T. Pl.-ziekten 67 (1961): 445 – 548

SEASONAL FLUCTUATIONS OF POPULATION DENSITY OF THE CABBAGE APHID, *BREVICORYNE BRASSICAE* (L.), IN THE NETHERLANDS, AND THE ROLE OF ITS PARASITE, *APHIDIUS (DIAERETIELLA) RAPAE* (CURTIS)[1]

Met een samenvatting:

Seizoenschommelingen in de populatiedichtheid van de koolbladluis, *Brevicoryne brassicae* (L.), in Nederland en de rol van haar parasiet, *Aphidius (Diaeretiella) rapae* (Curtis)

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[1] Accepted for publication 1 Nov., 1961.

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CHAPTER I

INTRODUCTION

In The Netherlands, as in most other countries, the cabbage aphid, *Brevicoryne brassicae* (L.), is one of the most important pests of cruciferous crops. Insecticides are in general use to control the pest. However, several serious problems arose from the extensive application of the insecticides which lead to drastic changes of certain environmental components. One of these problems is the rapid resurgence of the pest after treatment, which demands more frequent application of insecticides. This was demonstrated in The Netherlands by DE FLUITER (1959) who applied several organic phosphorous insecticides for the control of *B. brassicae*. He showed that these insecticides caused a sharp drop in aphid abundance in comparison to the non-treated plots. However, in most cases the infestation started again within few days and gradually increased while it remained more or less steady in the non-treated plots. This phenomenon may be partly explained by assuming that a high mortality occurred among the natural enemies, due to the application of insecticides.

These results showed that insecticides should not be applied haphazardly. Extensive studies should be carried out beforehand to find out, among other things, (1) the level around which the population densities of *B. brassicae* are naturally regulated and (2) the role played by natural mortality factors in the process of regulation. In this way it would be possible to know when and how a man-made mortality factor, such as application of insecticides, should be introduced to achieve the best economic results without disturbing the natural mechanism of regulation.

On the background of this effect of insecticides on populations of *B. brassicae*, the present work was initiated. The work was conducted during the years 1959, 1960 and part of 1961. The scope of the study was to contribute towards a better knowledge of:

1. The natural population densities of the cabbage aphid, *Brevicoryne brassicae* (L.) in The Netherlands.
2. The influence of the parasite *Aphidius (Diaeretiella) rapae* (Curtis) on the densities of the aphid.

Another main point worked out in this paper is the seasonal change in population density of the cabbage aphid. It has been demonstrated in this area of the world that in nature, populations of different species of the aphids follow a more or less particular trend in their seasonal changes. In most cases this trend has only been qualitatively described and it has been shown that on the whole aphid populations start to develop in the spring and gradually increase to reach a peak of abundance in early summer. A mid-season breakdown of the population follows and leads to a sharp decline in aphid abundance. Though the cabbage aphid is economically one of the most important aphids in Western Europe, the seasonal trend of its population densities has not been followed in detail. As will be shown in chapter III a mid-season decline in its abundance occurs. Hence it is thought that the present study may contribute to the more general problem of the mid-season breakdown of aphid populations.

CHAPTER II

SEASONAL HISTORY AND REPRODUCTIVE POTENTIAL OF THE CABBAGE APHID, *BREVICORYNE BRASSICAE* (L.)

1. INTRODUCTION

The cabbage aphid, *Brevicoryne brassicae* (L.) was reported as early as 1734 by FRISCH in Germany (ESSIG, 1948). A considerable proportion of the literature dealing with it is mainly concerned with its geographical distribution, host plants, economic injury to the cruciferous crops, bionomics, and studies of its chemical control. Some of the important investigations on the cabbage aphid are reviewed here.

HERRICK & HUNGATE (1911) studied the biology of the aphid in New York State. PETHERBRIDGE & WRIGHT (1938) reported on its seasonal history in England. ELZE (1944) described briefly the biology of the aphid in Palestine based on the results of rearings of five independent series of generations between November and July. ESSIG (1948) stated that its hosts belong almost entirely to the family Cruciferae and listed 51 species or varieties as hosts. BONNEMAISON (1951) carried out an extensive study of the factors which affect the appearance of alate and sexual forms of *B. brassicae* and studied the morphology and biology of the different instars and forms. MARKKULA (1953) thoroughly studied the aphid in South Finland. He worked out its bionomics and seasonal history and tested the suitability of several host plants. BODENHEIMER & SWIRSKI (1957) reported on the Aphidoidea of the Middle East and compiled the synonyms, biology, phenology, and ecology of the cabbage aphid.

Since the present study is mainly concerned with the population dynamics of the cabbage aphid, some elements of its bionomics and seasonal history are given in this chapter together with some quantitative data on its reproductive potential in the two years of observation.

2. SEASONAL HISTORY

A. Hibernation

It has been established that the production of sexuparae and sexuales depends on the combined action of photoperiod and temperature (BONNEMAISON, 1951; KENNEDY & STROYAN, 1959; LEES, 1959). Consequently overwintering of *B. brassicae* in different areas of the world ranges from exclusively as winter eggs to exclusively as virginoparae (table 1).

In The Netherlands, during the three winters 1958–1959, 1959–1960, and 1960–1961, the present writer examined a considerable number of brussels sprout plants kept for seed in the area of Wageningen, but did not encounter any of the active stages of the cabbage aphid. Only overwintering eggs were found.

Another main site of winter eggs is the large fields of Colza, *Brassica napus* L., which is planted in autumn, overwinters in the fields and is harvested the following summer. In years with favourable conditions for a heavy autumn infestation such as 1959, enormous numbers of winter eggs are deposited on the plants and a heavy infestation ensued the following spring. Late in June and early in July 1960 the vast fields of Colza in Flevoland and N.E. Polder were

TABLE 1. Overwintering of *Brevicoryne brassicae* (L.) in different areas of the world

Author	Locality	Condition of overwintering *B. brassicae*
MARKKULA (1953)	Finland	Exclusively as eggs
PETHERBRIDGE & WRIGHT (1938)	England	Normally as eggs, but small colonies of virginoparae may survive mild winters
VAN HOOF (1954).	Netherlands (North Holland)	Only as eggs
Personal observations of the present writer between 1959–1961 .	Netherlands (Wageningen district)	Only as eggs
BONNEMAISON (1951)	France (near Paris)	Mainly as virginoparae, but with small proportion of sexuales and eggs
BODENHEIMER & SWIRSKI (1957)	Israel	Exclusively as virginoparae
Personal observations of the present writer	Egypt (U.A.R.)	Exclusively as virginoparae

inspected; they proved to be heavily infested with the cabbage aphid. Owing to the effect of grouping of the aphids and ageing of the plants, at that date almost all the aphids were alatae. These eventually flew off the plants and were a very serious source of infestation for the newly cultivated cruciferous crops.

B. Early generations of B. brassicae on the overwintering plants

As will be shown later in this chapter, the average number of winter eggs per brussels sprout plant in the experimental field near Wageningen was about 5644 in the winter 1959–1960. Since about 70% of these eggs hatched, the apparent initial number of fundatrices could be placed at about 4000 per plant. The actual number, however, was far below this value; field observations showed that a large proportion of the newly hatched fundatrices failed to survive. Frequently they were found dead within a few millimeters from the empty egg shells. This high mortality may be attributed to the type of weather that prevailed in the spring of 1960 (fig. 1). During this period alternating spells of rather high temperature, up to a maximum of 19 °C, which stimulated the hatching of the eggs were followed by low temperatures, down to a minimum of −6 °C, which killed most of the young fundatrices.

In the beginning, the hatching fundatrices congregated mainly on the leaflets of the sprouts and then they moved towards the new growth of the flower stalks which coincided with the hatching period. By the time the new brussels sprout fields were planted, about six generations of *B. brassicae* had already developed on the old overwintered plants, and by the end of that period almost all the seed stalks were literally covered with aphids. Owing to the effect of grouping of the aphids and the drying and ageing of the flower stalks, the great majority of the larvae developed into alatae which dispersed to the newly planted fields. The observations support the idea that the seed plants are the main source of infestation for the new crops (VAN HOOF, 1954).

C. Infestation of the new crops

Once the alate adults dispersed from the old overwintered plants and settled down on the new ones, they started to form colonies and caused the infestation for the new season. The intensity of this infestation and the increase in popu-

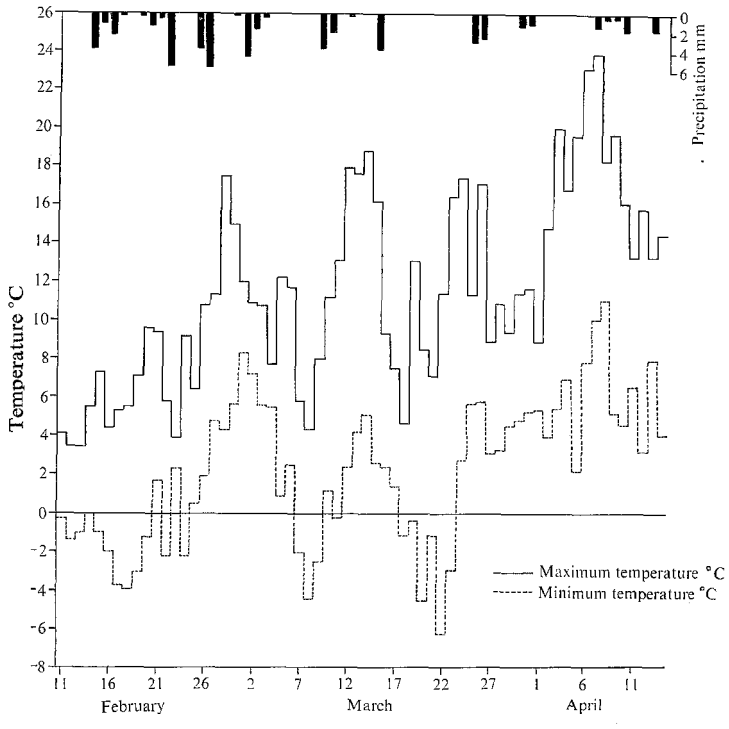


FIG. 1. Maximum and minimum daily temperature °C at 10 cm above soil level and precipitation in early 1960. (Data obtained from the meteorological station near the experimental fields near Wageningen)

lation density during the main part of the season will be dealt with in CHAPTER III. Later in the season, owing to low temperature and a short photoperiod, the sexual forms appeared. In the brussels sprout fields sampled near Wageningen, the first winter egg of *B. brassicae* was found in 1960 on September 15 while in 1959 it was found on September 4.

Late in the season the ratio of sexual females to viviparous females (alate and apterous) gradually increased. The last counts made in 1959 and 1960 showed the ratios given in table 2.

TABLE 2. Ratio of oviparous to viviparous females late in the season

Field and crop	Date	Average number of adult females of *B. brassicae* per plant			Percentage of sexual females to total of all females
		Apterous viviparae	Alate viviparae	Oviparae	
Brussels sprouts, field A, Wageningen	10-XI-'59	20	10	1230	97.6%
Brussels sprouts, field B, Wageningen	20-XI-'59	35	1	384	91.4%
Brussels sprouts, field C, Wageningen	27-X -'60	0	0	4	100 %

3. SOME QUANTITATIVE DATA ON THE SEASONAL HISTORY OF *B. brassicae* IN THE NETHERLANDS

A. Number of eggs per brussels sprout plant

Since the number of winter eggs per plant depends on the degree of aphid infestation in the previous autumn and early winter, it varies from year to year.

In order to determine the number of eggs of *B. brassicae* per sprout plant, in each of the two winters 1959–1960 and 1960–1961, a number of overwintering sprout plants, which were kept for seed production, were taken at random from the experimental field near Wageningen. The eggs present on the leaves, the sprouts, and the stalk of each of the plants were counted. The counts were made in winter time before any hatching took place. The results obtained during the winter 1959–'60 are shown in table 3.

TABLE 3. Number of overwintering eggs of *B. brassicae* on brussels sprout plants in 1959–1960

Plant number	Number of eggs per plant			
	Leaves	Sprouts	Stalk	Total
1	958	1834	324	3116
2	1299	4331	597	6227
3	2534	2848	2679	8061
4	1421	3182	942	5545
5	1744	1739	2286	5769
6	1319	6486	950	8755
7	1287	893	702	2882
8	905	2993	901	4799
Total	11467	24306	9381	45154
Mean number of eggs per plant	1433	3038	1173	**5644**

These results show the following:

1. In the year 1959, which was characterized by a very heavy infestation of *B. brassicae* late in the season, the number of overwintering eggs per sprout plant averaged 5644 with a minimum of 2882 and a maximum of 8755 eggs per plant.

2. More eggs were deposited on the sprouts. An average of 53.8 % was found on the sprouts while an average of 25.4 % was on the leaves and 20.8 % on the stalk.

This distribution is of practical importance, owing to the fact that by the time the eggs start to hatch, the sprouts would be removed from the field for marketing. A good proportion of the leaves would be aged and shed. Most of the eggs or the hatching fundatrices they carry would probably perish. In practice, it is probable that the fraction of the eggs deposited on the stalks, being about 20 % of the total, forms the main source of infestation for the new season.

In the year 1960 which had an extremely light infestation late in the season, 25 sprout plants were sampled. The average number of eggs per sprout plant was only 2.3 with a minimum of zero and a maximum of 25 eggs per plant. All the eggs were found on the sprouts.

B. Period and percentage of egg hatching

The period of hatching and the percentage of eggs that hatch vary from year to year and from place to place, depending on the conditions prevailing during the winter and early spring.

In 1959, one hundred eggs of *B. brassicae* were marked on overwintering sprout plants in the field near Wageningen. They were examined once every week starting 3-II-'59 till 20-IV-'59. Due to a lack of sufficient plants in the field, the initial number of eggs was too small to draw generalized conclusions. However, it was found that no eggs hatched until 2-III-'59. The first eggs were found hatched on 9-III-'59 and the last on 13-IV-'59. Most of the hatching of eggs took place late in March and early in April. Sixty percent of the eggs shrivelled and only 40% gave rise to fundatrices.

In the autumn of 1959 the infestation of *B. brassicae* was very high and resulted in a large number of eggs on the overwintering sprout plants (table 3). Every week, starting 11-II-'60, a large number of eggs varying between 2211 and 3272 was taken at random from the sprouts, the leaves and the stalks of the sprout plants and classified into sound, shrivelled and hatched eggs. This inspection continued until 14-IV-'60 when only 0.1% of the inspected eggs were still apparently healthy. The results obtained are shown in table 4 and fig. 2.

TABLE 4. Hatching of winter eggs early in 1960

Date	Total number of eggs inspected	Condition of eggs (in %)		
		Sound eggs	Shrivelled eggs	Hatched eggs
11- II-'60	3272	88.6	11.4	0
18- II-'60	2750	90.0	10.0	0
25- II-'60	3004	88.4	11.6	0
3-III-'60	2688	81.2	15.0	3.8
10-III-'60	3069	78.3	17.7	4.0
17-III-'60	2421	44.2	28.9	26.9
24-III-'60	3072	30.7	26.9	42.4
31-III-'60	2648	10.1	24.9	65.0
7-IV-'60	2211	2.3	27.8	69.9
14-IV-'60	2519	0.1	29.6	70.3

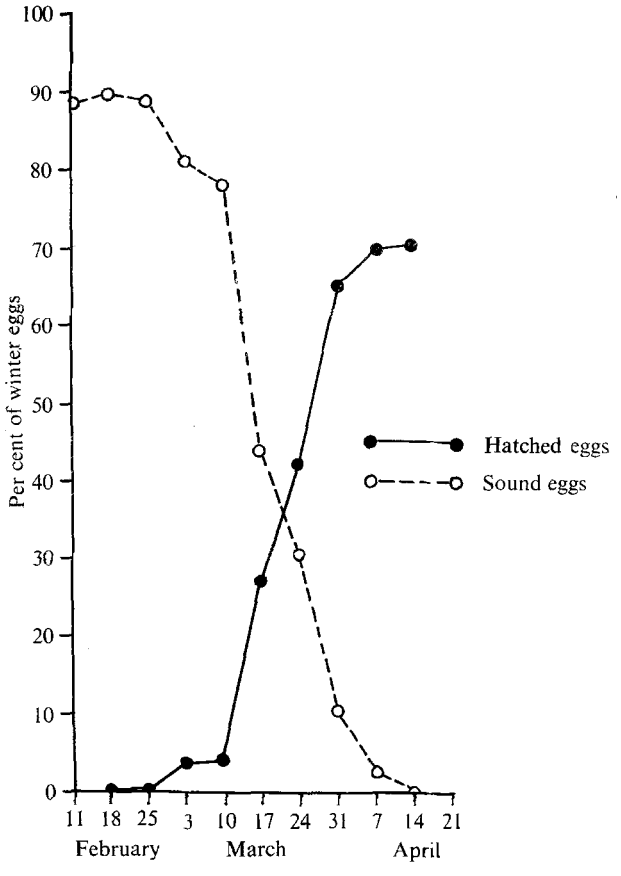
From the few observations made in 1959 and the more extensive data of 1960 the following conclusions can be drawn:

1. In 1959 the first eggs hatched some time between 2-III-'59 and 9-III-'59 and the last around the middle of April. Out of 100 eggs observed only 40% hatched whereas the remaining 60% shrivelled and gave no fundatrices.

2. In 1960 the first eggs hatched about one week earlier; between 25-II-'60 and 3-III-'60 and the last about the middle of April. By that date about 70% of the eggs were hatched while the remaining 30% had collapsed and failed to hatch. About 87% of the eggs which hatched did so in the last three weeks of March. The significance of this fact will be discussed in CHAPTER VII in relation to the role of parasitism in the control of the populations of the cabbage aphid in spring.

3. From the eggs which failed to hatch, 30% in 1960, only 11% had collapsed by the end of February and about 18% by the tenth of March. This ratio sud-

FIG. 2.
Hatching of winter eggs of *B. brassicae* early in 1960



denly increased during the week of 10 to 17-III-'60 from about 18% to about 29%. The last inspection made at the middle of April showed that 29.6% of the eggs had shrivelled.

