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Een oecologisch onderzoek over de appelbloedluis, *Eriosoma lanigerum* (Hausm.), en haar parasiet *Aphelinus mali* (Hald.) in Nederland

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parasitering die dan optreedt; zodoende ontsnapt dan nog een belangrijk deel van de waarddieren aan de parasitering. Door de veel grotere vermeerderingscapaciteit van de appelbloedluis krijgt deze in het voorjaar en in de voorzomer een steeds grotere voorsprong op de parasiet. Juist in deze periode vermeerdert de bloedluis zich sterk en richt de grootste schade aan. De parasiet is dan dus niet voldoende effectief.

Uit het onderzoek blijkt dus dat de bloedluisparasiet *Aphelinus mali* onder de omstandigheden, zoals die in ons land heersen, niet in staat is om de populatiedichtheid van de appelbloedluis beneden het economisch toelaatbare niveau te houden.

SUMMARY

1. INTRODUCTION

The woolly aphid is a serious apple pest. An account is given of the introduction of the woolly aphid parasite (*Aphelinus mali*) from N.-America into Europe and especially into the Netherlands from France by the Phytopathological Service in 1924. The initial attempt to establish the insect in Wageningen was succesful. But after some thirty years the woolly aphid is still a serious pest in the Netherlands.

This paper outlines the results of investigations made in relation to the influence of *Aphelinus mali* on its host, the woolly aphid.

2. BIOLOGY OF THE WOOLLY APHID AND ITS PARASITE IN THE NETHERLANDS

2.1. BIOLOGY OF THE WOOLLY APHID

In the Netherlands only the wingless, viviparous and parthenogenetically reproducing females are the forms responsible for the increase of the population density. They hibernate mostly in the form of young nymphs, usually in the first instar. During the latter part of March the insect becomes active and the secretion of wax starts again.

There are two forms of winged females, the virginoparae which occur in June and July and are considered very rare, and the sexuparae in August, September and October. The latter produce males and females. The fertilized female lays only one egg which may hatch in the spring; in this event, however, the fundatrix nymph invariably dies (DE FLUITER, 1931).

The woolly aphid occasionally occurs on the roots, but only when the latter are exposed by cultivation they can reach these by holes in the earth. In the laboratory they may be established on the roots of potted seedlings, especially on the part of the roots adjacent to the drainage hole at the bottom of pots. In my experiments the aphid has not been observed to migrate from branches and trunk of the trees to the roots.

The mortality may be very high especially in seasons when wheather conditions are very cold.

2.2. BIOLOGY OF THE WOOLLY APHID PARASITE

The woolly aphid parasite hibernates as a full-grown larva in a state of diapause within its mummified host, whose skin is hard and black. The ventral side of the mummified aphid is fastened on the twigs or the stem of the apple-tree. The first adults appear in spring, and there are several generations a year (cf. pg. 89).

3. CAPACITY OF INCREASE OF THE WOOLLY APHID AND ITS PARASITE

By „capacity of increase” should be understood the number of progeny of an animal species after a period of time, starting from one female, when there is no mortality by biotic factors. This is not meant to express the „capacity of increase” in an absolute sense, it is only meant to compare the capacity of increase of two animal species, which are ecologically connected: in this investigation the woolly aphid and its parasite.

There are five factors that fix the „capacity of increase”, namely 1. the rate of development from egg (or with viviparous forms from new-born larva) to adult state; 2. the number of progeny from one female; 3. the duration of the reproduction period; 4. the distribution of the progeny over the reproduction period; 5. the sex ratio.

3.1. CAPACITY OF INCREASE OF THE WOOLLY APHID

3.1.1. *Rate of development*

The rate of development may be expressed in 1. the duration of the period of development at different constant temperatures, 2. the number of generations during one season.

3.1.1.1. *Rate of development at constant temperatures*

Despite statements made in the literature it is not accepted there should be any relation between the atmospheric moisture content and the rate of development at a constant temperature of such an insect as the woolly aphid, that takes up an excess of moisture with its food.

