components of climate are the major factors keeping *A. lingnanensis* and *chrysomphali* from successfully controlling the California red scale in certain citrus areas. For instance, in the mild coastal climatic zone of southern California natural control of California red scale (control achieved without artificial periodic colonization of parasites) by *A. chrysomphali* or *lingnanensis* has occurred in every untreated citrus grove studied. In the less mild intermediate climatic zone, natural control of California red scale by *Aphytis* has occurred in certain groves and not in others, depending apparently upon microclimatic differences. In this intermediate zone, though, it has been possible to obtain biological control of the California red scale by yearly periodic colonizations of large numbers of *Aphytis* in all plots thus far studied. In the interior valley climatic zone, where extremes are greater, natural control rarely if ever occurs, and it has not been possible to achieve a consistent degree of successful biological control through the periodic colonization of parasites.

Parasite population density reflects the differences between climatic zones. A survey of 51 untreated groves in Los Angeles County in 1951 showed three times as many immature *Aphytis* per 100 scales in the intermediate climatic areas as in the interior climatic area of the San Fernando Valley. Actually, eradication of *Aphytis* nearly occurs following colder than normal winters in interior valley citrus areas. Often in such groves it is virtually impossible to find a live immature or adult *Aphytis* by March or April even though they were abundant the preceding fall.

Evidence that climatic factors may affect insect parasites and thus indirectly influence host populations has been given by Michelbacher and Leighly (1940) for field populations and by Burnett (1949) for experimental populations. Michelbacher and Leighly (p. 127-128) state, "Parasitism must be taken into account in any discussion of the climatic limitations of the alfalfa weevil. Climatic conditions favorable to the weevil may also be exceptionally favorable for one or more of

its parasites. It is therefore conceivable that the weevil may be more destructive, or at least more abundant, in a climatic zone other than its optimum if the conditions in the zone in question are not optimum for maximum parasitism. . . .

"In California our observations have yielded evidence of such a phenomenon. When the weevil was first found in lowland middle California, it was most abundant at Pleasanton, Alameda County, and in adjacent areas near San Francisco Bay. The populations encountered in the infested part of the San Joaquin Valley were rather small in comparison with those found near the Bay. In 1933 and 1934 the United States Department of Agriculture Bureau of Entomology and Plant Quarantine introduced the larval parasite *Bathyplectes curculionis* (Thoms.), into the infested areas. The parasite readily became established and is evidently more effective about Pleasanton and in the Bay area in general than in the San Joaquin Valley.

"As a result of depredations of the parasite, the weevil populations now found in the Bay area are smaller than those found in northwestern San Joaquin Valley, a condition that is the reverse of that which was obtained before the parasite was introduced. . . . If the trends of the weevil populations were studied without any attention to parasitism, however, the conclusion might be reached that the climate of the northwestern part of the San Joaquin Valley is more favorable to the weevil than that of the areas close to San Francisco Bay, with their cooler summers and more moderate winters. Such is evidently not the case."

In southern California, parasitization has never been seriously considered previously as a factor which might help explain the differences in severity of the California red scale in various climatic zones. It is quite possible, however, that differences in difficulty of obtaining chemical control of red scale infestations may be explained in the same manner as was done by Michelbacher and Leighly (1940) for the alfalfa weevil. For instance, in Orange County, a coastal area, insecticidal control of the red scale is much easier than in Riverside County, an interior area. *Aphytis chrysomphali* is fairly common even in regularly treated citrus groves in Orange County, whereas these parasites are rare in Riverside County groves. Orange County groves have been observed which were sprayed for red scale control when, unbeknownst to the owner, ninety per cent of the scales were dead due to the activity of *Aphytis*. It seems likely, therefore, that the parasites may be in large part responsible for the fact that red scale is not so difficult to control in

Orange County as in Riverside County. Usually these differences are explained by the fact that the number of generations per year of red scale is somewhat greater in interior areas; however, mortality because of summer and winter extremes is also greater, so that the net result, *if there were no parasites*, could be that red scale would be a worse problem in Orange County.

Burnett (1949) has shown with experimental populations of *Trialeurodes vaporariorum* (Westwood) and its parasite *Encarsia formosa* Gahan that different mean temperatures result in quite different population interactions between the host and parasite. At 18°C. the host population increased more rapidly than the parasite population; at 24°C. host and parasite rates of increase were about equal, whereas at 27°C. the parasite population increased more rapidly than that of the host so that it dominated the host. These results were due to a differential effect of temperature on the fecundity and rate of development of the host and parasite. Obviously such results could explain why natural control in the field occurs in certain years and not in others or in certain areas but not in others.

SUMMARY

Field data based upon a pupal mortality index show that *Aphytis* populations in southern California are more or less greatly reduced by low winter temperatures. The effect varies in different years and is relatively less in coastal (mild winter) areas than in interior valley (colder winter) areas. Close to 100 per cent pupal mortality has been recorded in interior areas; hence, natural control of California red scale usually occurs in untreated groves in coastal areas and rarely in such groves in interior areas. Subfreezing or average minimum temperatures are not necessarily the best index to mortality. Maximum temperatures (above 60°F.) have a favorable modifying effect, depending upon frequency and intensity. The *Aphytis* pupal mortality index also shows a decided increase during the hot dry months of July, August, and September in the more severe interior climatic areas.

Laboratory studies under controlled temperature and humidity conditions showed that all stages of *Aphytis* are adversely affected by low constant temperatures of from 30°F. to 50°F. and in some cases 60°F. depending upon duration of exposure. The adult stage was most susceptible, with 100 per cent mortality occurring after less than one day's exposure to 30°F. Cold-sterilization of sperm in the males and in the spermathecae of the females also occurs at low

temperatures. The pupal stage was most resistant; however, four days of exposure at 30°F. caused 66 per cent mortality. Effects on the egg and larval stages were intermediate. Complete mortality occurred to each of these stages after 2 to 4 days' exposure to 30°F. Four to eight days' exposure to 40°F. or 50°F. caused considerable to complete mortality to these stages. Prolonged exposure of 8 days at 60°F. caused some mortality. Eggs do not hatch up to 55°F. constant, and little or no development past young larvae occurs at 60° constant. Exposure of eggs to low temperatures had a carry-over effect after removal to optimum conditions. Rate of development under optimum conditions was reduced in relation to intensity of previous exposure to low temperatures. Equal but short alternating periods of high (80°F. for 12 hours) and low (40°F. for 12 hours) temperatures nearly eliminated the expected adverse effects which the low temperatures alone would have shown.

Aphytis adults are seriously affected by low atmospheric humidities, while immature stages, because of their protective niches, are less affected. Life expectancy of adults at 20 per cent R.H. was less than one-third as long as at 80 per cent R.H. High temperatures combined with low humidities produced extreme effects; life expectancy at 90°F. and 20 per cent R.H. was only one-twentieth of that at 70°F. and 80 per cent R.H.

High temperatures (90°F.) greatly reduced the life-expectancy of adult *Aphytis* regardless of humidity, and the same applies to immature stages. These data indicate that climatic zones in which an insect population is most abundant may not necessarily be the optimum zone. Biological control may occur in the zone optimum for the host; hence, the host will be scarce. Biological control may be neutralized by climatic factors in a zone suboptimum for the host; hence, the host will be relatively abundant. The net result will be a host most abundant in a suboptimum climatic zone.

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