C. Number of generations per year

In *B. brassicae*, as in most other aphids, the generations inevitably overlap right from the beginning. This is due to a considerably shorter developmental period as compared with a rather long reproductive period. This means that the early born nymphs complete their development and start depositing nymphs of a new generation while their own mothers are still reproducing. This leads to the fact that, whether in the field or in the laboratory, all stages of the aphids will be found in the colonies within a rather short time after the initial infestation has taken place. It is therefore impossible to speak about definite separated generations in *B. brassicae*.

However, to get an idea about the number of generations per year in The Netherlands, a group of nymphs born on one particular day were reared on potted cauliflower plants in cages (plate 1, A) in an open outdoor insectary. Two series of generations were followed until winter when the generations

ended through the development of oviparous females which deposited winter eggs. Series A, which represented the maximum number of generations, consisted always of the first born nymphs, reared until they deposited their first progeny. Series B, which represented the minimum number of generations, consisted of nymphs, reared until they developed into adults; these adults were allowed to deposit their nymphs until the day on which the last nymph was deposited. This day marked the end of the generation. A new generation was then started with the newly born nymphs. In this way, starting on 2-IV-'59 and on 17-III-'60, the maximum and minimum number of generations were determined. The results are shown in tables 5 and 6.

These results show that in The Netherlands a maximum of 14 generations of *B. brassicae* and a minimum of 3–4 generations occurred in 1959 and 1960. These figures, however, represent the ultimate extreme cases by taking always on one hand the very first reproducing adult and on the other hand the very last nymph produced by the very last producing adult. Judging from the observations taken from the normal breeding, so excluding the extreme individuals and taking only the more representative middle groups, it could be stated that, for all practical purposes, the number of generations of *B. brassicae* in The Netherlands ranges between 6 and 11 per year.

In 1959 the rate of development was highest in August, when it took 10 days for one generation to develop, whereas in 1960 the maximum rate occurred in June, when a generation developed in 8 days. Longer durations prevailed earlier and later in the seasons so that in the period under investigation in 1959 the longest duration of a generation was 27 days in April and 56 days in October and November. In 1960 it was 31 days in March and April and 37 days in October and November. The length of the reproduction period of the individual, which is in fact the main factor responsible for the overlapping of generations, is also affected by seasonal conditions. It ranged from a maximum of 29 days in the middle of the season to a maximum of 44 days at the end.

D. Effect of temperature on the rate of development

It has been shown in the previous section that the duration of the generations varied in the different periods of the season. As temperature is believed to be one of the most important factors responsible for this variation, an experiment was carried out to determine the extent of its effect.

Ten newly-born nymphs were placed on each of a cut cauliflower leaf inserted into a small glass vial filled with water and stoppered with a plug of cotton wool. Each leaf was placed in a glass dish covered with cheese cloth (plate 1, B). The vial and the leaf were laid flat on a filter paper covering the bottom of the dish. Leaves were changed every other day while the water in the vials was replaced daily. Five of such dishes were put in each of seven chambers of a serial thermal cabinet. When the cauliflower leaves were changed the nymphs were carefully transferred from the old leaf to the new one. The nymphs of chambers 3, 4, 5, 6 and 7 (with a lowest temperature of 10 °C) had been deposited by their mothers inside these chambers. The nymphs of chambers 1 and 2 (average temperature about 5 °C) had been deposited at room temperature and a few hours later they were placed in the dishes in their respective chambers. A photoperiod of sixteen hours was used in all cases. The results are shown in table 7 and fig. 3.

TABLE 5. Maximum and minimum number of generations of *B. brassicae* (1959)

Generation number	Series A: Maximum number of generations				Series B: Minimum number of generations			
	Date		Duration of generation in days	Remarks	Date			Duration of generations in days (longest developmental period + longest depositing period)
	Mother born	First nymph of following generation born			Mother born	Last aptera of following generation giving birth to		
						First nymph	Last nymph	
1	2-IV	29-IV	27		2-IV	10-V	20-VI	38 + 41 = 79
2	29-IV	14-V	15		20-VI	9-VII	7-VIII	19 + 29 = 48
3	14-V	30-V	16		7-VIII	22-VIII	30-IX	15 + 39 = 54
4	30-V	13-VI	14		30-IX	1-XII[2])		62
5	13-VI	27-VI	14					
6	27-VI	10-VII	13					
7	10-VII	23-VII	13					
8	23-VII	4-VIII	12					
9	4-VIII	14-VIII	10					
10	14-VIII	24-VIII	10					
11	24-VIII	5-IX	12					
12	5-IX	18-IX	13	some sexuales				
13	18-IX	7-X	19	mostly sexuales				
14	7-X	2-XII[1])	56	all sexuales				

[1]) This date marked the first nymph to moult into adult because they were all sexuales, so no nymphs were further deposited.
[2]) This date marked the last nymph to moult into adult, they were all sexuales so no nymphs were deposited.

TABLE 6. Maximum and minimum number of generations of *B. brassicae* (1960)

Generation number	Series A: Maximum number of generations				Series B: Minimum number of generations			
	Date		Duration of generation in days	Remarks	Date			Duration of generations in days (longest developmental period + longest depositing period)
	Mother born	First nymph of following generation born			Mother born	Last aptera of following generation giving birth to		
						First nymph	Last nymph	
1	17-III	17-IV	31		17-III	30-IV	7-VI	44 + 38 = 82
2	17-IV	11-V	24		7-VI	21-VI	20-VII	14 + 29 = 43
3	11-V	27-V	16		20-VII	7-VIII	20-IX	18 + 44 = 62
4	27-V	9-VI	13		20-IX	27-IX	all breeding	
5	9-VI	17-VI	8				died out	
6	17-VI	28-VI	11					
7	28-VI	12-VII	14					
8	12-VII	25-VII	13					
9	25-VII	5-VIII	11					
10	5-VIII	19-VIII	14					
11	19-VIII	5-IX	17					
12	5-IX	24-IX	19	some sexuales				
13	24-IX	21-X	27	mostly sexuales				
14	21-X	27-XI	37	nearly all sexuales				

TABLE 7. Effect of different temperatures on rate of development of *B. brassicae*

Chamber number	Temperature in °C			Duration in days						
				Development from newly born nymph to newly moulted adult		Pre-larviposition period		Total duration of generation from first nymph till first nymph in the next generation		
	Max.	Min.	Aver.	Max.	Min.	Max.	Min.	Max.	Min.	Aver.
1	6	3.5	4.9	All died, in the first nymphal instar, within 10 days.						
2	9	2	5.5	All died before moulting to adult. The last one died in the fourth nymphal instar after 29 days in that instar.						
3	16	10	13.1	36	26	7	5	43	31	37
4	21	15.5	17.8	16	9	4	2	20	11	16.5
5	26.5	19	23.2	13	8	1	1	14	9	11
6	32	24	28.2	11	8	-[1]	-	11	8	10
7	34.5	27	30.9	13	10	-	-	13	10	11.5[2]

[1]) It took only a few hours for the newly moulted adults to start depositing nymphs.
[2]) All but two of the fifty nymphs died before reaching maturity.

This experiment shows that temperature significantly affected the duration of a generation of *B. brassicae*. At low temperatures, a complete generation could not develop due to the fact that all first instar nymphs died. At a mean temperature of 5.5 °C, some of the nymphs survived till the fourth instar, but none of them reached maturity.

With an increase of the average temperature, generations were completed. At an apparent optimum range of temperature of about 28 °C, the duration of a generation was at a minimum (fig. 3). When the temperature increased still further, the few surviving individuals showed a slightly prolonged development, 11.5 days at a mean temperature of 30.9 °C. At this high temperature only two adults were finally obtained from an initial number of 50 first instar nymphs, while most nymphs died in the first instar. On the whole, under the conditions applied in this experiment, the shortest duration of a generation was 8 days whereas the maximum duration was 43 days.

From this experiment and from the results of field and laboratory observations in 1959 and 1960, it can safely be concluded that the above mentioned values (8–43 days) represent the actual extreme limits for *B. brassicae* in The Netherlands.

Temperature is therefore a very important factor affecting population growth in the cabbage aphid.

4. FECUNDITY

An essential factor determining the rate of growth of an insect population is the reproductive potential. Investigations on this factor in aphids are more complicated than in most other insects because of the presence, almost throughout the season, of two different types of adult females, *viz.* apterous and alate virginoparae with different potentials. Furthermore, a third type, the sexual oviparous females, appears later in the season.

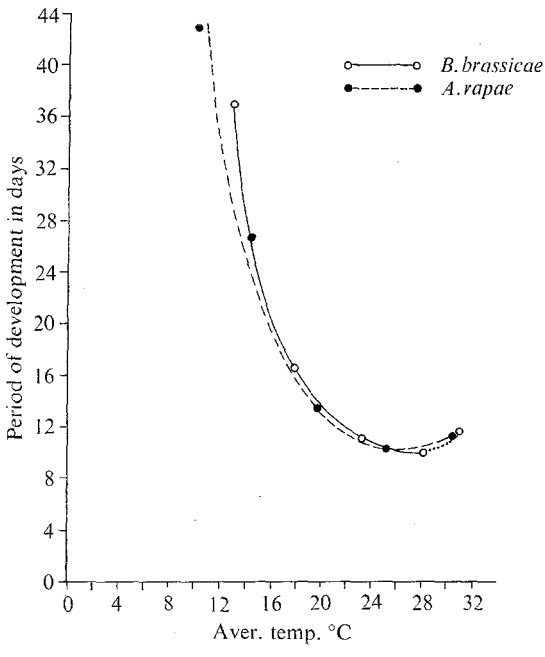


FIG. 3.
Effect of temperature on rate of development of *B. brassicae* and *A. rapae* (from newly born nymph to adult *B. brassicae*, and from egg to adult *A. rapae*)

The fecundity of females of *B. brassicae* has been studied in different parts of the world and the results were different (HERRICK & HUNGATE, 1911; ELZE, 1944; BROADBENT, 1949; BONNEMAISON, 1951; MARKKULA, 1953). So far the fecundity of the cabbage aphid has not been studied in The Netherlands. It is believed, however, that data on the fecundity of viviparous adults under local conditions are essential in studies of the population dynamics of the aphid.

A. Material and method

Several groups of apterous and alate virginoparae were secured in various periods of the season 1959 and 1960 by isolating last instar nymphs individually in glass dishes. The newly moulted adults were reared, also individually, either on leaves of brussels sprouts or cauliflower in glass dishes or in lamp glasses. The glass dish (plate 1, B) and the method of providing and changing the plant leaf is the same as has been described earlier (p. 456).

Lamp glasses (plate 2, A) were more convenient for the leaves of the brussels sprouts. A piece of cotton wool was wrapped around the upper part of the leaf petiole to fit it into the neck of a 25 cc Erlenmeyer flask. The petiole was then inserted into the flask which was filled with water. The leaf was provided with a rather stiff paper collar to prevent the aphid from falling off and failing to crawl back onto the leaf. The flask was placed on a petri dish covered with a filter paper disc and the whole "set-up" was covered with a lamp glass closed at the top with cheese cloth. Twice a week the water in the flasks was replaced and a slice of the petiole was cut off to promote water uptake. In this way it was possible to change the leaves at longer intervals than in the glass dish method.

BONNEMAISON (1951), rearing *B. brassicae* on such cut leaves dipped in water, stated that the aphids developed in an excellent way. Their fecundity was generally superior to those reared on potted plants. The use of several nutritive solutions instead of water did not keep the leaves in better condition.

In the present work, it was observed that, though the aphids were very carefully transferred from their original host plants to the leaves, some of them did not readily settle down on the new hosts. This led to an abnormally high initial mortality which occurred in the first few days. Therefore, aphids which died within less than one week, were considered as dying prematurely and were excluded from the experimental data. Each unit was inspected daily throughout the life of the adults and the nymphs deposited daily were recorded and removed.

B. Results

The results of these series of experiments are summarized in table 8.

Three important values can be obtained from these results, *viz.*:

1. The average total number of nymphs deposited per female.
2. The average longevity of the female.
3. The average number of nymphs deposited per female per day.

Still another important characteristic of *B. brassicae* could be obtained from these series of experiments, *viz.* the daily rate of reproduction per female throughout its life (fig. 4 and 5).

The results of these series of experiments can be summarized as follows:

1. The apterous virginoparae deposit more nymphs than the alate ones. Under the various experimental conditions involved, the number of nymphs deposited per apterous female varied between about 26 and 29. These numbers agree with the averages obtained in some previous studies (ELZE, 1944; MARKKULA, 1953) but they are lower than the numbers given by other authors, especially BONNEMAISON (1951) who obtained considerably higher numbers. He also used cut leaves, but he worked under more optimum conditions either by using constant temperatures (17 °C or 24 °C) or by alternating these same temperatures daily. In the latter case he obtained the highest averages ranging from 47 to 63 nymphs. Still it has to be stated that, even under naturally fluctuating temperatures, BONNEMAISON's numbers are higher than the present results. This could be attributed, at least partly, to the fact that he reared the aphids exclusively on white cabbage whereas the present rearings were carried out on cauliflower or brussels sprout leaves. MARKKULA (1953) concluded that females of *B. brassicae* reared on white cabbage leaves yield more progeny than those reared on the other two crops.

2. The alate virginoparae deposited an average number of nymphs ranging from about 13 to 23 nymphs per female. These results agree with the results of other authors (BROADBENT, 1949; BONNEMAISON, 1951; MARKKULA, 1953) who found an average of 12 to 21 nymphs per alate female. It is obvious that apterous virginoparae respond to different conditions more than alatae. The latter are naturally predisposed for dispersion and so may live under more varying conditions than the former.

3. Under conditions used in these series of experiments, the maximum number of progeny per apterous virginopara was 53 nymphs whereas it was 35 for the alate one.

TABLE 8. Fecundity and longevity of *Brevicoryne brassicae*

A. APTEROUS VIRGINOPARAE

Exp. no.	Site	Food plant and condition	Date of start of experiment	Number of virginoparae	Longevity of adults in days		Progeny				Temperature °C		
					Max.	Aver. and S.E.[1]	Aver. no. of nymphs per ♀ and S.E.	Range of total progeny per ♀	Aver. no. of nymphs per ♀/day[2]	Max. no. of nymphs per ♀/day	Max.	Min.	Aver.
1	Outdoor insectary	Cauliflower, in glass dishes	11-VIII-'59	45	49	21.2±1.56	27.5±1.8	7–53	1.29	7	29.2	1.7	19
2	Laboratory room	Sprouts, in lamp glasses	31-VIII-'59	46	35	21.1±0.96	28.5±1.55	16–49	1.35	12	22.1	13.9	19
3	Laboratory room	Cauliflower, in glass dishes	29-IX-'59	50	33	24.2±0.9	26.2±1.04	8–42	1.08	9	19.8	12.0	17
4	Outdoor insectary	Cauliflower, in glass dishes	23-VI-'60	22	43	27.8±2.03	29.3±2.78	7–43	1.05	6	30.0	6.0	16

B. ALATE VIRGINOPARAE

1	Outdoor insectary	Cauliflower, in glass dishes	11-VIII-'59	45	34	19.4±1.13	18.5±0.95	7–32	0.95	7	29.2	1.7	19
2	Laboratory room	Sprouts, in lamp glasses	17-IX-'59	22	36	23.5±1.47	16.1±0.59	12–21	0.68	12	21.3	13.9	18
3	Laboratory room	Cauliflower, in glass dishes	29-IX-'59	48	30	16.3±1.08	13.1±0.7	4–21	0.8	10	19.8	12.0	17
4	Laboratory room	Sprouts, in lamp glasses	13-X-'59	20	48	26.2±3.31	18.8±1.11	11–33	0.72	15	19.8	12.0	16
5	Laboratory room	Cauliflower, in glass dishes	25-X-'60[3]	16	30	19.4±2.01	23.4±2.11	10–35	1.21	9	23.0	15.0	20

[1]) S.E. = standard error = standard deviation of the mean.
[2]) This value is obtained by dividing the total number of nymphs produced by all females involved in the experiment by the total number of days those females lived.
[3]) This group was given 16 hours of day-light per day.