In my own experiments I determined the rate of development of the woolly aphid at different constant temperatures. The aphids were bred on apple-trees (Cox's Orange Pippin) in a room with a constant temperature. Parts of selected branches of the tree were enclosed by square metal cases with a glass lid on each side (Fig. 1). In a curved metal tube within each case warm water of a constant temperature could be circulated by means of a „Höppler thermostat”. The temperature within the case could be read on a bulb thermometer. On each branch in its case five wounds were made by a knife, each wound being surrounded by a ring of tacky grease. The wounds were inoculated with young woolly aphids which were not more than a day old. Above the plant an electric lamp was placed that automatically switched on and off with a continuous day period of light and dark of thirteen and eleven hours respectively. Observations on moulting were made every day. The results are given in Table 1, from which the following may be concluded: 1. The duration of the first nymphal instar varied considerably at different temperatures. 2. The duration of the second, third and fourth instars varied much less. 3. Generally speaking the duration

of the first instar is comparatively long when compared to those of the other instars.

The variation of the duration of the first instar may be accounted for by the fact that the newly-hatched nymph may walk about on the plant for some time before it selects a suitable site for feeding upon.

The following conclusions may be drawn from Table 2: 1. The rate of development of the three last instars is about equal. 2. The quickest rate of development of the first instar is in most cases equal to the average of the last three instars. Thus the actual rates of development of the four nymphal instars of the woolly aphid are about equal.

The graph in Fig. 2 represents the relation between the real duration of the development of the woolly aphid and the temperature.

The data from these experiments have been compared with totally different data obtained by MARCOVITCH (1934), EHRENHARDT (1940b) and BODENHEIMER (1947). It must be noted, however, that the first two authors have results based upon experiments where whole plants are enclosed in a container of a constant temperature (controlled by thermostat), so that the harmful effect of high temperatures affected the whole rather than a small part of the plant, as was the case in my experiments. BODENHEIMER did not have constant temperature conditions, indeed his graphs were constructed from values which he calculated from average temperature records under natural conditions.

3.1.1.2. *Number of generations in one season*

The aphids were reared in metal cages placed on apple-trees in the field (Fig. 3). The observations were started with overwintering nymphs in the spring when these showed their waxy secretions. When these insects reached maturity and had produced a few nymphs, the former were killed, and the latter allowed to breed until they in their turn had started to reproduce. This process was repeated several times until the following winter.

Generally speaking there are eleven or twelve generations each year as shown in Table 3.

3.1.2. *Number of progeny*

3.1.2.1. *Number of progeny at constant temperatures*

The experiments made to determine the number of progeny at constant temperatures were conducted in a manner similar to those on the determination of the rate of development at constant temperatures (Fig. 1).

The newly-hatched nymphs were counted and discarded every day. Frequently the adult woolly aphids were caught in the grease, used to prevent their escape, before they had finished laying their progeny. In such cases it was possible to determine their full complement by counting the living young and the number of embryos within the mother aphid, provided the cells at the beginning of each ovariole had stopped producing eggs (cf. EHRENHARDT, 1939). It will be seen in Table 4 that the average number of progeny of 4 aphids at $15\frac{1}{2}^{\circ}\text{C}$ is 170, of 6 aphids at 26°C 135 and of 4 aphids at alternating temperatures from $15\frac{1}{2}^{\circ}$ to 26°C amounts to 160. The differences of these figures are not significant, however.

3.1.2.2. *Number of progeny at inconstant temperatures*

The aphids were bred in the laboratory at room-temperature on potted apple-seedlings. Rings of grease were used to prevent the aphids escaping. Generally the records were made every two or three days. The following conclusions may be drawn from Table 5:

1. From 28 aphids (1a up to and including 19), which produced the whole of their progeny as nymphs, the mean number of progeny being 149 (minimum 115, maximum 195).

2. From 19 aphids (12a up to and including 10e), which were caught in the grease, and from which the cells at the beginning of the ovarioles had stopped producing eggs, the mean number of progeny being 151 (minimum 112, maximum 187).