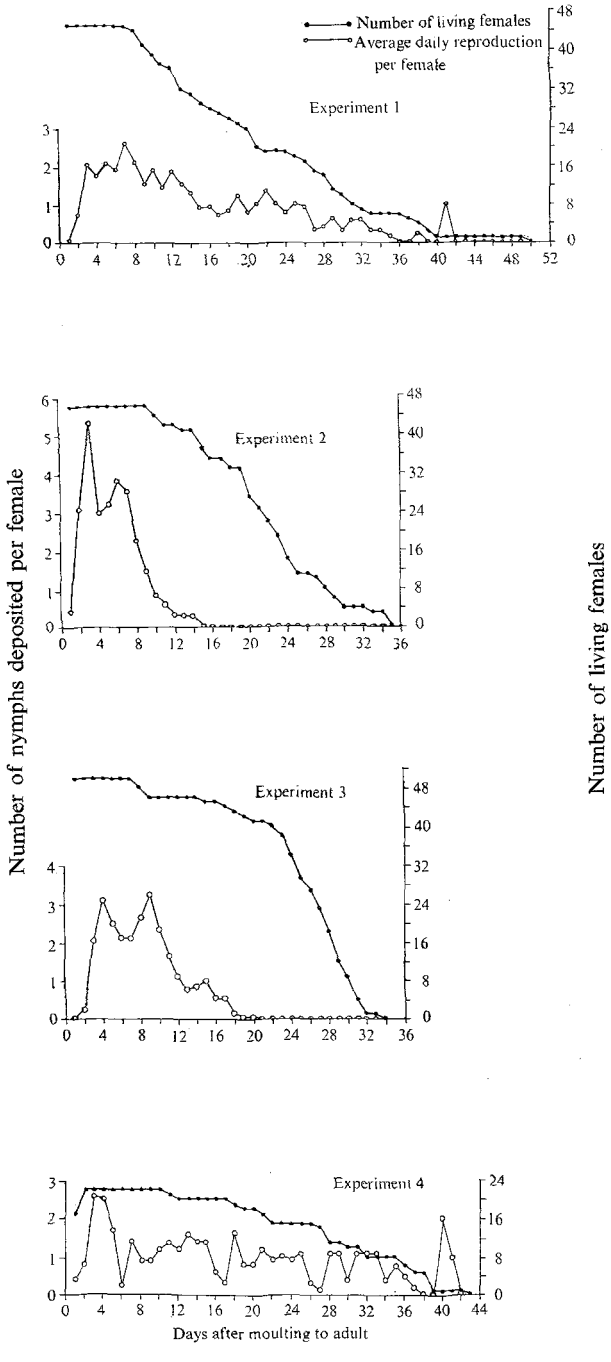


FIG. 4. Daily rate of reproduction and mortality of *B. brassicae* (apterous virginoparae). Explanation see table 8

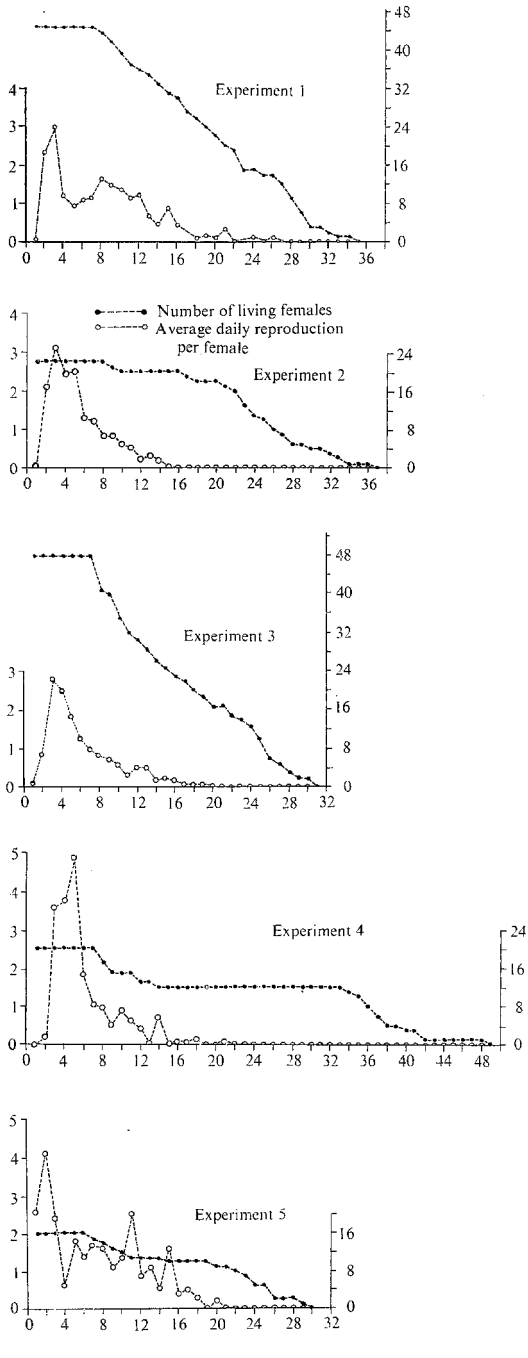


FIG. 5. Daily rate of reproduction and mortality of *B.brassicae* (alate virginoparae). Explanation see table 8 and fig. 4

4. When apterous and alate virginoparae were reared under the same conditions, there was a tendency for the apterous to live longer than the alate ones.

5. The value representing the number of nymphs deposited per female per day is generally higher in case of the apterous virginoparae than in the alate ones.

6. Fig. 4 and 5 show that, though deviations may exist, the average daily reproduction follows a general pattern in either the alate or the apterous virginoparae. Other conditions being equal, the alatae reach the peak of their daily reproductivity slightly earlier than the apterous ones, after which the rate drops more sharply and finishes also earlier.

In most cases in apterous virginoparae, two peaks in the daily larviposition could be discerned a few days apart, followed by a gradual decline. This type of daily reproduction means that normally the alatae effectuate most of their reproduction capacity at a comparatively earlier date than the apterae. This fact is of importance in determining the effect of parasitism in reducing the number of progeny produced by each of the two forms of aphids when parasitized in a late stage (see p. 513).

CHAPTER III

SEASONAL COURSE OF ABUNDANCE OF *BREVICORYNE BRASSICAE* (L.) IN THE FIELD

1. INTRODUCTION

Having obtained the basic information mentioned in the previous chapter, the next step was to follow the population changes of the aphid throughout the season. As mentioned in chapter I, aphid populations in the temperate regions show a characteristic seasonal trend. Four examples of such a trend will be given here, concerning aphids infesting different groups of host plants.

DE FLUITER (1954) studied the phenology of the strawberry aphid, *Pentatrichopus fragaefolii* Cook. in The Netherlands and stated that after mild winters or with favourable climatic conditions in spring and early summer, the populations of the aphid increase to a high peak in late June or during July which is always followed by a rapid decline. Low population densities persist in August and early September but increase again with favourable autumn weather in late September and October.

DUNN & WRIGHT (1955) studied the populations of the pea aphid, *Acyrthosiphon pisum* (Harris) in England from 1948 to 1951 on several leguminous crops. They have demonstrated that the aphid follows a more or less typical trend of abundance, with an acute increase early in the season to a peak followed by a sharp decline. Later, if conditions are favourable, a new peak of abundance may occur. The timing of the first peak shifted back and forth from May to July according to the different crops, different planting time and different years. On late crops the same trend of abundance occurs with a peak in September or October.

The same trend of a population increase followed by a sudden depression

has been observed for aphids on potatoes. BROADBENT (1953) stated that typically in England the aphid infestation of potatoes starts with a few alatae depositing nymphs which develop into apterae and multiply until a maximum is reached usually during July. The aphid populations then decline rapidly and occasionally rise again towards the end of the season. However, he added that sometimes under favourable conditions the decline may not be appreciable and the population may remain high throughout the late summer.

EVENHUIS (1958, and unpublished notes) studied the population dynamics of the woolly apple aphid, *Eriosoma lanigerum* (Hausm.), at Wageningen and the Province of Zealand. He has shown that generally the population of the aphid starts with a very low initial density in May which gradually increases till it reaches its maximum late in July. This is followed by a gradual decline to reach a minimum late in September. A second increase may occur and reach another peak of infestation towards the end of October followed by a decline late in November.

It is thus indicated that generally the aphid populations are characterized by two declines in numbers, one occurs in mid-season and one in late autumn. The autumn decline could easily be attributed to physical factors such as low temperature and a short photoperiod. In most of the above mentioned instances these factors cause the occurrence of sexual forms, hence winter eggs instead of virginoparae are deposited. On the other hand, many ecological factors are responsible for the mid-summer decline. Thus, there are more speculations about the cause of that decline which affects both autoecous non-migrating species of aphids, such as *A. pisum*, *P. fragaefolii*, and *B. brassicae*, as well as heteroecous migrating species, such as *Myzus persicae* (Sulz.).

In most of the examples referred to, the most probable physical factor causing the mid-summer decline was heavy rain (BROADBENT, 1953; DUNN & WRIGHT, 1955). Also other factors such as very high temperature and strong light which inhibit reproduction have been mentioned (MÜLLER, 1952; BROADBENT, 1953; DUNN & WRIGHT, 1955).

The biotic factors which have been mentioned in this connection are:

1. Condition of the host plant: In several occasions in case of pea aphid infestations on various leguminous crops, DUNN & WRIGHT (1955) mentioned cutting of the crop as one of the main factors for the drop of the aphid population. The physiological condition of the plant is more likely to be of particular importance in the population dynamics of the aphids because it affects their survival, development and reproduction (KENNEDY & STROYAN, 1959). In several cases the decline in aphid populations has been attributed to increased maturity of the host plant which rendered it unfavourable as food. However, this explanation seems improbable in some cases, such as the pea aphid referred to above, where a later increase in populations might occur in the same progressively more mature and dessicated plants (DUNN & WRIGHT, 1955). Furthermore, during a particular mid-season period, the decline is usually general on different cultivated crops, as well as weeds, all in different conditions of growth and maturity. Therefore, generally the number of most species of aphids is simultaneously very low during that period (MÜLLER, 1952; BROADBENT, 1953).

In case of the strawberry aphid, *P. fragaefolii*, DE FLUITER (1954) concluded that the peaks of aphid infestation always correlate with periods during which young strawberry leaves, which are preferred by the aphids, are abundant.

EVENHUIS (1958) stated that the mid-summer decline in the woolly apple aphid cannot be readily attributed to the effect of natural enemies or to the climatic factors. He believed that such a decline may be related to the physiological condition of the host plant.

2. The production of winged forms: The change from apterae to alatae, which leads to a mass migration of the winged adults, has been mentioned as a cause of the rapid decline after the summer maximum (BROADBENT, 1953; DUNN & WRIGHT, 1955). However, this also cannot stand the same argument that the decline is general, regardless of the condition of the host plants which affects the appearance of the alate forms. Moreover, the decline occurred irrespective of the proportion of immature winged forms in the population (DUNN & WRIGHT, 1955).

3. Natural enemies, such as predators, parasites and pathogens: EVENHUIS (1958) concluded that the effect of natural enemies cannot offer a satisfactory explanation to the summer decline of the woolly apple aphid. He stated that aphids enclosed in cages in the absence of parasites and predators also show a similar decline of population density. On the other hand, the natural enemies were mentioned in other instances as one of the factors responsible for the decline in aphid populations (BROADBENT, 1953; DUNN & WRIGHT, 1955).

BROADBENT (1953) cited instances where the Hymenopterous parasites and the Coccinellid predators prevented a population of *M. persicae* from developing on potatoes in England. Furthermore, he mentioned that entomogenous fungi occasionally deplete potato aphid populations when the weather is warm and damp. The natural enemies mentioned by DUNN & WRIGHT (1955) as partly responsible for the mid-season decline of the pea aphid are Hymenopterous parasites, Coccinellidae (especially *Coccinella septempunctata* L.), Syrphid larvae and entomogenous fungi.

It has been mentioned in CHAPTER I, that such a study of the numerical changes in a field population of the cabbage aphid was not carried out in detail before. In the following part the seasonal abundance of the aphid in The Netherlands will be dealt with.

2. POPULATION CHANGES OF B. BRASSICAE IN THE FIELD IN 1959 AND 1960

The population changes of the cabbage aphid were followed throughout the main season of infestation in the years 1959 and 1960 in brussels sprout fields located on a heavy clay soil near Wageningen.

A. Material

In 1959 two adjacent fields were used for sampling:

Field A: The area of this field was about 250 m^2 (18×14 m). Eight hundred cauliflower plants (variety Climax) were transplanted into the field on 7.IV.'59 in 32 rows of 25 plants each. On 17.VI.'59, 744 brussels sprout plants (variety Westlandse) were transplanted alternatively between the cauliflower rows, so as to form 31 rows of 24 plants each. The distance between the brussels sprout plants was about 60 cm in each direction. On 7.VIII.'59 the cauliflower plants

were removed and the sprout plants were allowed to remain till the end of the season.

Field B: The area of the field was about 308 m² (22 × 14 m). On 23.IV.'59 twelve rows of potato plants (variety Dore) were planted, each row had 42 hills, which gave a total of 504 hills. On 11.VI.'59, brussels sprouts, same variety as field A, were transplanted into the field in rows between the potato rows, so that 468 sprout plants were transplanted in 13 rows each with 36 plants. The distance between the sprout plants was 60 cm in each direction except across the potato rows where it was 180 cm. On 17.VII.'59, the potato plants were removed and the brussels sprouts were allowed to remain till the end of the season.

The summer of 1959 was dry and so the two fields were water-sprinkled several times during the season. Sprout plants in field A were less vigorous than those in field B mainly because some parts of field A were higher and so the soil was comparatively drier than in field B. Besides, the plants were more crowded in field A.

The two fields A and B were designed so as to represent roughly what happens in practice when early crops, such as early potatoes and cauliflower, are infested with aphids (mainly *B. brassicae* and *M. persicae* on cauliflower, and *M. persicae* on potatoes). These infested early crops are thought to act as a suitable habitat for building up populations of predators and parasites of aphids. These natural enemies would disperse to the new crop of brussels sprouts either when the early crops are removed or when dispersal is induced by decrease of the aphid density.

In 1960 only one field (field C), about 192 m² in area (16 × 12 m), was sampled. This field was situated on the same site of the fields of the previous year. It was surrounded on each side by a row of brussels sprout seed plants. On 18-V-'60, 567 brussels sprout plants were transplanted into the field in 27 rows each with 21 plants. Distance between the plants was about 60 cm in all directions.

In all three fields no chemical treatments were applied.

B. Sampling and counting

The "three-leaf method" was used in sampling all three fields. The method was used by ANSCOMBE (1948) for estimating aphid numbers on potato plants and later was adopted by CHURCH & STRICKLAND (1954) for cabbage aphids on brussels sprouts. In general terms the method comprises the counting of aphids on each of three stratified leaves per plant (one upper, one middle and one lower leaf), sampling a number of plants scattered over the field. Knowing the mean number of each of the three categories of leaves per plant, it is possible to calculate the mean number of aphids per plant.

CHURCH & STRICKLAND (1954) have tested the method by uprooting a number of brussels sprout plants, taking several three-leaf samples till the plants were stripped (each plant producing eight to ten of such samples), and counting the number of cabbage aphids per leaf. They concluded that the three-leaf method is accurate enough to estimate the population densities of the aphid.

The actual method of estimating the cabbage aphid populations in the present work is as follows:

1. The border rows were excluded from sampling.

2. Once every week 50 plants out of each field were sampled. To determine the first plant to be sampled, each week any plant of the four corners of the field was picked at random. This plant was given any random number between and including 1 and 10. Proceeding from this number to any one of the two directions of rows, plant number 10 was selected as the first plant to be sampled. This procedure assured that the first plant would be taken at random from any one of 76 different plants in the field (only of 58 plants in field B, 1959).

3. Once the first plant had been selected and sampled, the next plant in the row was given number 1 and moving in the same direction plant number 10 was sampled again. This procedure was continued until the end of the row and then backwards in the following row. In this way each tenth plant was sampled up to a total number of fifty plants. In field B, with less than 500 plants, every seventh plant was sampled.

Because of the wide range of positions of the first plants and since in course of the season some of the plants in the field died and were removed, leading to a new arrangement almost every week, it was practically impossible to sample the same set of fifty plants per field twice during the season.

4. As stated above from each sampled plant three leaves were taken; one leaf at random from each of the upper, middle and lower parts of the plant. Usually the upper leaf was taken from the crown or slightly lower, the middle leaf from the mature ones around the middle part of the plant and the lower leaf from the old senescent ones near the base of the plant.

CHURCH & STRICKLAND (1954) stated that "approximately 95% of the aphids infesting a sprout plant at this time (September 1951 in England) were on the leaves". The present writer could generally confirm this statement, but at the period of extremely high density in the autumn of 1959, a considerable fraction of the population occurred also on the sprouts. In such cases ignoring the sprouts would account for a considerable error. Hence, in the present work the sprouts were taken together with their leaves, and the aphids on both parts were added together.

5. The aphids were counted and recorded immediately in the field. However, in case of a heavy infestation, to save time and to render it possible to sample all the fifty plants on one day, some of the heavily infested leaves were kept separately in plastic bags in cold storage to be counted within the following two or three days.

6. Because the counts were mostly carried out in the field, it was not possible to classify the nymphs accurately into their four instars. Thus the aphids were classified into the following groups:

Young nymphs; representing mainly the first and early second nymphal instars.

Middle nymphs; representing mainly the late second and early third nymphal instars.

Advanced nymphs; representing mainly the late third and all fourth nymphal instars.

Apterous viviparae; easily distinguished by the young nymphs usually around them and by the anal plates.

Alate viviparae.

Apterous oviparae; sexual females late in the season.

The alate males, also late in the season, were not included in the counting.

7. At the same time the following groups were also counted:
   1. Mummies of *B. brassicae*, which resulted from parasitized aphids, classified into intact mummies and mummies with emergence holes.
   2. Any stages of predators.
8. Simultaneously all the leaves of every other brussels sprout plant, so 25 out of 50 plants, were counted and classified into upper, middle and lower leaves. Mostly these classes correspond with the upper, middle and lower thirds of the plant. So it was possible to obtain the mean number of leaves of each of the three categories per plant.
9. These counts were continued once every week as follows:
   Field A; from 10-VII-'59 till 20-XI-'59 inclusive.
   Field B; from 6-VII-'59 till 10-XI-'59 inclusive.
   Field C; from 1-VI-'60 till 27-X-'60 inclusive.
10. In order to obtain the average number of each of the counted items per plant, the following formula was applied:

$$n = \frac{1}{N} (\bar{r}_1 \Sigma x_1 + \bar{r}_2 \Sigma x_2 + \bar{r}_3 \Sigma x_3)$$

where: n = average number of a counted item per plant
N = number of plants sampled (50 in each case in the present work)
$\bar{r}_1$ = average number of upper leaves per plant
$\bar{r}_2$ = average number of middle leaves per plant
$\bar{r}_3$ = average number of lower leaves per plant
x_1 = number of counted item (e.g. stage of aphid, mummy, predator) per upper leaf
x_2 = number of counted item per middle leaf
x_3 = number of counted item per lower leaf

This method of sampling proved to be satisfactory to describe the population changes in the course of the season. It is time consuming, but after some training and adaptation, it was possible in all cases, even when the infestation was extremely high, to finish the sampling of the fifty plants within about ten hours.

C. Results

The results of the counts of *B. brassicae* in the two years are given in tables 9, 10 and 11 and in fig. 6.