3. From 3 aphids (21a, 28, 29a), which were also caught in the grease and from which the cells at the beginning of the ovarioles had not stopped producing eggs, the progeny was 83, 106 and 110 respectively.

By comparing 1., 2. and 3. it is permissible to determine the number of progeny of aphids that died before producing their whole progeny by adding the hatched nymphs and the number of embryos, provided the cells at the beginning of the ovarioles have stopped producing eggs.

4. The mean number of progeny from 6 aphids (14a up to and including 26c) reared on unhealthy food plants was 131 (minimum 98, maximum 162), not very much less than the number of progeny on healthy seedlings. The mean number of progeny bred in favourable conditions at room-temperature may be fairly estimated at 150. A similar figure probably applies to field conditions.

3.1.3. *Duration of reproduction period*

Table 4 shows that the mean reproduction period of the aphids 3 : 2a, 3 : 3b and 3 : 5 is almost twice their period of development at 26°C.

Table 5 shows that the period of development is about 65 % of the reproduction period at room-temperature (28 aphids: 1a up to and including 19). From Tables 5 and 6 it is seen that at room-temperature the reproduction period is about one and a half times the period of development. It is thought likely that this phenomenon happens in the field.

3.1.4. *Distribution of the number of progeny over the reproduction period*

In Table 4 it will be observed that the aphids 3 : 2a, 3 : 3b and 3 : 5 produced all their progeny as young nymphs at a constant temperature of 26°C. The progeny of the aphids observed every twenty four hours is given in Table 7. If the newly-hatched nymphs of the three aphids are totalled up every two days, it is shown that the rate of production of nymphs continues to increase until half way through the reproduction period. After this period the rate of production of nymphs tends to decrease again (see Fig. 4). In Fig. 5 the reproduction of nymphs by three aphids (10a, 14b and 15a) is shown at an inconstant room-temperature. This follows the same trend as noted in Fig. 4, except for slight differences which may be attributed largely to temperature influence.

3.1.5. *Sex ratio*

The viviparous, parthenogenetically reproducing generations are 100 % females.

3.1.6. *Summary of the investigations on the capacity of increase of the woolly aphid*

1. The rate of development at constant temperatures is considered in Fig. 1; in the Netherlands there are eleven or twelve generations per annum. 2. The number of progeny in the field when conditions are favourable is approximately 150. 3. The duration of the reproduction period in the field is considered to be one and a half times the period of development. 4. At the middle of the reproduction period the peak of hatching occurs. 5. The viviparous forms always produce one hundred per cent females.

3.2. CAPACITY OF INCREASE OF THE WOOLLY APHID PARASITE

3.2.1. *Rate of development*

3.2.1.1. *Rate of development at constant temperatures*

3.2.1.1.1. *Duration of the egg-stage*

A number of female parasites were placed in a petri-dish together with a number of woolly aphids, usually of the third nymphal instar and kept at room-temperature. After one to two and a half hours the parasites were discarded, and the aphids in the petri-dish were put in a series-thermostat of ZWÖLFER (1932). By dissecting the aphids at intervals and examining the eggs of the parasite, the duration of development of the egg could be ascertained (Table 9).

3.2.1.1.2. *Duration of the pupal stage*

The yellowish parasitised woolly aphids were collected in the field. The parasitised yellow aphids which are devoid of the waxy secretion, and on which a black spot is visible (which is in fact the contents of the gut of the larva of the parasite) contain the nearly full-grown parasite larva. Within a few days the parasitised aphids turn black and die and become mummified. Within these mummified aphids the pupa is formed. Every day the yellow parasitised aphids were examined, and when they reached the mummified state they were transferred to a petri-dish in the series-thermostat at different constant temperatures. Every day the adult parasites were observed to emerge from the mummified aphids. In addition to the temperature influence the influence of the humidity was examined. To facilitate this the mummified aphids were placed in small dishes contained in the petri-dish filled with water (relative air moisture content 100 %) or a saturated solution of cooking-salt (relative air moisture content 75 %) or a saturated solution of calcium chloride (relative air moisture content at temperatures recorded from 26 % to 39 %). The following deductions may be drawn from Table 9:

1. The spreading in the time of hatching of both males and females at a fixed air moisture content increases from the higher to the lower temperatures and is at $16\frac{1}{2}^{\circ}\text{C}$ and at $13\frac{1}{2}^{\circ}\text{C}$ rather pronounced.