It is clear that, though there are some differences in the number of aphids between the two fields A and B (1959), the general trend of infestation in both fields more or less follows the same pattern. It is also seen that counts on the sprout plants in 1959 did not start early enough to show the starting point of the infestation as has been the case in 1960. However, judging from counts that have been made weekly on the cauliflower plants in field A for four weeks, starting 1-VI-'59, and from the counts on brussels sprouts in 1960, a picture of the population changes of the cabbage aphid throughout the season could

TABLE 9. Average number of *B. brassicae* per brussels sprout plant
Field A – 1959

Date	Average number of aphids per plant								
	Nymphs				Adults				Total no. of all stages
	Young	Middle	Advanced	Total no. of nymphs	Apterous viviparae	Alate viviparae	Apterous oviparae	Total no. of adults	
10-VII	648	171	62	881	49	12	0	61	942
17-VII	743	331	151	1225	105	6	0	111	1336
24-VII	112	102	47	261	13	2	0	15	276
31-VII	32	27	14	73	2	1	0	3	76
7-VIII	20	16	10	46	0	1	0	1	47
14-VIII	19	17	4	40	3	1	0	4	44
21-VIII	39	13	12	64	3	1	0	4	68
28-VIII	136	39	21	196	16	1	0	17	213
4-IX	149	58	58	265	24	2	0	26	291
11-IX	1142	221	231	1594	257[1])	10		267	1861
18-IX	1428	506	345	2279	327[1])	13		340	2619
26-IX	2438	822	414	3674	496[1])	31		527	4201
2-X	3231	1601	1072	5904	474	72	460	1006	6910
9-X	2276	1520	1840	5636	156	99	1755	2010	7646
16-X	500	549	676	1725	156	41	1265	1462	3187
23-X	271	576	743	1590	95	13	943	1051	2641
31-X	311	596	728	1635	89	8	961	1058	2693
6-XI	127	297	411	835	35	7	499	541	1376
20-XI	72	115	296	483	35	1	384	420	903

TABLE 10. Average number of *B. brassicae* per brussels sprout plant
Field B – 1959

Date	Average number of aphids per plant								
	Nymphs				Adults				Total no. of all stages
	Young	Middle	Advanced	Total no. of nymphs	Apterous viviparae	Alate viviparae	Apterous oviparae	Total no. of adults	
6-VII	578	192	100	870	54	4	0	58	928
13-VII	307	193	125	625	49	8	0	57	682
20-VII	1032	437	317	1786	144	9	0	153	1939
27-VII	336	190	125	651	31	8	0	39	690
3-VIII	107	105	48	260	15	3	0	18	278
10-VIII	51	12	6	69	3	3	0	6	75
17-VIII	26	27	6	59	0.5	0.5	0	1	60
24-VIII	63	24	11	98	7	2	0	9	107
31-VIII	241	69	38	348	15	2	0	17	365
7-IX	279	36	29	344	33	2	0	35	379
14-IX	1129	286	107	1522	119[1])	9		128	1650
21-IX	1055	364	123	1542	88[1])	68		156	1698
28-IX	1885	778	291	2954	261[1])	86		347	3301
5-X	2294	1198	1010	4502	173	200	447	820	5322
12-X	1126	1199	1015	3340	157	142	1601	1900	5240
20-X	790	916	1171	2877	76	67	1555	1698	4575
26-X	283	560	383	1226	22	18	982	1022	2248
2-XI	212	612	585	1409	30	21	1265	1316	2725
10-XI	101	327	547	975	20	10	1230	1260	2235

[1]) These numbers represent the total of viviparous and oviparous females.

TABLE 11. Average number of *B. brassicae* per brussels sprout plant
Field C – 1960

Date	Average number of aphids per plant								
	Nymphs				Adults				Total no. of all stages
	Young	Middle	Advanced	Total no. of nymphs	Apterous viviparae	Alate viviparae	Apterous oviparae	Total no. of adults	
1-VI	0	0	0	0	0	0	0	0	0
8-VI	0.9	0.4	0	1.3	0	0.1	0	0.1	1.4
15-VI	19	3	1	23	2	0.4	0	2.4	25.4
22-VI	81	28	11	120	8	7	0	15	135
28-VI	477	161	49	687	7	63	0	70	757
6-VII	677	275	105	1057	29	32	0	61	1118
13-VII	225	109	230	564	154	6	0	160	724
20-VII	684	148	96	928	91	4	0	95	1023
26-VII	266	145	173	584	121	3	0	124	708
3-VIII	29	20	45	94	14	0	0	14	108
10-VIII	46	9	14	69	4	0	0	4	73
17-VIII	4	4	10	18	1	0	0	1	19
24-VIII	6	2	3	11	2	0	0	2	13
1-IX	8	1	1	10	1	0	0	1	11
8-IX	0	1	1	2	1	0	0	1	3
15-IX	1	1	3	5	1	0	0	1	6
22-IX	23	1	2	26	3	0	1	4	30
28-IX	59	18	3	80	7	1	7	15	95
5-X	22	18	8	48	6	0	4	10	58
13-X	0	0	1	1	0	0	1	1	2
20-X	0	1	4	5	0	0	5	5	10
27-X	0	0	0	0	0	0	4	4	4

be drawn. In general, the pattern fits into a bimodal curve with one maximum early in the season (17-VII-'59 in field A, 20-VII-'59 in field B and 6-VII-'60 in field C) and another maximum late in the season (9-X-'59 in field A, 5-X-'59 in field B and 28-IX-'60 in field C) separated by a minimum in mid-season (14-VIII-'59 in field A, 17-VIII-'59 in field B and 8-IX-'60 in field C). However, there may exist great variation in the rate of population growth from field to field and from year to year. For instance, during the first maximum the population of *B. brassicae* per sprout plant averaged 1336 in field A (year 1959), 1939 in field B (year 1959) and 1118 in field C (year 1960). At the second maximum, however, the difference was most conspicuous; the average number of all stages of *B. brassicae* (winter eggs excluded) per sprout plant was 7646 in field A and 5322 in field B while it was only 95 in field C. The mid-season minimum averaged 44 aphids in field A, 60 in field B and 3 in field C.

This shows that in 1959 and 1960 there was no striking difference between the number of aphids per plant during the first peak while the difference was very large during the second peak late in the season.

The picture of the population changes of the cabbage aphid in 1959 and 1960 clearly showed drastic fluctuations, especially during mid-summer. Furthermore, it is shown that a considerable difference in the aphid abundance occurred between the two years, especially during the second peak of infestation.

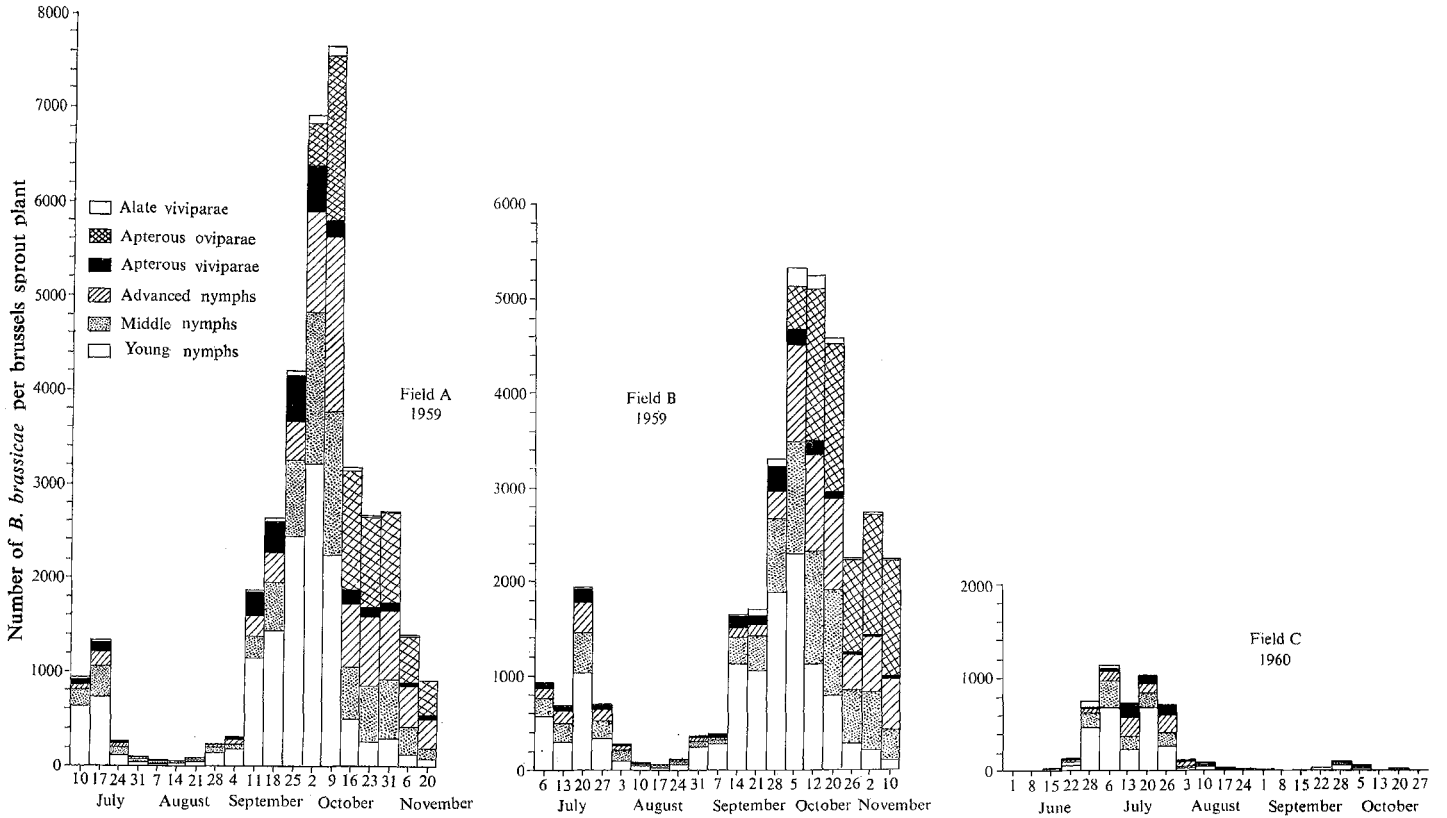


FIG. 6. Average numbers of *B. brassicae* per brussels sprout plant in fields A and B. (1959) and C (1960), near Wageningen

In the following chapter an attempt will be made to discuss some of the mortality factors of the aphid, not intendedly to determine their precise role in the whole complex of natural resistance, but rather to compare their relative importance during the two almost extreme succesive seasons with such large differences in aphid populations.

CHAPTER IV

ANALYSIS OF THE SEASONAL FLUCTUATIONS IN POPULATION DENSITY OF *BREVICORYNE BRASSICAE* (L.)

1. INTRODUCTION

It has been shown in CHAPTER III that the population density of the cabbage aphid fluctuates widely in the course of the season and from year to year. A complex of factors must have played a role in inducing these changes in the population densities both in different periods within the same season and in the two years 1959 and 1960. These factors may cause the changes by affecting the reproduction, migration and mortality. It would have been worth while to analyse the combined influence of these factors and treat the three above mentioned components separately. However, such an analysis would be inadequate and meets so many difficulties that the results would only be a rough approximation of the facts. Some of these difficulties are:

1. The generations of the aphid overlap almost right from the beginning of the population growth in spring.
2. Most of the factors involved interact in a complicated way.
3. It was impossible to obtain systematic observations on reproduction and migration as affected by the complex of conditions prevailing in the field.

In view of these facts, it proved more useful to investigate the effects of some of the abiotic and biotic factors on the numbers of the cabbage aphid, in order to determine whether or not they can account for the remarkable changes in population density.

2. LITERATURE

A complete analysis of the seasonal trend in the growth of the cabbage aphid populations has not been made before. Moreover, the results given by different authors are not in accordance, possibly because of the different conditions under which they were obtained. Sometimes the role of parasites and predators proved to be of primary importance. Thus, HERRICK & HUNGATE (1911) mentioned instances in New York State where *B. brassicae* never reached high densities, because parasites and predators kept the aphid in check. They recorded and commented on four species of parasites and on certain predators belonging to the families Coccinellidae, Syrphidae and Chrysopidae. STRICKLAND (1916), working in Western Canada, presumed that the main factor preventing infested cabbages from being destroyed is the activity of several natural enemies. He

mentioned in particular that in 1914 and 1915 in South Alberta (Canada) the only parasite was *Aphidius rapae* Curtis and that it was very valuable in preventing outbreaks of *B. brassicae*. BARNES (1931) thought that late in the season 1929 the cabbage aphid attack was controlled in a particular district in England as a result of heavy parasitism.

In other cases the effect of parasites proved to be of minor importance. PETHERBRIDGE & MELLOR (1936) concluded that although the parasites were active during the summer, they were unable to prevent the cabbage aphid from multiplying rapidly when the weather conditions were favourable. In their opinion parasites were less important in reducing the numbers of the aphid than larvae of the predator *Syrphus luniger* Mg. Unfortunately they included as parasites *Asaphes vulgaris* Wlk. and *Lygocerus testaceimanus* Kieff. which are now known to be definitely secondary and tertiary parasites.

In The Netherlands, WOLDA (1956) has observed that, in the garden under investigation, the larvae of *Phaenobremia* sp. and Syrphids were the most important factors which decreased colonies of *B. brassicae* on brussels sprout plants during August 1956.

RIPPER (1944) explored the possibilities of integrated control measures by applying biological control as a supplement to chemical control against the cabbage aphid in England. He used nicotine vapour for an exposure of about one minute as a selective insecticide which resulted in a high mortality of the aphid whereas the predators and the parasite survived. Hence the fraction of aphid population that survived the treatment was eventually eliminated either immediately by the predators or within three weeks by the parasites.

MARKKULA (1953) recorded as natural enemies of the cabbage aphid in Finland six species of Syrphids, four Coccinellids, one Hemerobiid, two *Aphidius* spp. and one Chalcid parasite.

BÖRNER & HEINZE (1957) recorded a list of names of 44 predators and 14 parasites of the cabbage aphid. Unfortunately some of these names proved to be synonyms, some need more verification and some have been proven not to be primary parasites.

GEORGE (1957) gave some preliminary results about the effect of parasites and predators on the cabbage aphid in East England. *Aphidius rapae* was the only primary parasite and its rate of parasitism was rather low. Predators comprised three species of Syrphids and one *Phaenobremia sp.* with the former apparently the most efficient. Coccinellids were remarkably absent.

As for an important effect of the climatic factors, PETHERBRIDGE & WRIGHT (1938) stated that in England the climatic factors were more important than biological factors in governing the natural rate of increase of the cabbage aphid. They added that the main predators were Syrphids and *Phaenobremia* sp., while the Coccinellids were never numerous enough to become an important factor. Parasitism was very low ranging from 2–5% only.

3. THE EFFECT OF MORTALITY FACTORS

From the data in the literature, it can be concluded that the changes in population density of the cabbage aphid are mainly due to actual mortality factors rather than to effects on reproduction or migration. Some evidence is given

here to show that the mid-season decline in the abundance of the cabbage aphid, as was demonstrated in the present work, is caused by actual mortality factors.

1. If reproduction is inhibited and no mortality factors are operating, at least the total number of nymphs counted in the week preceding the decline should survive till the following week. However, from tables 9, 10 and 11 it was shown that this was not the case and that in each of the three brussels sprout fields the total number of aphids per sprout plant just after the decline is far less than the number of nymphs one week earlier. This means that, even if reproduction completely ceased, mortality factors were still responsible for the sharp decline.

2. The data concerning the proportion of young nymphs to adult *B. brassicae* as obtained in each of the three fields, just before and during the mid-season decline is given in table 12.

TABLE 12. Proportion of young nymphs to adult *B. brassicae* before and during the mid-season decline

Field	Date	Total no. of *B. brassicae* per sprout plant	No. of young nymphs per plant	No. of adults per plant	Aver. no. of young nymphs to one adult
A	17-VII-'59	1336	743	111	6.7
	24-VII-	276	112	15	7.5
	31-VII-	76	32	3	10.6
B	20-VII-'59	1939	1032	153	6.7
	27-VII-	690	336	39	8.6
	3-VIII-	278	107	18	5.9
	10-VIII-	75	51	6	8.5
C	20-VII-'60	1023	684	95	7.2
	26-VII-	708	266	124	2.1
	3-VIII-	108	29	14	2.1
	10-VIII-	73	46	4	11.5

These data show that, judging from the proportion of young nymphs to adults, in fields A and B (1959) reproduction was not inhibited or slowed down during the decline as compared to the period before the decline. In field C, however, reproduction was slowed down for two weeks and then increased again while the total number of aphids was still decreasing. This means that the decline in aphid populations occurred with or without the inhibition of reproduction and so most probably other factors may be responsible for it.

3. From observations in the three fields already mentioned and in other fields in The Netherlands in 1959 and 1960, in most cases the remains of the destroyed colonies could still be found on the plants and the effect of some mortality factors such as predators or fungous disease could be discerned on them.

Some of the mortality factors that might be responsible for the population changes will be dealt with in this part.

A. The effect of abiotic factors

In the present work the effects of temperature and precipitation were studied in some detail.

1. Temperature: It has been shown on page 7 that the alternation of comparatively high and low temperatures early in the spring of 1960 (fig. 1) destroyed a large number of fundatrices which had hatched in warm periods and subsequently died during a following cold spell. Moreover, it was also found (table 7) that it was not possible to maintain a complete generation of *B. brassicae* at an average temperature of 4.9 °C (the minimum was 3.5 °C). All nymphs died while still in the first instar. The threshold of development for the species is reported to be 1.7 °C in Finland, 3.1 °C and 8 °C in France and 3–4 °C in Israel.

On the other hand, only 2 individuals out of 50 survived a high temperature averaging 30.9 °C (maximum 34.5 °C). BROADBENT & HOLLINGS (1951) obtained a thermal death point of 41 °C by exposing the aphid, after removal from the host plant, for one hour at 60% R.H. Presumably a slightly higher temperature or longer exposure would be needed if the aphid was kept on the host plant. Between the two lethal extremes, temperature influences the rate of development, survival, and reproduction. Furthermore, temperature would have an influence through the effect it exerts on the biotic factors (e.g. activities and development of parasites and predators). Two main questions have to be considered regarding the effect of temperature on the sharp population changes of *B. brassicae* in the sampled sprout fields in 1959 and 1960.