2. At the lower temperatures the duration of the pupal stage of the female is a little longer than that of the male (statistically significant).

3. At lower temperatures there is a tendency that the development is more rapid at a higher than at a lower air moisture content, but the figures showing this are not significant.

4. At higher temperatures the size of the time unit (one day) between two succeeding observations is too great to show the tendency, stated in 2 and 3.

3.2.1.1.3. *Duration of egg- and larval stage combined*

It was not possible to study the duration of the larval stage separately, but the duration of the egg- and larval stage combined was investigated. In these experiments potted apple-seedlings with woolly aphids were used. They were infected with the woolly aphid parasite, and were kept at different temperatures which were thermostatically controlled. Records were made every day and the mummified aphids were noted. Table 10 presents the influence of the different temperatures on the duration of development. The variation in the length of the egg- and larval state combined is found to be considerable. This is largely attributed to the wide variation of the duration of the larval stage.

3.2.1.1.4. *Discussion of the duration of development of the woolly aphid parasite at different constant temperatures*

The graph given in Fig. 6 shows the relation between the temperature and the duration of development of the egg-stage, the pupal stage and the egg- and larval stage combined. For these three different factors three different graduations are used, which are in the proportion of 1 : 5 : 5. From Fig. 6 it will be seen that the development of the egg, the larva and the pupa are about proportional in the ratio of 1 : 4 : 5.

3.2.1.2. *Number of generations of the parasite in one season*

Colonies of the woolly aphid were reared in metal boxes (Fig. 3) on branches of apple-trees in the field. Some males and females of *Aphelinus mali* were put in these boxes and were left for several days. The colonies were observed every two or three days; the mummified aphids were isolated. When adult parasites emerged new colonies of aphids were inoculated. At the end of the season the full-grown larva went into diapause and no more parasites emerged.

In Table 11 it will be noted that in the Netherlands there are normally five generations each year. In some suitable seasons there may be a partial sixth generation.

3.2.2. *Number of progeny*

Males and females were reared separately from parasitised aphids. Observations were made daily, and as soon as they hatched they were used in the investigations. Every day about thirty or forty healthy aphids were each put in a separate petri-dish together with a female (and occasionally a male) of the parasite. The experiment continued until the female parasites died. The parasitised aphids were dissected daily and the number of eggs of the parasite recorded. From Table 12 it will be observed that the number of ova laid by a female may vary considerably, but the average number is about 85. The maximum number recorded was 177.

3.2.3. *Duration of reproduction period and distribution of eggs laid over that period*

In Table 13 the data of the females nos. 8-25 are given. Although the number of eggs laid daily may vary considerably the following conclusions may be drawn from Tables 12 and 13.

1. The mean number of eggs laid daily fluctuates about a constant level; at room-temperature this amounts to about 11.

2. The number of eggs laid by a female varies according to the longevity of the insect.

3. From 25 observations the mean number of eggs laid totalled 85; the mean longevity amounted to 8 days.

The length of life of the female parasite may vary because the aphid emits a liquid substance from its siphunculi, which hardens when exposed to the air. This substance may readily contaminate the mouth-parts, the antennae and the legs of the female parasite, thus causing its death (cf. LUNDIE, 1924). This fact was observed in several experiments, and it is also considered to take place in the field. Therefore it is better to regard the number of eggs laid as 85, rather than to consider the maximum number of 177 eggs as the egg-laying capacity of the parasite.

3.2.4. *Sex ratio*

Tables 14 and 15 show that the proportion of females, bred from the hibernating full-grown larvae was 49 %, while of those collected in the summer the proportion was 66 %. The difference is statistically significant. In nature it may be said that the proportion of females is about 50 %.