1. Were there such drastic and sudden changes in temperature, in the three fields late in July and early in August in both years 1959 and 1960, as to account for the sudden and persistent drop in the population of the aphid in that period?
2. Was the temperature sufficiently more near the optimum in September and October of 1959 than in the same period in 1960, to account for a peak of 7646 aphids per sprout plant in autumn of 1959 compared with only 95 aphids per sprout plant in autumn of 1960?

To help answering these two questions, the maximum and minimum daily temperatures at 10 cm above the soil surface, throughout the counting periods of 1959 and 1960, were obtained from a meteorological station situated on the border of the sprout fields (fig. 7 and 8). Furthermore, it is shown from fig. 6 that a sudden mid-season decline in the aphid population took place within a certain week late in July or early in August. To find out if a drastic change in temperature has coincided with the sudden decline in population, the temperature during the week when the decline occurred has to be compared with the temperature taken one week earlier when the population was still at a high level. These temperatures are given in table 13.

From fig. 7 and 8 and table 13 it seems unlikely that the sharp mid-season decline in the aphid density was affected by temperature. Only a drastic change in temperature during the week when the decline occurred as compared to the preceding week, when the population was high, could be responsible for the observed drop in numbers. It is obvious, however, that such a change in temperature did not take place either in 1959 or in 1960.

To answer the second question, the temperatures in September and October 1959 and 1960 will be considered (table 14).

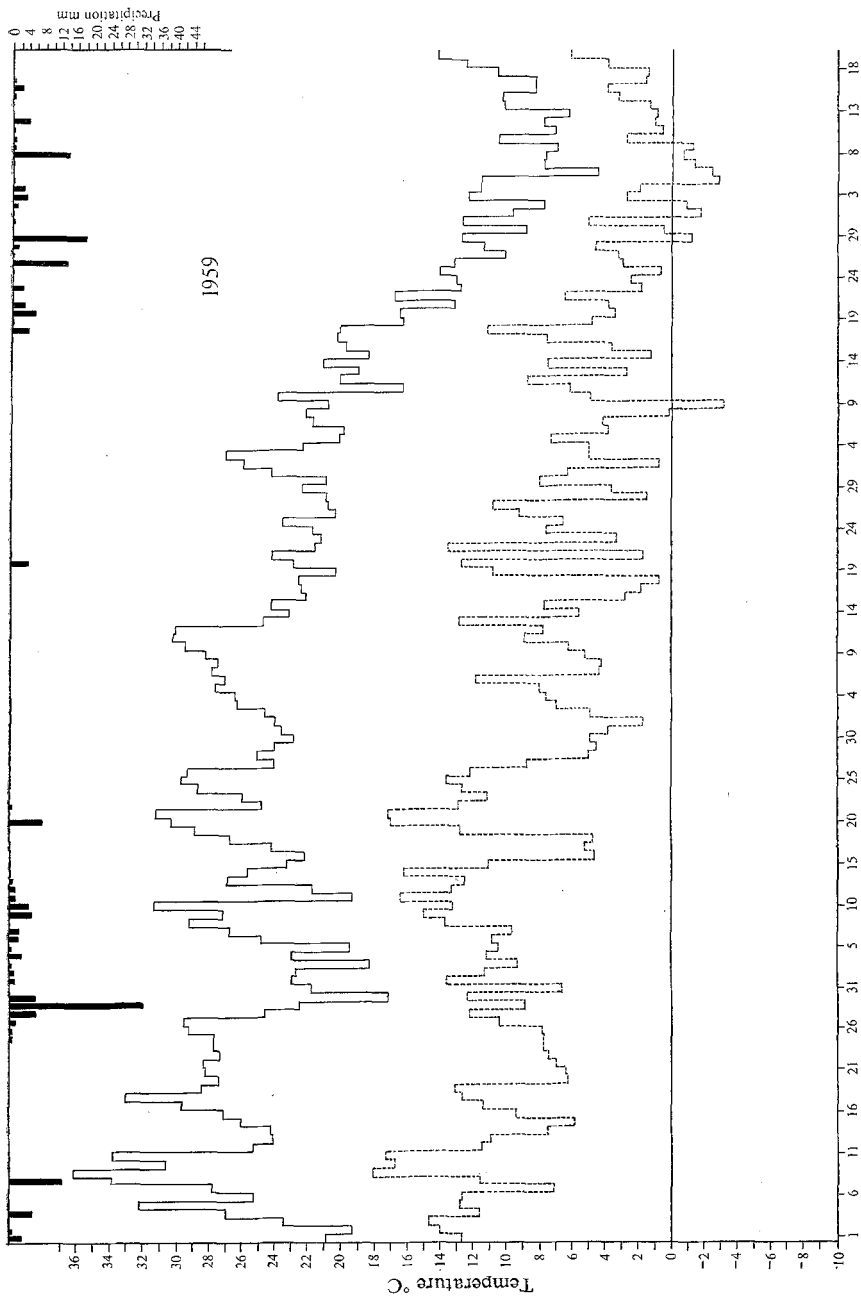


FIG. 7. Daily maximum and minimum temperature (°C) at 10 cm above soil level and precipitation (mm) from July until November 1959. (Data obtained from the meteorological station near the experimental fields near Wageningen)

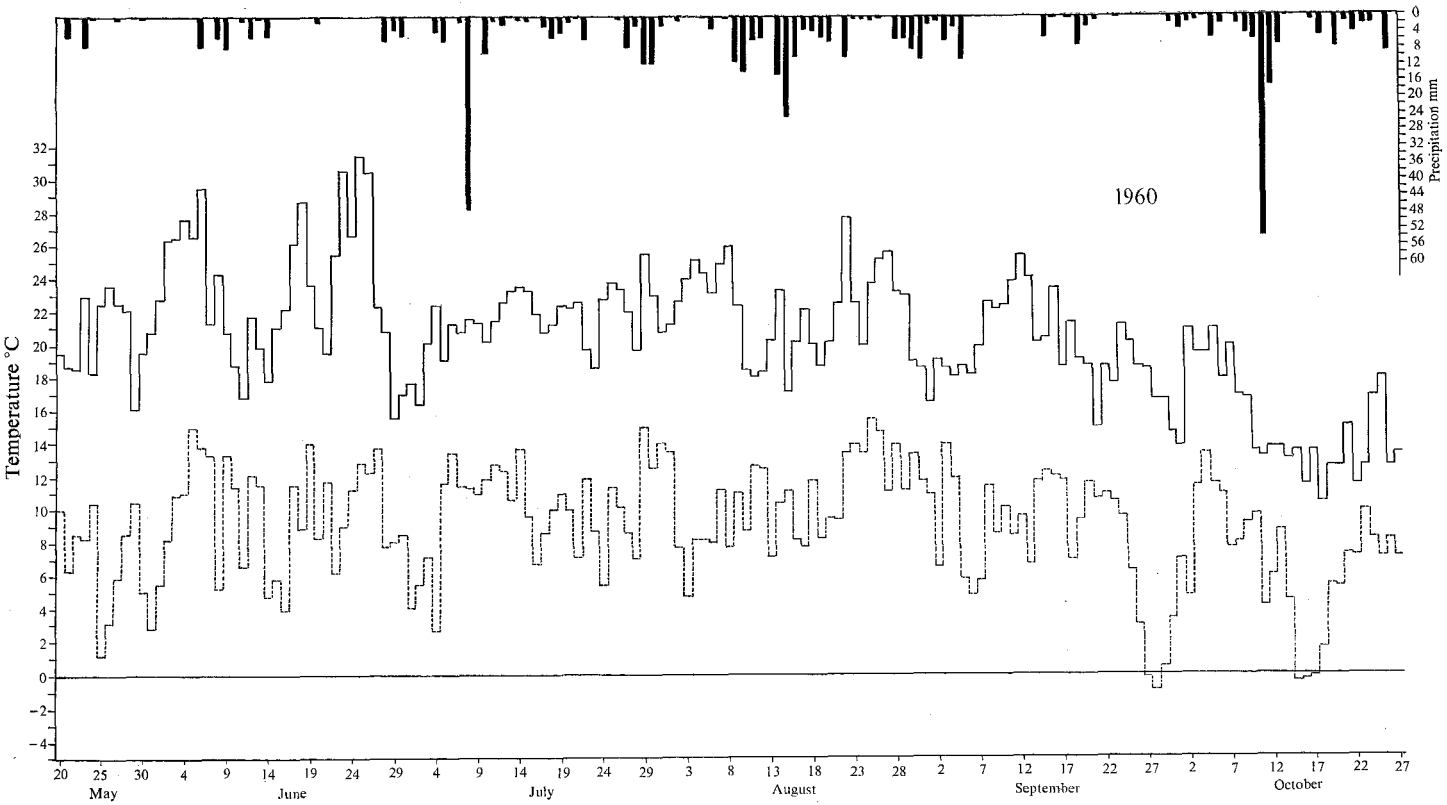


FIG. 8. Daily maximum and minimum temperature and precipitation from May until October 1960. Explanation see fig. 7

TABLE 13. Temperature °C at 10 cm above soil surface during the week when the decline in the cabbage aphid occurred and during one week earlier when the population was still high

	Field A		Field B		Field C	
	Before the population decline	During the population decline	Before the population decline	During the population decline	Before the population decline	During the population decline
Counting day	17-VII-'59	24-VII-'59	20-VII-'59	27-VII-'59	26-VII-'60	3-VIII-'60
Total number of *B. brassicae* per sprout plant .	1336	276	1939	690	708	108
Average maximum temperature for the previous week	27.3	28.9	27.6	28	21.7	22.3
Absolute maximum temperature in the previous week	33.8	29.7	33.1	29.1	23.8	25.6
Average minimum temperature for the previous week	10.5	8.6	9.4	7.8	9.1	10.4
Absolute minimum temperature in the previous week	5.7	6.2	5.7	6.4	5.4	4.7
Average temperature at 9.00 A.M. for the previous week	21.4	21.1	21.7	20.1	16.7	16.8

TABLE 14. Average monthly temperature °C at 10 cm above soil surface in autumn of 1959 and 1960

Month	Max.	Min.	Mean
September 1959	24.3	6.6	17.8
September 1960	19.7	8.1	13.8
October 1959	17.9	3.9	11.7
October 1960	14.9	6.8	10.6

It is shown in table 14 that the maximum and minimum temperatures were more widely apart in 1959 than in 1960. No accurate conclusions could be drawn from these data concerning the effect of this difference on population density of *B. brassicae*, but it is rather doubtful that it accounts for the large differences observed in the two years. On the other hand, the mean temperature of September '59 was higher than that of September '60, a fact that might have partly helped the higher level of the population in autumn '59 compared to '60. However, it is unlikely that temperature is the decisive factor, because the mean temperature in October '59 was only 1 °C higher than October '60 whereas the aphid populations in the same months were totally different. Furthermore, the mean temperature in October '59 was about 2 degrees lower than September '60 and still the aphid population was extremely higher in the former than the latter month.

2. Precipitation: The year 1959 was remarkably drier than 1960. This was

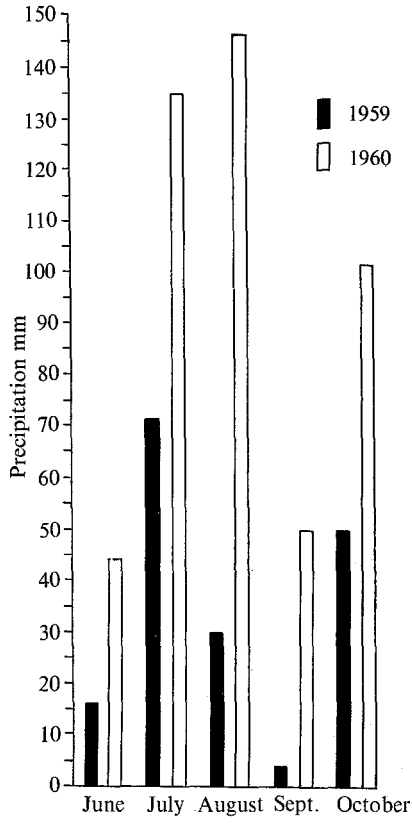


FIG. 9.
Total monthly precipitation (mm) from June until October 1959 and 1960

especially true in August, September and October (fig. 7 and 8). Actually there was almost no precipitation in late August, September and the first half of October 1959 at the time when the second peak of aphid abundance started and reached tremendous numbers. In the same period of 1960, however, with few exceptions, it rained every day. Fig. 9 shows the difference between the total monthly precipitation from June till October in 1959 and in 1960.

Extensive rainfall in 1960 compared to 1959 may have affected the abundance of *B. brassicae* in two ways. Firstly, a spread of a fungous disease was favoured by the high humidity. This disease was found responsible for eliminating whole colonies in 1960 whereas it was not encountered in 1959. Secondly, it was found during the weekly counts (tables 9, 10 and 11) that the beginning of the aphid infestation, whether early in the season or after the mid-season drop, often originated from an invasion of alate viviparae, which settled down on the plants and started forming colonies. This fact is clearly demonstrated by the immigration of alates into field B where in one week (14 to 21-IX-'59) the average number of alate viviparae per sprout plant increased from 9 to 68 whereas the number of apterous viviparae decreased from 119 to 88. In another instance, during the flight of alatae which eventually led to the first maximum in field C, within nearly one week (22 to 28-VI-'60) the number of alate viviparae per

sprout plant increased from 7 to 63 whereas the number of apterous viviparae decreased from 8 to 7.

This type of colonies, formed around alate viviparae, prevailed in the second half of August '59 and started the new infestation. Such an infestation, however, could not be started in any considerable numbers in autumn of 1960 owing to the failure of alate viviparae to fly because of almost continuous rainfall.

B. The effect of biotic factors

Biotic factors are of paramount importance in affecting the abundance of any organism. In its broad meaning, the term should include the effect of the quantity and quality of food on the organism. This effect is more pronounced in aphids because they are more closely associated with their host plants and because the condition of food will eventually lead to the formation of alate or apterous individuals. Thus it has been demonstrated in several instances that the physiological condition of the host plant is of great importance in affecting the abundance of aphids (KENNEDY & BOOTH, 1951; KENNEDY & STROYAN, 1959). The study of the physiological condition of the host plant, however, is beyond the scope of the present work and so this discussion will be limited to the natural enemies.

1. Entomophagous fungi: As has been mentioned before (p. 481) fungous outbreaks were not found at all in the colonies in 1959. In 1960, however, fungous infected colonies were very abundant during the week 26-VII to 3-VIII. On 10-VIII practically no living colonies were left and the remains of the old diseased colonies could be found on all plants. The few surviving aphids were scattered individually or in very small groups.

Hence, outbreaks of fungous diseases were partly responsible for the mid-season decline in 1960 but not in 1959.

2. Predators: Four groups of predators were found among the aphid colonies on the sprout plants:

a. Coccinellids: The main species was *Coccinella septempunctata* L. Early in the season 1959, the adults and larvae were very numerous in the field. Unfortunately it was not possible to count them because the great majority was present on the soil rather than on the plants. Any attempt to determine their population density per plant seemed rather questionable. Furthermore, since they were mostly on the soil, it could not be stated with certainty that all of them were actually feeding on the cabbage aphid. Such a situation was also found by GEORGE (1957), who stated that adult Coccinellids were frequently noticed in the brussels sprout fields but were rarely found actually on the aphid host-plants.

Just prior to the sudden decline in the two fields in July 1959, there were, especially on the soil, enormous numbers of adults and advanced larvae of *C. septempunctata* L. Probably they were partly responsible for the drop in aphid abundance in 1959. Later in the season they were present in negligible numbers.

In 1960, however, the number of Coccinellids was remarkably low in the brussels sprout fields under investigation.

Other Coccinellids that sometimes were found associated with the cabbage aphid are *Coccinella bipunctata* L., *C. bipunctata a. 4 maculata* Scop. and *Halyzia 14 punctata* L., but they were always present in very low numbers.

b. Syrphids: According to WOLDA (1956), the most important species of Syrphidae feeding on colonies of *B. brassicae* in The Netherlands is *Epistrophe balteata* Deg. The species *Sphaerophoria scripta* L., *Syrphus vitripennis* Meig. and *Lasiopticus pyrastri* L. are less frequent.

In the present work the larvae of the different species of Syrphidae were counted, as one group, on 50 sprout plants each week using the three-leaf method as has been mentioned on page 468. The counts were carried out in all three fields together with the aphid counts. The results are shown in fig. 10.

c. Phaenobremia aphidovora Rübs. (Fam. Cecidomyidae): Next to *C. septempunctata* L. this was the most generally prevailing predator in the sprout fields. The eggs were deposited within the aphid colonies on which the hatched larvae preyed. The larvae were counted in the same way as mentioned previously and the results are given in fig. 11.

d. Larvae of the family Chrysopidae: These larvae were also counted but their number was negligible throughout the counting period in 1959 and 1960.

3. Parasites: In the years 1959 and 1960 about 25,000 mummies of *B. brassicae* were collected in different areas of The Netherlands and on different cruciferous crops. About 6,000 of them gave rise to primary parasites and they all belonged to the species *Aphidius* (*Diaeretiella*) *rapae* (Curt.). In all probability this is the only primary parasite of *B. brassicae* in The Netherlands. The role of this parasite in controlling the populations of the cabbage aphid is one of the main themes of the present work and will be discussed later.

4. DISCUSSION

It is difficult to conclude which of the above factors, if any, might be responsible for the mid-season decline in population density of *B. brassicae* or for the considerable difference in its abundance late in the seasons of 1959 and 1960. However, the following points should be raised:

1. From table 13 and fig. 7 and 8, temperature and rainfall do not seem to show any sudden change that could be directly responsible for the mid-season decline mentioned above.
2. Every month from June till October had more precipitation in 1960 than in 1959. The period between, and including, the second half of August and the first half of October 1959 was almost completely dry whereas during the same period of 1960 most of the days were rainy.
3. *Coccinella septempunctata* L. frequently occurred in the sprout fields during July 1959; its number was low in 1960.
4. In 1959, two peaks of larval abundance of *Phaenobremia aphidovora* Rübs., ranging between 10 and 14 per plant, occurred coinciding with the peaks of the cabbage aphid. In 1960, the density of the larval populations of this predator was much higher, reaching a peak of 124 larvae per plant in the first week of August, also coinciding with the early peak in the density of the aphid.
5. In 1959, Syrphid larvae were mostly low in numbers, not exceeding an average of 2 per plant throughout the counting period. In 1960, they were more numerous in July and early August, reaching a top of about 8 per plant on 13-VII-'60, coinciding with the mid-season drop in the aphid population.

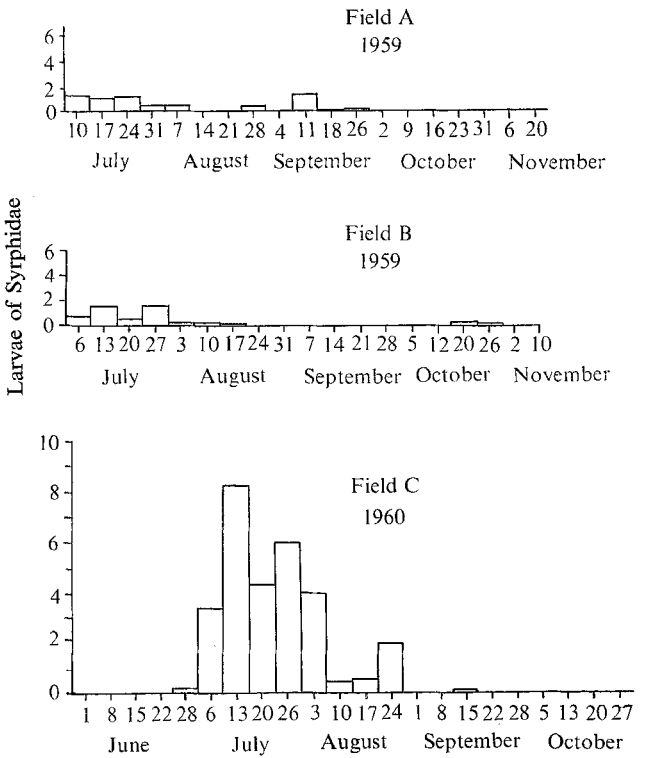


FIG. 10. Average numbers of Syrphid larvae per brussels sprout plant in fields A and B (1959) and C (1960)

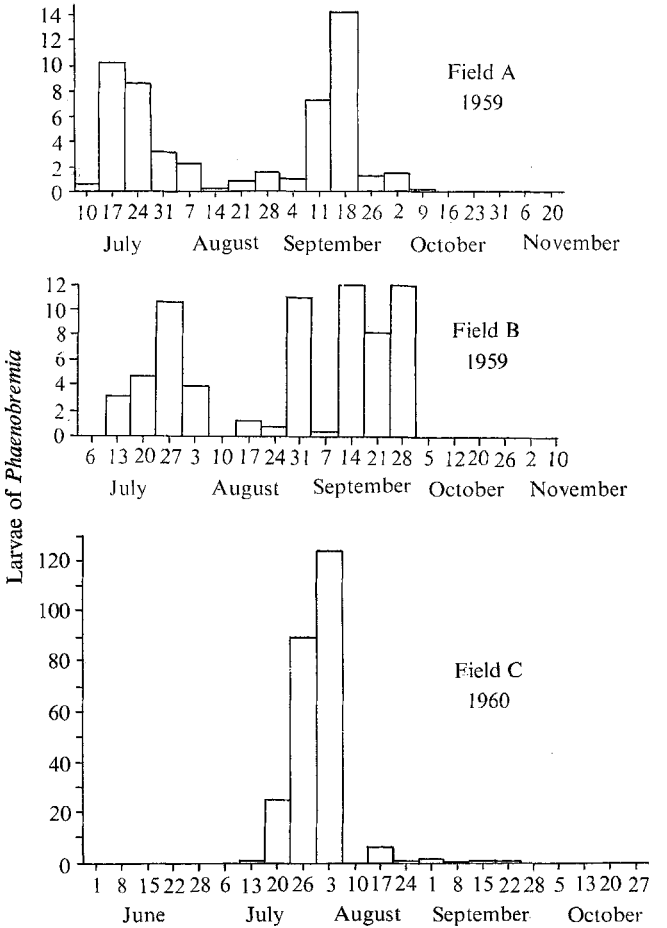


FIG. 11. Average numbers of larvae of *Phaenobremia aphidovora* per brussels sprout plant in fields A and B (1959) and C (1960)

6. At the time of the mid-season decline, most of the remains of the destroyed colonies showed that they were definitely preyed upon by predators.

7. In 1959 no fungous disease was found in the colonies whereas in 1960 the disease generally prevailed prior to and coinciding with the mid-season drop.

8. It will be shown later that at the time of the first aphid peak in both years, parasitism was rather low, so that it could not account for a high mortality. It was also low later in the season, during the second peak.

9. *Phaenobremia aphidovora* had a second peak of abundance (maximum about 14 larvae per plant) late in 1959 after the new high peak of aphid population density was already established. By that time all other predators were low in numbers. They were definitely scarce at the time when the second peak started.

In 1960 the numbers of all predators were very low from mid-August onwards.

10. The mean temperature was 4 °C higher in September 1959 than it was in September 1960. However, it was only 1 °C higher in October 1959 than in October 1960.

All these points give circumstantial evidence to draw a conclusion as to the cause of the population changes of *B. brassicae* in 1959 and 1960, which may be summarized as follows:

1. In 1959 the cabbage aphid built up a population early in the season and the predators, mainly *Phaenobremia aphidovora* Rübs. and probably *Coccinella septempunctata* L., have subsequently caused a sharp decline in aphid abundance. Later in the season alate viviparae started a new infestation that reached a very high peak of abundance owing to the scarcity of the predators, low rate of parasitism and favourable weather conditions which were at the same time unfavourable for an outbreak of the fungous disease.

2. In 1960 the early build-up of the aphid population proceeded as in the previous year. It was then checked in the same way, mainly by Syrphids and *P. aphidovora* and the outbreak of a fungous disease. It is of importance to note that the numbers of Syrphids and *P. aphidovora* were significantly higher during the first peak of 1960 than 1959. This might suggest that the dry weather which is favourable for the aphid abundance is at the same time unfavourable for those predators. There was no possibility to establish a second aphid peak of any importance. No new colonies could be established, because of the heavy and continuous rains during the period it might have started.

CHAPTER V

THE BIONOMICS OF THE PARASITE *APHIDIUS (DIAERETIELLA) RAPAE* (CURTIS) (HYMENOPTERA, APHIDIIDAE)

1. INTRODUCTION

Aphidius rapae Curt. was described in 1885 and has frequently been recorded as being the only parasite of the cabbage aphid. In several instances it was

recorded as very valuable, either alone or together with other natural enemies, in controlling outbreaks of the aphid (see p. 30). Nevertheless, no detailed study of the life history of the parasite has been published. In the present study the writer is primarily interested in the role of the parasite as a mortality factor of the cabbage aphid. However, it is obvious that more basic information concerning the life history of the parasite was needed before conclusions could be drawn as to the possible effect of the parasite on the population density of the aphid.

The present chapter will deal mainly with the bionomics of *A. rapae*. A following chapter will be concerned with host-parasite interrelations.

In the literature detailed information concerning the parasite is rather scarce. WHEELER (1923) described the mature larva of the parasite. SPENCER (1926) studied the biology of the parasites and hyperparasites of some Aphids in Ohio, U.S.A., and discussed the relationships which existed between the host plants, aphids, primary parasites and hyperparasites. *B. brassicae* and *Aphidius rapae* were included in his study. He also studied the embryonic development of the parasite *A. rapae*, its immature forms, and the internal effects of the parasite larvae on the tissues of the host. ULLYETT (1938) described the larval stages of the parasites which belong to the genus *Aphidius* as "drawn from the species which is found parasitizing *Brevicoryne brassicae*" in South Africa. Most probably he was referring to *A. rapae*. SEDLAG (1957/'58) published some short notes about the bionomics, anatomy of the reproductive system, and populations of the parasite. SEDLAG (1958a), during a collecting trip in East Germany in the summer of 1957, has studied the occurrence of the parasites affecting aphids of cruciferous crops. He concluded that *A. rapae* was the only parasite of the cabbage aphid and that the rate of parasitism was sometimes rather high. However, the population of the parasite was generally under a serious influence by the hyperparasites, most important of which were *Charipinae*. The same author (SEDLAG, 1958b) published some notes about the bionomics of the parasite. He stated that *A. rapae* parasitized both *B. brassicae* and *Myzus persicae* and that it comprised about 99.9 % of the total primary parasites emerging from the cabbage aphid. Furthermore, he believed that the effect of the parasite was limited in controlling the cabbage aphid especially in early season because of lack of available hosts at the time the overwintering parasites emerged.

2. TAXONOMY AND NOMENCLATURE

Taxonomic work concerning the parasite and related genera and species has been published by SMITH (1944) in his study on the Aphidiidae of North America and by STARY (1960) who placed the parasite under the new genus *Diaeretiella*. MACKAUER (1961, in press) suggests the new nomenclature *Aphidius* (*Diaeretiella*) *rapae*.

The parasite was first described by CURTIS (1855) in "MACINTOSH's Book of the Garden" as *Aphidius rapae*. Several synonyms have since been used for the same species as follows:

Trioxys piceus Cresson (1880), *Aphidius brassicae* Marshall (1891), *Diaeretus californicus* Baker (1909), *Diaeretus rapae* (Curtis) Gahan (1910).

In a private correspondence, Dr. M. MACKAUER suggested to the writer that in order to complete the list of synonyms, some other names may be in-

cluded. He added that possibly all, or at least some, of the synonyms "represent distinct sibling species, geographical races or biological strains but morphologically they cannot be separated; the different characters used for a separation are all within the range of variation".

The present writer believes that the above mentioned list of synonyms does not by any means constitute a complete one. Most probably when more taxonomical and biological work is done, it will be revealed that many other names represent forms that actually fit within the range of this species.

The name *Diaeretus rapae* (Curtis) has been in general use until quite recently when STARY (1960) came to the conclusion that "the genus *Diaeretus* Forster is monotypic including only the genotype *Aphidius leucopterus* Hal. as it was originally stated by FORSTER in 1862". He then suggested that the other species which were included by various authors in the genus *Diaeretus* should be transferred to other genera of the family Aphidiidae. Furthermore, STARY (1960) described a new genus "*Diaeretiella*" with one single species, *D. rapae*, and so its type species is *Aphidius rapae* Curtis. He added, however, that a revision of the genus *Diaeretiella* is being prepared by him at present to include a group of species that were erroneously placed in the genus *Diaeretus*.

MACKAUER (1961, in press), does not accept this view. He believes that the partially reduced wing venation which characterizes the genus *Diaeretus* (and so genus *Diaeretiella* of STARY) cannot stand to be a generic character of taxonomic reliability within the family Aphidiidae because this type of reduced wing venation can be found in each of the various genera of the family. Besides, all the other main characters, including the female genitalia, in *rapae* are typical to the genus *Aphidius*. Therefore, he concludes that the species should be included in the genus *Aphidius* under a subgenus *Diaeretiella*, and thus its name should be *Aphidius* (*Diaeretiella*) *rapae* (Curtis).

It thus appears that the name *Diaeretus rapae* (Curtis), which has been in common use for about fifty years, should be changed according to the rules of nomenclature. However, the species *rapae* is not quite justified to be included in the new genus *Diaeretiella* and should rather be placed under the subgenus *Diaeretiella* within the genus *Aphidius*.

Since the verification of the name is beyond the scope of the present study, the writer conforms with MACKAUER's views. However, for simplicity, the parasite is indicated briefly as *Aphidius rapae* Curtis.

3. GEOGRAPHICAL DISTRIBUTION

Though the main host, *Brevicoryne brassicae* L., is almost cosmopolitan in its geographical distribution, the parasite *Aphidius rapae* Curtis is only occasionally recorded. Outside Europe (including U.S.S.R.) it is recorded in U.S.A. (including Hawaii), Canada and New Zealand. Actually this does not mean that it does not exist in other areas, but it means that more study is needed on the distribution of the parasite in other localities. The writer believes that it might be as widely distributed as its host *B. brassicae*.

4. HOST RANGE

The parasite has been recorded from the following aphids: *Macrosiphum*

euphorbiae (Thos.) [Syn. *M. solanifolii* (Ashmead)], *Brevicoryne brassicae* (L.), *Myzus persicae* (Sulz.), *Lipaphis erysimi* (Kltb.) [Syn. *Rhopalosiphum pseudobrassicae* (Davis)], *Aphis gossypii* Glov. and *Aphis nasturtii* Kltb. (Syn. *A. abbreviata* Patch).

Its main host, however, is *B. brassicae*, but *Myzus persicae* is also of importance because generally this latter aphid infests the cruciferous crops simultaneously with *B. brassicae*. GEORGE (1957) collected parasitized material of *M. persicae* from cabbage plants and from potato plants adjacent to sprout fields, furthermore he collected other parasitized material of *B. brassicae* from adjacent sprout plants. Without any exception all the primary parasites emerging from *M. persicae* were *Aphidius matricariae* Haliday, while all those emerging from *B. brassicae* were *Aphidius rapae* Curt. SEDLAG (1958b) collected mummies of *M. persicae* from cruciferous crops in East Germany. He obtained 923 primary parasites out of which 11.5% were *A. rapae*.

In The Netherlands, as has already been mentioned on p. 483, about 6000 primary parasites emerging from *B. brassicae* mummies collected in 1959 and 1960 proved to be *A. rapae*. Mummies of *M. persicae* were also collected in two different fields at Wageningen and gave the following primary parasites belonging to four different species: *A. rapae* Curt., *A. matricariae* Haliday, *Aphidius sp.* (near *avenae* Haliday) and *Praon volucre* (Haliday) *myzophagum* Mackauer (table 15).

TABLE 15. Parasites of *Myzus persicae* on two types of crops at Wageningen

Crop	Total number of mummies of *M. persicae* collected	Number of primary parasites emerging		
		A. rapae	*A. matricariae* & *A. avenae*	*Praon volucre*
Brussels sprouts and cauliflower (also infested with *B. brassicae*)	834	277	21	6
Potatoes (far from cruciferous crops and with no *B. brassicae*)	133	21	20	0

Thus it is shown that, in The Netherlands, contrary to the findings of GEORGE (1957) in England and SEDLAG (1958b) in East Germany, *A. rapae* parasitizes *M. persicae* in the field in a greater proportion than other species of Aphidiidae when the host is on cruciferous crops and so associated with *B. brassicae*. When mummies of *M. persicae* were collected on potato plants far from any fields of Cruciferae and with no infestation of *B. brassicae*, about half of the emerging primary parasites were *A. rapae*. Hence it could be stated that, next to *B. brassicae*, *M. persicae* is also an important host for the parasite *A. rapae*.

As host preference is an important feature in host specificity, the question arises as to which of the two hosts is preferred when offered simultaneously to *A. rapae*. The following experiment may clarify this point.

In each of ten glass dishes (plate 1, B), five half-grown nymphs of *B. brassicae* and five half-grown nymphs of *M. persicae* were confined simultaneously. One female of *A. rapae*, about 24 hours old, was placed in each dish for 24 hours.

No plant leaves were provided to eliminate the interference of a possible host plant attraction to either host or parasite. After 24 hours all nymphs were dissected and the number of parasite eggs deposited in each was counted. The results are given in table 16.

TABLE 16. Preference of *A. rapae* for nymphs of *B. brassicae* and *M. persicae*, when offered simultaneously

Female	*B. brassicae*		*M. persicae*	
	No. of nymphs parasitized	No. of eggs deposited	No. of nymphs parasitized	No. of eggs deposited
1	1	1	1	1
2	2	6	0	0
3	5	15	0	0
4	2	3	0	0
5	1	1	1	4
6	1	1	0	0
7	3	4	1	1
8	0	0	0	0
9	4	6	1	2
10	1	1	0	0
Total	20	38	4	8

More nymphs of *B. brassicae* parasitized $P < 0.005$
More eggs deposited in *B. brassicae* $P < 0.005$

These results show that *A. rapae* parasitizes both aphids but it prefers *B. brassicae* more than *M. persicae.*

From the emergence of mummies collected in the field it is concluded that in samples collected in different parts of The Netherlands, *A. rapae* was the only parasite of the cabbage aphid. Furthermore, it also parasitizes *M. persicae* in the field whether the host is on cruciferous crops or on potatoes, but more if on cruciferous plants (see table 15). From the results given in table 16, it is shown that if the parasite is given the choice to parasitize both aphids simultaneously, it parasitizes more individuals and in total deposits more eggs in *B. brassicae* than in *M. persicae.*

The fact that *M. persicae* is parasitized by *A. rapae* is of practical importance, especially during the early generations of the parasite. The infestation of early potato and brussels sprout plants by *M. persicae* helps the parasite to find an appropriate host, in addition to *B. brassicae* on the seed plants, early in the season. Thus it is probable that an early population of the parasite would be built up on those early crops and eventually moves to the new cruciferous crops. Furthermore, the fact that *B. brassicae* is more preferred by the parasite than *M. persicae* is also important, because generally both aphids infest cruciferous crops simultaneously. Hence, more parasitism by *A. rapae* would occur on *B. brassicae* than on *M. persicae.*

5. LIFE HISTORY

A. Development of the parasite

A. rapae is an internal parasite. The female deposits its eggs internally

within the body of the host. It was found in this work that under normal field conditions, the parasite eggs hatched within about 48 to 72 hours. Though more than one egg may be deposited in one individual host and normally all these eggs hatched into first instar larvae, only one larva survived. The other larvae died while still in their first instar. Consequently, only one adult emerged. At first the parasite larva feeds on the body fluids and the adipose tissue so that no external symptoms of parasitism can be recognized. A few days later, however, the growing parasite larva gradually starts to feed also on the host embryos and some of the internal organs. Then, the host aphid, though still alive, shows a sluggish appearance and some change in colour. By the time the parasite larva attains its full grown stage, all the internal contents of the aphid are already consumed and only the thin integument remains and turns into a hardened, straw-coloured, almost hemispherical body; a "mummy". The last instar larva opens a slit in the ventral surface of the host integument and thus fastens the mummy to the plant surface. This is done by means of the threads of the cocoon it starts to spin to line the inside of the host integument. The prepupa discharges the meconium, which is composed of about 10 to 20 shining, black, cigar shaped pellets, and transforms into a pupa. The adult emerges through a small circular hole generally cut dorsally near the posterior end of the mummy. Frequently the circular cap cut off the place of emergence remains hinged to it. The texture of the mummy, the shape and position of the emergence hole and the form of the meconium are characters of importance in differentiating the mummies that had given rise to an *Aphidius* adult from those that contained a secondary or tertiary parasite.