It was observed that four unfertilized females laid eggs, of which the progeny were all males. The figures were 1, 14, 11, 19 respectively. Four fertilized females laid eggs which produced males and females in the following proportions: 0 + 3; 7 + 21; 15 + 47; 6 + 12 respectively.

3.2.5. *Summary of the investigations on the capacity of increase of the woolly aphid parasite*

1. Fig. 6 shows the duration of the development of the egg, the pupa and the egg and larva combined at different constant temperatures. In the Netherlands there are five or sometimes six generations of the parasite during one year.

2. The average number of progeny from 25 female parasites is 85 eggs.

3. The average reproduction period at an inconstant room-temperature lasts 8 days. The period of development at a temperature of 18°C (Fig. 6) is about 28 or 29 days; the mean longevity of the female parasite amounts to about 0,3 times the period of development from the egg to the adult stage.

4. The number of eggs laid daily at room-temperature fluctuates about a constant level and numbers about 11.

5. The proportion of hibernating females is about 50 %; in the summer generations it is a little higher (average 66 %).

3.3. COMPARISON OF THE CAPACITY OF INCREASE OF THE WOOLLY APHID AND ITS PARASITE

The graph depicted in Fig. 7 shows the capacity of increase of the woolly aphid and its parasite at a temperature of about 18°C. It will be seen that the capacity of increase of the former is much greater than that of the latter.

4. PHENOLOGY OF THE WOOLLY APHID AND ITS PARASITE

4.1. PHENOLOGY OF THE WOOLLY APHID

The woolly aphid usually hibernates as a young nymph, mostly in the first instar. It starts producing its flocculent woolly secretion in the second half of March (Table 3). As the reproduction period is about one and a half times as great as the period of development, overlapping of generations starts during the second generation. When weather conditions are favourable the aphid may continue in its active state until December or even later.

4.2. PHENOLOGY OF THE WOOLLY APHID PARASITE

The parasite hibernates as a full-grown larva in a state of diapause within the parasitised dead woolly aphid.

In Table 16 the results are shown of observations (Wilhelminadorp, 1951) made every two or three days of 100 mummified aphids with a living larva, prepupa, pupa or adult of the parasite. On May 13th the first adults were found inside the mummified aphids; the diapause state of the larva had ended by May 7th. Mummified aphids collected in the field during the preceding autumn and winter were enclosed in glass tubes, the opening being closed with a piece of cotton wool; they were examined every two or three days in spring. The glass containers were kept in the open air, but away from direct sunlight. From the spring of 1950 up to and including 1955 observations were made on the hatching period of the adults of the overwintering generation. These results are given in Tables 17 and 18.

It will be seen in Table 18 that during the six years of the investigations the first parasites hatched from May 2nd to May 23rd; the last ones emerged from May 15th to June 11th; 50% hatched between May 7th and May 31st. Thus in the different years the adult parasites hatched at various times.

It appears from Table 17 that in most years there is a distinct proterandry. An experiment was made to illustrate the influence of heat produced by direct sunlight on the break of diapause and on the rate of development. In this experiment a number of parasitised aphids were collected in the autumn and winter and were collared on pieces of hardboard which were mounted at a height of about 1½ m on a post in the field, viz. each one being placed vertically on the North, East, South and West, with one horizontally above. Observations were made mostly every two days to determine whether emergence holes were present in the parasitised aphids, thus indicating that the parasites had left their hosts. The results are shown in Table 19. In the second column the number of parasitised aphids were all reduced to the same number 30. The parasites from the parasitised aphids on the pieces of hardboard facing South, East, West and above hatched much earlier than those on the North and also the controls, the latter being kept in the same situation as the parasitised aphids in the glass tubes.

In 1951 parasitised aphids were marked and observed every two or three days in an orchard at Wilhelminadorp. Table 20 shows that the first parasites hatched much earlier (April 30th) than in the glass tubes, screened from direct sunlight (May 23rd: Table 18). In the field in 1951 the first wasps were noticed on April 30th too.