Mating may take place a few minutes after emergence but the female parasite starts ovipositing whether it has mated or not. The parasite is arrhenotokous, so an unmated female gives rise to an all-male progeny.

B. Sex ratio

On the whole females slightly exceed males in number. Out of the mummies of *B. brassicae* collected in 1959, 4321 *A. rapae* emerged; 2601, or 60.2%, of

TABLE 17. Sex ratio of *A. rapae*

Month	Total adults emerged	Percentage of females
June 1959	425	73.4
July	265	64.2
August	185	65.4
September	132	59.1
October	219	59.4
November	27	33.3
December	4	25.0
January 1960	17	23.5
February	112	49.1
March	369	48.0
April	1713	60.2
May	1594	60.5
June	162	60.5
July	416	59.6
August	21	52.4

which were females. Almost the same ratio of females; 782 out of 1297, or 60.3 % was obtained in 1960.

Actually the sex ratio has a seasonal variation as it was noticed that males are later in entering diapause and earlier in emerging from the overwintering mummies than females. This trend leads to a decline in the ratio of females in winter and early spring in comparison to other months as shown in table 17.

C. Longevity

A number of newly emerged adults were kept in glass tubes (16 × 4.5 cm) and provided with honey droplets, a piece of cotton wool soaked in water, and a leaflet of brussels sprouts to serve as a hiding place. The tubes were placed in the open air insectary and mortality was recorded daily. The results are summarized in table 18.

TABLE 18. Longevity of adults of *A. rapae*

Time	Females				Males			
	Total no.	Longevity in days			Total no.	Longevity in days		
		Min.	Max.	Aver.		Min.	Max.	Aver.
Early in the season (16–22.III.'60)	19	11	19	14	30	9	20	14
Early in the season (24–30.III.'60)	69	7	16	10.3	65	6	18	10.7
Mid-season (1–5.VII.'60)	79	3	16	7.4	56	3	14	7.4

These results indicate that, under the same conditions, there was no difference in longevity between males and females. In early spring the mean longevity was about two weeks. This period gradually decreased to one week under mid-summer conditions.

Furthermore, 54 females used for oviposition experiments under room temperature, provided with honey droplets, water, sprout or cauliflower leaves, and cabbage aphids for oviposition, lived for 9 days on the average, with a minimum of 4 days and a maximum of 15 days.

D. Fecundity

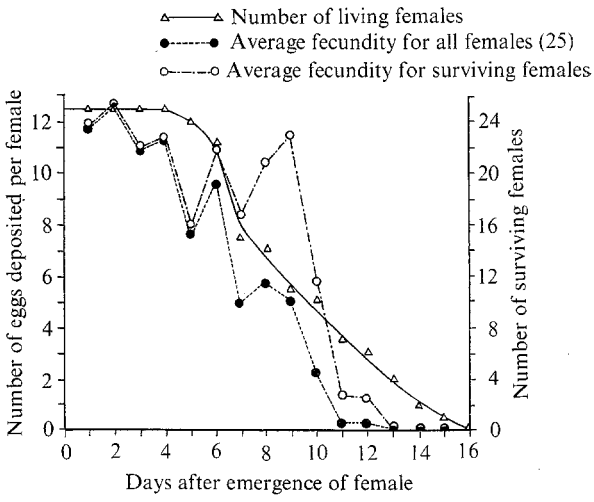
The total number of eggs deposited by one female of *A. rapae* throughout its life was determined by rearing newly emerged females individually in glass dishes (plate 1, B). Ten half-grown nymphs of *B. brassicae* were provided daily throughout the life of the female and were placed on a leaf of cauliflower or brussels sprouts. No filter paper was placed on the bottom of the dish so as to prevent the possibility of some of the nymphs hiding beneath it and escaping the parasite attack. Fine honey droplets were added on the wall of the dish to provide food for the parasite. For facilitating the process of determining the number of eggs deposited, the removed nymphs were reared for two days in similar glass dishes at a temperature of about 25 °C before dissecting them. By that time the parasite eggs had developed into advanced embryos or early first instar larvae and in either case were easier to find than the newly deposited eggs. The results obtained with 25 females are shown in table 19 and fig. 12.

TABLE 19. Fecundity of *A. rapae*

Female	Number of eggs deposited on successive days after emergence														Total no. of eggs
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1	21	10	17	8	0	0										56
2	4	16	9	1	0	24	15	47	28	17						161
3	7	16	24	10	0	20	1	5	22	14						119
4	7	1	1	3	0	3	3	3	4							25
5	0	5	13	11	0	11	15									55
6	2	11	8	5	13	0										39
7	6	0	4	2	5	12	7	21	10	0						67
8	4	6	3	17	0	0										30
9	11	9	8	4	3											35
10	9	20	11	4	0											44
11	9	6	17	7	0	0										39
12	30	16	11	1												58
13	19	15	16	5	3	1	0	0								59
14	3	12	3	6	5	10	13	0								52
15	14	18	7	0	0	1										40
16	3	20	2	0	2	13	1	4	0	0	0	0				45
17	1	1	0	4	6	10	6	4	3	5	1	1	0	0		42
18	1	6	3	19	15	15	11	18	9	6	3	4	0	0	0	110
19	4	7	15	23	17	20	11	12	16	3	1	0				129
20	13	12	16	15	16	11	7	10	13	6	3	3	0			125
21	11	20	9	10	16	12	15	2								95
22	44	30	18	14	9	9	10	6	7	0	0	0	0			147
23	16	16	10	45	39	32										158
24	30	25	14	17	12	26	9	14	15	7	0					169
25	29	19	35	55	28	9										175
Total	298	317	274	286	189	239	124	146	127	58	8	8	0	0	0	2074
Mean for 25 females	11.9	12.7	11.0	11.4	7.6	9.6	5.0	5.8	5.1	2.3	.3	.3	0	0	0	83
Mean for surviving females .	11.9	12.7	11.0	11.4	7.9	10.9	8.3	10.4	11.5	5.8	1.4	1.3	0	0	0	

From these results it can be concluded that, under the conditions of this experiment, females of *A. rapae* deposited 83 eggs on the average with a maximum of 175 and a minimum of 25 eggs. The maximum number of eggs deposited by a female of *A. rapae* under any condition, as obtained by the writer, was 205. These figures would seem lower than the corresponding figures obtained by other authors for this species and some other related species of the same family. However, the present figures may prove of more practical value as they represent the capacity of ovipositing with regard to the longevity, the searching and oviposition abilities of the parasite and the ability of the host to escape parasite attack. For instance, SEDLAG (1958b) reported that more than 400 ripe eggs were counted in the ovaries of *A. rapae* female. He added that by dissecting the exposed nymphs, he could find at least 207 eggs that were actually deposited. Unfortunately he did not mention the conditions under which he obtained those results. ULLYETT (1938) estimated that a female *Aphidius sp.* can deposit between 300 to 400 eggs during her life time. He added, however, that "this is her biotic potential but it does not follow that she will be able to deposit the full number; premature death may occur or she may not be able to find sufficient hosts". SCHLINGER & HALL (1960) stated that the total number of eggs per

FIG. 12.
Daily rate of oviposition and mortality of *A. rapae*



female of *Praon palitans* Muesebeck ranged from 118 to 194, but these numbers were taken from dissections of the ovaries under the assumption that "when hosts are available, females are capable of depositing their full complement of eggs".

In table 19 it is also shown that in almost all cases, 24 out of 25, females started to oviposit right from the first day after their emergence. However, it was not exceptional that, after few days of oviposition, a female completely stopped the oviposition, or deposited only 1 or 2 eggs per day, for one or more days and then again started to deposit larger numbers of eggs. In general, females deposited more eggs early in their life; 8 to 13 eggs per day were laid during the first nine days. The rate of oviposition then dropped sharply for the following three days. No female oviposited after the twelvth day though one specimen lived as long as 15 days (see fig. 12).

As will be shown later, *A. rapae* deposits indiscriminately in parasitized and non-parasitized hosts, so this trend of daily rate of oviposition is not expected to change much with the change of number of hosts available.

The number of eggs deposited per female per day ranged from a minimum of 0 to a maximum of 55, with a mean number of 10.3 eggs. The frequencies of numbers of eggs deposited daily throughout the life of the females are shown in table 20 and fig. 13.

The data obtained from the last day of life of each female were excluded from the table because it is not exactly known how long within that day the female was still alive. It appears from table 20 that in more than half of the days the females only produced a small number of eggs (10 eggs or less) or did not deposit at all. In only about 10% of the days a female deposited more than 20 eggs per day.

6. SEASONAL HISTORY

A. Hibernation

With the decline in temperature and photoperiod in autumn, *A. rapae* starts

TABLE 20. Frequencies of number of eggs deposited per day per female *A. rapae*[1])

Classes of number of eggs deposited per female per day	Frequency	Percentage
0 eggs per day	23	12.1
1– 5 ,, ,, ,,	48	25.1
6–10 ,, ,, ,,	40	21.0
11–15 ,, ,, ,,	34	17.8
16–20 ,, ,, ,,	26	13.6
21–25 ,, ,, ,,	7	3.7
26–30 ,, ,, ,,	7	3.7
31–35 ,, ,, ,,	1	0.5
36–40 ,, ,, ,,	1	0.5
41–45 ,, ,, ,,	2	1.0
46–50 ,, ,, ,,	1	0.5
51–55 ,, ,, ,,	1	0.5
Total	191	100.0

[1]) Last day of life of the female is excluded.

to hibernate. Mummies of *B. brassicae* were collected in large numbers twice a week in 1959 and in comparatively smaller numbers once a week in 1960. A high fraction of the mummies collected early in the autumn gave emergence to adult parasites before winter. This rate of emergence gradually decreased

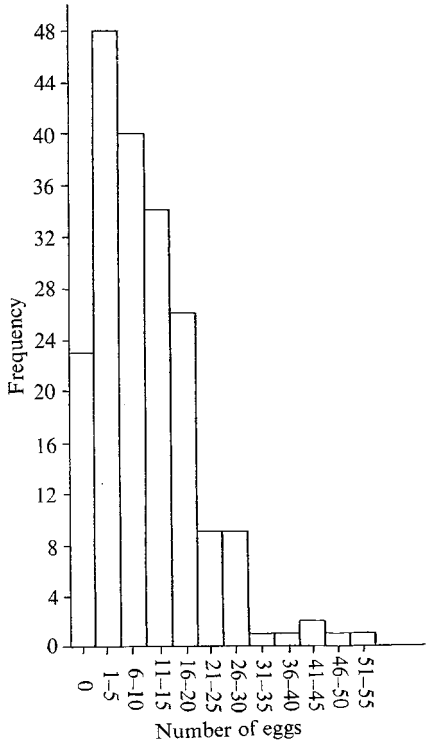


FIG. 13.
Frequencies of number of eggs deposited per day per female *A. rapae*

to reach a minimum in late October, after which very few adults emerged till spring. The first group of mummies with overwintering parasites in 1959 was collected on 26-IX (last autumn adult emerged on 6-X-'59 and first spring adult emerged on 19-IV-'60). In 1960, however, a group of mummies collected on 1-VIII-'60 did not give rise to adult parasites before 9-V-'61 (at least 281 days within the mummies).

The hibernation could easily be broken by exposing the mummies to room temperatures and long photoperiod.

To find out the hibernating stage of the parasite, 150 mummies of the cabbage aphid were collected and dissected once per week starting the middle of November 1959 and continued till late in April 1960 (during January and February collections were made once in two weeks).

The results of the dissections revealed that the parasite hibernates as a last instar larva within the mummy. Until the end of February only seven mummies contained living prepupae or pupae, which presumably emerged during the winter, while 912 mummies contained living last instar larvae. Starting the first week of March, the proportion of pupae, and eventually of emergence, gradually increased till the last overwintering parasite emerged 20-VI-'60 (from mummies collected 7-XII-'59).

In the Netherlands, the cabbage aphid normally overwinters exclusively in the egg stage, all other stages being inevitably eliminated during the winter. Consequently all earlier stages of the parasite die within their perishing hosts and so the parasite hibernates only as a last instar larva inside the mummy.

B. Emergence of hibernating parasites

Actually *A. rapae* emerged under natural conditions in all months of the year, though only in very small numbers in winter. Of 3358 adults which emerged after hibernation from mummies collected between 11-IX-'59 and 29-II-'60, very few emerged in January and the first half of February. Emergence then increased gradually, with the exception that an extraordinary high emergence occurred in the last week of February coinciding with a sudden spell of high temperature. A first peak of emergence occurred in the second week of April and a second peak in the second week of May. Thereafter, emergence of overwintered parasites gradually declined till it ended in the third week of June (See fig. 21). It was not possible to obtain any reliable data from mummies collected during the winter of 1960–1961 owing to the scarcity of mummies available in that period.

It is obvious that the trend of emergence, rather than the exact timing is more important because probably the dates of emergence vary from year to year. The significance of the time of emergence will be discussed later in relation to its coincidence with hatching of the overwintering eggs of *B. brassicae*.

Under natural conditions the early emerged parasites could still deposit some eggs even in November, December and January, if hosts are available for oviposition. This ability, however, is of no practical importance because most probably the hosts perish during the winter months. The fundatrices which hatch in late February and early March are more important. They can also be parasitized, and if they survive the type of weather in early spring, they give rise to the first generation of the parasite. These, together with the parasites emerging

later from the overwintering mummies, may cause an early high rate of parasitism as will be shown later.

C. Number of generations per year

To determine the number of generations of *A. rapae* per year in The Netherlands, the following method was used: A potted cauliflower plant, heavily infested with *B. brassicae*, was placed in a cage (plate 1, A) and an adequate number of both sexes of adult *A. rapae* were introduced into the cage under room temperature for oviposition. Twenty-four hours later, all parasites were removed and the cage was sealed and kept in an open air insectary. The plant was inspected daily and all mummies were carefully removed and kept in glass vials also under outdoor conditions. As has been mentioned before with *B. brassicae*, two series of generations were followed throughout the year. In series A, representing the maximum possible number of generations, a new cage, representing a new generation, was started on the day the first female of the previous generation emerged. In series B, representing the minimum possible number of generations, the last group of females emerging from a previous generation was kept in glass vials in the open air insectary. Every day some aphid nymphs were exposed to the females for oviposition. These nymphs were dissected the next day for parasite eggs. This procedure was continued until the last eggs were deposited. This day marked the extreme end of a generation and a new generation was started the same day. The generations were determined in this way in 1959 starting 18-III-'59 and in 1960 starting 26-II-'60. The results are shown in table 21.

These results show that in The Netherlands the extreme number of generations of *A. rapae* per year varied from 6 to 11 in 1959 (starting 18-III-'59) and 5 to 11 in 1960 (starting 26-II-'60). In 1959 the shortest generation took 14 days in July and August whereas in 1960 it took 16 days in July. Early in the season a generation took a minimum of 37 days, starting March 1959, and of 47 days, starting February 1960. Some of the mummies of the late generations, which mummified from September to January, overwintered and the adults emerged in the following spring. The extreme case was the eleventh generation of 1960 which started 2-XI-'60 and took 110 days for the first adult to emerge.

D. Effect of temperature on the rate of development

Observations indicated that temperature appeared, at least in part, to affect the great variation that occurred in the rate of development of the parasite. An experiment was conducted to determine that effect.

Non-parasitized half-grown nymphs of *B. brassicae* were exposed individually to parasites of *A. rapae* in a glass vial. When the host was observed to be definitely parasitized, it was removed from the vial and placed in a glass dish. Eight to twelve of these newly parasitized nymphs were reared on a cauliflower leaf in each dish (the dishes and the procedure of rearing are similar to that already described on page 456). Three of these dishes, containing a total of 24–36 parasitized nymphs, were placed in each of six chambers of a serial thermal cabinet. The parasitized nymphs were checked daily and mummies were collected and placed in glass vials at the respective temperatures till emergence. In all cases a photoperiod of 16 hours was used. The results are given in table 22 and fig. 3.