The difference in the time of hatching of the parasites, those screened from direct sunlight and those in the field, may be explained by the influence of heat, induced by direct sun radiation.

4.3. OBSERVATIONS ON THE DIAPAUSE OF THE WOOLLY APHID PARASITE

In 1955 parasitised aphids collected in the field at different times, and placed in glass tubes closed by a piece of cotton wool, and screened from direct sunlight, were observed every two or three days. Table 21 presents the results, namely that the percentage of larvae going into diapause increased rapidly during September and the beginning of October.

5. MUTUAL INFLUENCE OF THE WOOLLY APHID AND ITS PARASITE

5.1. HOST RANGE OF THE PARASITE

Although very many hosts of the parasite *Aphelinus mali* are quoted in the literature, only *Eriosoma lanigerum* may be regarded as the real host. In some experiments it was noted that the parasite laid eggs in the woolly aphid of pear, *Eriosoma lanuginosum* (HTG), but in no case mummified aphids were obtained.

5.2. NUMBER OF EGGS LAID IN ONE APHID

It will be seen in data of Table 13 that the parasite prefers to lay her eggs in healthy aphids, which have not been parasitised already. It has been noted that a parasite may sting an aphid more than one time; only as an exception, however, more than one egg was found in one aphid.

As the parasite lays more than one egg in one aphid only if she cannot easily find unparasitised hosts, superparasitism will only occur at high parasitising percentages. As it is very difficult for the female parasite to find all hosts that are available, a hundred per cent parasitism is impossible. Observations confirm that only one parasite hatches from one aphid.

5.3. THE STAGES OF THE WOOLLY APHID THAT ARE PARASITISED

The female parasite shows no preference for any particular instar of the aphid. Even newly-hatched aphids are parasitised, and the progeny develop normally. The nymphs of winged aphids are also subject to parasitism.

5.4. DURATION OF THE REPRODUCTION PERIOD AND NUMBER OF PROGENY OF THE WOOLLY APHID AFTER IT HAS BEEN PARASITISED

Table 22 shows the duration of the reproduction period and the number of progeny of 6 aphids, kept at room-temperature after parasitism. From this table the following may be concluded:

1. At room-temperature the production of progeny of the woolly aphid continues after parasitism until the larva of the parasite is about half grown.
2. During this period a large number of progeny may be produced, in fact about a third of the potential maximum, namely 59.

5.5. INFLUENCE OF LIGHT ON PARASITISM

Only in a few cases parasitism in the dark was observed.

5.6. FEEDING OF THE PARASITE

In a few instances it was observed that a female parasite stung its hosts and then proceeded to feed on the exuding fluid. In one instance microscopic examination showed that little holes were present in the body wall of the aphid, but dissection did not reveal the presence of an egg. It is concluded that there is little or no mortality caused by hostfeeding.

6. OTHER BIOTIC FACTORS WHICH INFLUENCE THE POPULATION DENSITY OF THE WOOLLY APHID

6.1. INFLUENCE OF PREDATORS

A large number of predators are mentioned in the literature on the woolly aphid. Some data concerning the influence of some of the more important predators are given, in this account the unpublished investigations of Mrs. F. NIJHOFF-ROMBACH, which were made in the Province of Zeeland in 1952.

Among the *Neuroptera*, *Chrysopa septempunctata* WESM. appeared to be the most important species; in one orchard from 4 to 10 larvae were found feeding among 1000 aphids; one larva, for example, fed on 264 nymphs of the woolly aphid of the third or fourth instar to be able to complete its development.

Among the *Coleoptera*, the Ladybird *Exochomus quadripustulatus* (L.) is the most important species, especially because it feeds on the woolly aphid early in the season, when the population of the latter is still small.

Among the *Diptera*, the larvae of the species *Epistrophe balteata* (DE GEER), *Syrphus ribesii* (L.) and *Cnemodon vitripennis* (MEIG.) are important. One larva of the first species devoured 197 woolly aphid nymphs of the third and fourth instar before reaching larval maturity; one larva of the second species consumed 225 nymphs and one larva of the third species 173. During the summer the larval stage of *Epistrophe balteata* extended over ten days; those of the two other species were somewhat longer in their development.

Generally speaking the predators associated with the woolly aphid cannot be regarded as economic in commercial orchards.

6.2. INFLUENCE OF HYPERPARASITES

Three species of hyperparasites were bred during the investigations. They are *Pachyneuron aphidis* (BOUCHÉ), *Asaphes vulgaris* WALK. and *Ceraphron spec.* The writer is indebted to Dr CH. FERRIÈRE, Geneva for the determination of these species. Until now the *Ceraphron spec.* was not recognised as a hyperparasite of the woolly aphid. The hyperparasites are not regarded as important since the percentage of hyperparasites did not exceed 1 %.

6.3. INFLUENCE OF OTHER PARASITES

Only very scanty data are found on other parasites of the woolly aphid in the literature.

6.4. INFLUENCE OF THE OCCURRENCE OF WINGED FORMS

Only the winged sexuparae may be regarded as important in relation to the population fluctuations of the woolly aphid, as in Western Europe at least the

progeny of this form never survives. As the winged forms appear after the woolly aphid has reached its highest population density, their presence is considered to be of minor importance.

7. INFLUENCE OF CULTIVATION MEASURES ON THE POPULATION DENSITY OF THE WOOLLY APHID AND ITS PARASITE

7.1. INFLUENCE OF SOIL CULTIVATION

The cultivation of the soil may materially affect the growth of plants and in turn diminish the number of predators that may feed upon the woolly aphid.

7.2. INFLUENCE OF PRUNING

The routine pruning of the trees tends to encourage new growths, and in particular „water growths”, which are ideal for the breeding of the woolly aphid.

7.3. INFLUENCE OF SPRAYING

The effect of spraying may influence the woolly aphid population in two ways: 1. mechanically and 2. the effect of the insecticide. As will be seen in Table 23 some commonly used winter washes don't affect the parasite, since it is protected by the hollow „shell” of the mummified aphid. The influence of spraying may be considerable when some potent summer insecticides are used, but it has not been possible to study this very wide field of research.

8. TREND OF THE POPULATION DENSITY OF THE WOOLLY APHID AND ITS PARASITE IN THE FIELD

8.1. POPULATION FLUCTUATIONS OF THE WOOLLY APHID IN THE COURSE OF THE SEASON

It proved impossible to access accurately the population density at different moments during the growing season, and only approximate figures could be obtained. During winter the population density sinks to a very low level; only a few individuals on a tree seem to have survived in the second half of March. During the first part of spring the population density increases rapidly and this continues until August or somewhat earlier when a decline takes place.

The population decline continues in September, by which time very few, unhealthy aphids, almost without wax secretion are present on the trees. During the latter part of September and in October the population density rises again and then drops until breeding starts again during mid March.

The population decline in the winter can be explained by the influence of low temperatures and frosty conditions.

However, the low density which occurs in August and early September is not readily understood. The predator and parasite factor does not offer a satisfactory answer since aphids enclosed in cages in the absence of the beneficial insects also show a decline of population density.

In a preliminary experiment using high temperatures and differing air humidities it was noted that a high temperature with a low air moisture content in summer cannot be responsible for the drop in the population density.

The decrease of the woolly aphid population in summer may be related to the physiological condition of its host plant. Woolly aphid infested potted apple-seedlings kept in the laboratory showed a similar tendency of population fluctuation to colonies of aphids observed under natural conditions. On the seedlings at first a rapid increase of the population density was observed; after some months, however, a sharp decline was noticed although the plants appeared quite healthy. When most of the unhealthy aphids were removed, leaving a low population, it was observed that the wax secretion of the remaining aphids started again in a few days. It is not known in how far the increase and the decline of the population density in the field and the laboratory may be correlated.

8.2. POPULATION FLUCTUATIONS OF THE WOOLLY APHID PARASITE IN THE COURSE OF THE SEASON

Similar to the woolly aphid it was not possible to measure the exact population densities of the parasite in the field.

From Tables 24 and 25 it will be seen that the percentage of adults that hatch after hibernation in the glass tubes screened from direct sunlight and from rain, hail a.s.o. (Table 24), as well as of those hatching in the field (Table 25), is roughly 50 % (Table 24: 41 %, Table 25: 66 %). Besides this mortality, however, much more aphids in winter are mechanically removed by rain, hail, frosty conditions a.s.o.

When the parasites start emerging in the spring the population density is low, but as the season advances the density will gradually increase.

8.3. COMPARISON OF THE POPULATION DENSITY OF THE WOOLLY APHID AND ITS PARASITE AT THE BEGINNING OF THE SEASON

At the beginning of the season there is little difficulty in determining the population density of the woolly aphid and its parasite. The populations are low as represented by the figures of Table 25.

In 1954 the population density of the parasite was about three times that of the aphid, in 1955 the population densities were about equal, and in 1956 the aphid population was negligible owing to the severe winter weather.

9. COURSE OF THE PARASITISM DURING THE SEASON

The percentage parasitism was noted for a number of years, the records being made weekly. In this experiment 100 healthy aphids in about the third instar were collected from 10 different trees and were dissected under the binocular microscope, and the number of eggs and larvae counted. In Fig. 8 till 13 inclusive the graphs of these records are presented. It will be noted from Fig. 9 to 13 inclusive that the total number of eggs and larvae on any one date may not always be the same as the total of parasitised aphids (superparasitism at high parasitism percentages).

The graphs of the different years are of interest since some striking similarities will be noted.

10. FINAL DISCUSSION

1. In the years 1951 to 1955 inclusive there was a distinct peak of parasitism at the beginning of the season. This peak was notably high in 1951, 1952 and 1954 and less pronounced in 1953 and 1955. In 1951, 1952, 1953 and 1955 at this period there was a distinct peak in the egg-curve, followed one or two weeks later by one in the larval curve. Table 26 shows that there is a correlation between the hatching of the overwintering generation and the appearance of eggs in the samples.

Parasitism may be very high as was experienced in the spring of 1954, when it was calculated that the number of parasites was sufficient to parasitise the entire aphid population. However, the fact that there was not a hundred per cent parasitism suggests that the parasite was unable to find all hosts. At this time a considerable superparasitism was observed. In some years the density of the parasite is not great enough in the spring to parasitise all the aphids and indeed in 1953 and 1955 the peak of parasitism was low. The difference in the degree of parasitism in 1954 and 1955 may be partially explained by reference to Table 25. For example the ratio of the parasites and the aphids in 1954 was higher than in 1955.

Moreover in 1954 the development of the parasite was at the same date more advanced than in 1955 (Table 16); the development of the woolly aphids that had hibernated was at the same date about equal in both years.

2. In most years the percentage of parasitism is low in the early part of the year after the peak in spring. By midsummer the degree of parasitism steadily begins to rise. This is extended in most years to the late summer and autumn. The apparent rise in the rate of parasitism is mainly explained by the fall in the aphid population density. The latter is mainly explained by the condition of the host plant.

The percentage of parasitism drops off in the autumn when the parasite goes into a state of diapause; the woolly aphid continues developing until late in winter. In 1954 the peak of parasitism was very low and decreased early in the autumn; this is probably due largely to the cool, wet summer.

3. Between the peaks of parasitism in the spring and the summer (or the autumn) there may be lesser peaks, which may be correlated to the second and third generations of the parasite.

In a neglected orchard at Kloetinge in 1952 the woolly aphid population remained quite low during the whole season; the peaks of the second and third generations were very noticeable in this orchard.

The capacity of increase of *Eriosoma lanigerum* being much greater than the capacity of increase of *Aphelinus mali* and the fact that in early spring the parasite is not able to find all hosts, may account for the parasite being of little importance for the control of the woolly aphid in the Netherlands.