TABLE 21. Maximum and minimum number of generations of *A. rapae* in The Netherlands in 1959 and 1960

I. 1959

Generation number	Series A: Maximum number of generations						Series B: Minimum number of generations					
	Date					Duration in days	Date					Duration in days
	Host exposed	First mummy	Last mummy	First adult	Last adult		Host exposed	First mummy	Last mummy	First adult	Last adult	
1	18-III	14-IV	17-IV	24-IV	2-V	37– 45	18-III	14-IV	17-IV	24-IV	2-V	37–45
2	27-IV	12-V	17-V	19-V	25-V	22– 28	3-V	15-V	21-V	21-V	1-VI	18–29
3	19-V	1-VI	6-VI	6-VI	11-VI	18– 23	6-VI	17-VI	28-VI	23-VI	5-VII	17–29
4	6-VI	17-VI	28-VI	23-VI	5-VII	17– 29	9-VII	19-VII	27-VII	23-VII	3-VIII	14–25
5	23-VI	4-VII	8-VII	8-VII	13-VII	15– 20	10-VIII	20-VIII	3-IX	24-VIII	11-IX	14–32
6	9-VII	19-VII	27-VII	23-VII	3-VIII	14– 25	20-IX	4-X	19-X	13-X	16-XI	23–57
7	24-VII	4-VIII	15-VIII	9-VIII	22-VIII	16– 29	26-XI	No mummies. All aphids died during winter				
8	10-VIII	20-VIII	3-IX	24-VIII	11-IX	14– 32						
9	26-VIII	6-IX	17-IX	12-IX	26-IX	17– 31						
10	13-IX	27-IX	12-X	4-X	24-X	21– 41						
11	5-X	24-X	13-XI	21-XI	16-V-'60[1])	47–224						
12	26-XI	No mummies. All aphids died during winter										

II. 1960

1	26-II	4-IV	16-IV	14-IV	12-V	47– 75	26-II	4-IV	16-IV	14-IV	12-V	47– 75
2	20-IV	11-V	18-V	15-V	27-V	25– 37	16-V	31-V	10-VI	6-VI	17-VI	21– 32
3	16-V	31-V	10-VI	6-VI	17-VI	21– 32	24-VI	6-VII	23-VII	12-VII	30-VII	18– 36
4	6-VI	17-VI	25-VI	23-VI	3-VII	17– 27	11-VIII	23-VIII	1-IX	28-VIII	9-IX	17– 29
5	24-VI	6-VII	23-VII	12-VII	30-VII	18– 36	13-IX	27-IX	9-X	6-X	15-V-'61	23–244
6	13-VII	24-VII	1-VIII	29-VII	7-VIII	16– 24						
7	30-VII	10-VIII	24-VIII	17-VIII	31-VIII	18– 32						
8	17-VIII	29-VIII	5-IX	5-IX	15-IX	19– 29						
9	6-IX	18-IX	27-IX	26-IX	8-X	20– 32[2])						
10	26-IX	17-X	25-X	2-XI	14-XI	37– 49[3])						
11	2-XI	17-XII	7-I-'61	20-II-'61	25-IV-'61	110–174						

[1]) Some of the mummies overwintered till following spring.
[2]) One mummy hibernated giving emergence on 12-V-'61, so a duration of 248 days.
[3]) One mummy hibernated giving emergence on 8-V-'61, so a duration of 224 days.

TABLE 22. Effect of different temperatures on rate of development of *A. rapae*

Chamber number	Temperature °C			Duration in days						
				Oviposition to mummification		Mummification to emergence		Oviposition to emergence		
	Max.	Min.	Aver.	Max.	Min.	Max.	Min.	Max.	Min.	Aver.
1	5.5	3	4.5	All died within 29 days without mummification						
2	13	7.5	10.3	28	22	21	15	49	37	43.0
3	16	12	14.5	21	17	11	8	29	25	26.8
4	22	18	19.7	9	8	6	5	14	13	13.5
5	27	24	25.3	7	6	5	3	11	9	10.3
6	32	29.5	30.6	6	6	6	5	12	11	11.3

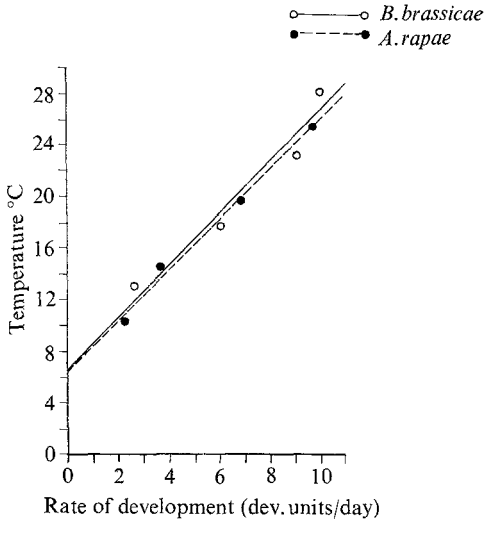
This experiment showed that temperature plays an important role in influencing the rate of development of the parasite both before and after mummification. However, because *A. rapae* is an internal parasite the effect of temperature before mummification may be indirect due to an effect on the host. After the host has been transformed into a mummy, the effect of temperature must be directly on the parasite.

It was observed that, on the whole, the rate of development as influenced by temperature showed almost the same trend in both *B. brassicae* and *A. rapae*. The duration decreased with an increase of temperature to an apparent optimum, above which there was an indication of a slight increase if the temperature was increased still further (see fig. 3).

When the temperature ranged between 3 to 5.5 °C (aver. 4.5 °C) all the parasitized nymphs died within 29 days. Another attempt was made at this particular temperature with a new group of 25 parasitized nymphs but they also died within 16 days. On dissection they contained parasite eggs in various stages of development. It was shown on p. 459 that unparasitized *B. brassicae* could not survive at these temperatures also. This might lead to the assumption that the development of the parasite is checked due to the lethal effect of these temperatures on the host. However, when the threshold of development of both *B. brassicae* and *A. rapae* was estimated (fig. 14), the lines indicating the rate of development for both host and parasite at the different temperatures almost coincided. The same threshold, about 6.5 °C, is obtained for both species. This indicated that the low temperatures used were lethal for both the cabbage aphid and for the parasite.

With an increase of temperature the rate of development of *A. rapae* increased until it reached a minimum of about 10 days at about 25 °C. It has been stated before that, in case of *B. brassicae* a further rise in temperature beyond the optimum reduced its survival rate. In this experiment also, about 90 parasitized nymphs had to be reared at an average temperature of 30.6 °C to secure only 16 mummies, whereas all the remaining host individuals died, generally within the first four days. Furthermore, this high temperature had a very detrimental effect on the parasites within the mummies and actually most of the 16 mummies failed to give adults. When such mummies were dissected, they all contained dead parasites still in their last larval instar. This meant that they probably died within less than 24 hours after mummification.

FIG. 14.
Effect of temperature on rate of development of *B. brassicae* and *A. rapae*



Hence, it is obvious that high temperatures seriously affect the parasite in the last larval instar whereas, as mentioned before, this stage is very tolerant to low temperature. In fact it is the only stage that hibernates and survives through winter.

The rate of development of the parasites which survive the detrimental high temperature seems to be prolonged as compared with the apparent optimum. However, owing to the scarcity of emerging individuals, the difference proved not to be statistically significant.

Table 22 shows that the minimum duration of a generation of *A. rapae* was 9 days whereas the maximum was 49 days. Under outdoor conditions this minimum was never achieved and appeared to be 14 days in July and August 1959. The maximum duration of a generation for a non-hibernating parasite under outdoor conditions was 75 days.

CHAPTER VI

HOST-PARASITE INTERRELATIONS

In this chapter, some elements of the parasitism of *A. rapae* and the interrelation between the host and the parasite are studied. This study serves in a discussion of the role of the parasite in regulating the population of the cabbage aphid.

1. OVIPOSITION

A. Preoviposition period

Newly emerged females of *A. rapae* contain a number of complete eggs and start oviposition shortly after emergence, provided an appropriate host is encountered.

The preoviposition period was determined as follows: Just after emergence, ten parasite females were isolated individually in glass vials (16 × 4.5 cm) with colonies of *B. brassicae* on leaves of cauliflower. The time between emergence and the first deposited egg (confirmed by dissection of the host) was recorded in every case. Temperature ranged between 18 and 21.5 °C, average about 20 °C. The results showed that the period between emergence and deposition of the first egg is rather short, ranging from about 20 to 111 minutes with an average of 48 minutes. Subsequently, oviposition proceeded with very short intervals. In five cases the time which elapsed between the first and the second egg was recorded; the range was from 1 to 24 minutes, average about 8 minutes.

B. Behaviour during oviposition

The process of oviposition is similar to that of related species, the abdomen of the female parasite is bent anteriorly beneath the thorax and between the legs to reach well in front of its head. The ovipositor is then inserted with a quick movement and an egg is deposited in the host. Thus, in most cases, the ovipositing female remains within some distance of the host and contacts it only with the ovipositor.

To observe the reaction of the parasite to the host over an extended period of time, several one-day old parasite females which had no previous access to hosts, were isolated individually in glass tubes with a cauliflower leaf heavily infested with *B. brassicae*. Each female was observed for six successive hours and the observations are summarized as follows:

The parasite generally finds its host within a few minutes. Normally, several unsuccessful attempts to oviposit precede an actual oviposition. Early in the exposure period, the parasite deposits its eggs in succession interrupted by short intervals of rest. Sometimes eggs are deposited less than one minute apart, either in the same host or in different hosts. After one or two hours, however, the rate of oviposition slows down, the parasite takes longer rests and walks around, sometimes even encounters the aphids without reacting to them. Few hours may elapse before the parasite tries to oviposit again. In the second period of active oviposition, the parasite deposits a smaller number of eggs, usually with longer intervals between ovipositions. Then it stops again and acts as mentioned above. These periods of gradually decreasing oviposition and gradually increasing intervals of rest alternate several times. After a few periods of active oviposition the parasite goes to hide for one or more hours, usually on the lower surface of the leaf. Under field conditions other appropriate sites for hiding will be present. The periods of "inactivity" are spent in walking around, cleaning its antennae, legs, wings and tip of abdomen or simply resting with no apparent movement. Sometimes, especially towards the end of the observation period, the parasite seems indifferent to the host, flying or walking to a place far from the host colonies, such as the glass walls or an uninfested part of the leaf, where it stays still and/or walks around for hours.

Since *B. brassicae* normally occurs in colonies in the field, the movements of the parasite in oviposition could be better studied by offering the host in colonies. Thus a disc was cut from a cauliflower leaf infested with colonies of *B. brassicae* and was fitted into the bottom of a petri dish. A cellophane paper was

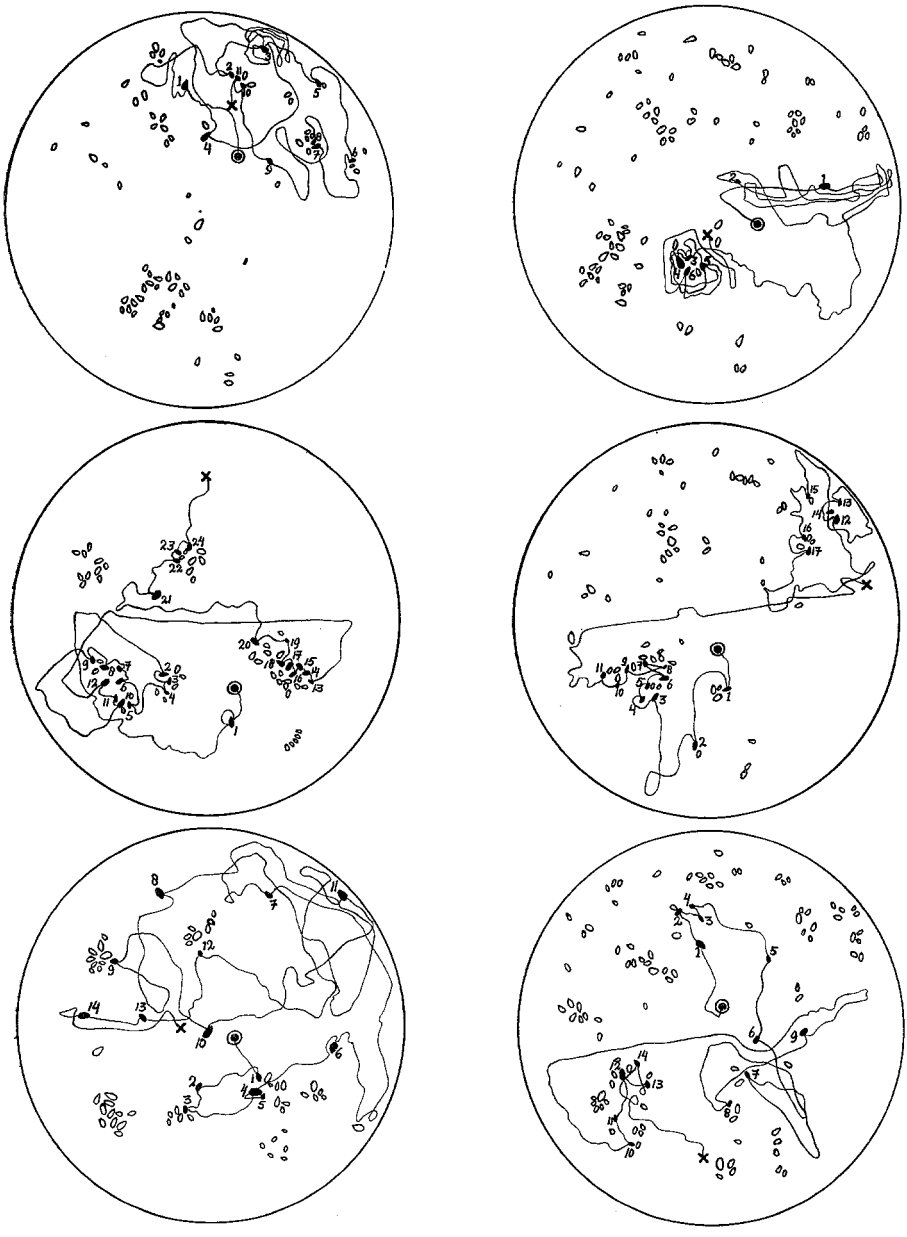


FIG. 15. Diagrams showing movements of female *A. rapae* in colonies of *B. brassicae*. Numbers indicate the sequence of apparently parasitized aphids

placed on the glass top of the dish and the position of colonies and individuals were marked on it. A parasite female of about one day old was introduced into the dish and its movements were recorded for 30 minutes on the cellophane paper. The results obtained with six females are shown in fig. 15.

It could be concluded from the diagrams of fig. 15 and the observations made during the experiments that generally the parasite percieves the host only at a very short distance. Even when it passes a host within one or two millimeters the parasite still might go its way without being attracted to it. Apparently the parasite does not react to the host till it nearly contacts it, almost invariably with the antennae first. Because of this lack of long-distance perception, the parasite is no more attracted to a colony than to an individual aphid. Similarly it is not attracted to a certain size of the host more than to another. However, there is always more chance that the parasite will encounter a colony because of its larger size. Once it encounters such a colony, there is more chance for other individuals within the same colony to be also encountered and so a parasite moves from one host to another in the same colony. However, it leaves the colony without having encountered all its individuals and it may also leave the colony after encountering only one individual. After having infested a certain host, the parasite may move around this host within a short distance. This behaviour could be interpreted as being an adaptation to the colony life of the host. In doing so, the chance to find another individual of the same colony increases considerably. However, in some cases it leads to a second meeting with the same host and superparasitism will generally be the result.

It was also confirmed in this series that once a host is encountered, several oviposition attempts are made before an actual oviposition takes place. This point will be illustrated numerically later in this chapter. Moreover, several actual ovipositions may occur in the same individual before the parasite finally leaves it.

C. Number of eggs per insertion of ovipositor

Three hundred and seventeen nymphs of *B. brassicae* were exposed individually to a few female parasites and when a single insertion, apparent insertion, or even an attempt to insert took place, the host was immediately removed before any other oviposition could occur. Upon dissection of those hosts, 206 out of the original 317 proved not to be parasitized. Each of the remaining 111 nymphs had one parasite egg only. This is in accordance with the general opinion concerning related parasites, though SCHLINGER & HALL (1959) have stated in the case of *Trioxys utilis* Muesebeck that "normally one egg is deposited per insertion of the ovipositor but occasionally 2 to 4 may be deposited".

2. HOST PREFERENCE

A. Discrimination between parasitized and non-parasitized hosts

It was of importance to investigate whether or not the parasite oviposits indiscriminately in parasitized and non-parasitized hosts. For this purpose, ten newly emerged female parasites were reared individually in glass dishes and each was given 20 half-grown nymphs of *B. brassicae* per day throughout its life. The nymphs were removed daily and dissected in order to count the num-

TABLE 23. Distribution of eggs of *A. rapae* within 20 host individuals as compared with a binomial distribution

No.	Total no. of eggs	No. of nymphs with									P[2])
		0 eggs	1 egg	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	7 eggs	8 eggs	
1	18	8 8.0	7 7.6	4 3.4	1 1.0	0 [1]) 0.2[1])					0.75
2	41	5 2.4	5 5.2	3 5.6	3 3.8	2 1.8	1 0.8	0 0.2	0 0.0	1 0.0	0.20
3	13	9 10.2	9 7.0	2 2.2	0 0.4						0.35
4	34	6 3.4	6 6.2	2 5.4	4 3.0	1 1.2	0 0.4	0 0.0	0 0.0	1 0.0	0.12
5	10	11 12.0	8 6.4	1 1.4	0 0.2						–[3])
6	10	14 12.0	3 6.4	2 1.4	1 0.2						–[3])
7	25	9 5.6	4 7.2	5 4.6	0 1.8	0 0.6	1 0.2	1 0.0			0.15
8	13	13 10.2	2 7.0	4 2.2	1 0.4						0.01
9	22	4 6.4	10 7.4	6 4.2	0 1.4	0 0.4					0.18
10	14	9 9.8	8 7.2	3 2.4	0 0.6						0.70
11	15	7 9.2	11 7.4	2 2.6	0 0.6						0.10
12	18	4 8.0	14 7.6	2 3.4	0 1.0	0 0.2					0.01
13	42	0 2.4	11 5.2	2 5.6	2 3.8	4 2.0	1 0.8				0.01
14	18	6 8.0	10 7.6	4 3.4	0 1.0	0 0.2					0.25
15	32	2 3.8	7 6.6	8 5.4	3 2.8	0 1.0	0 0.4				0.30
16	31	3 4.0	8 6.6	6 5.2	2 2.6	0 1.0	1 0.2				0.65
17	22	3 6.4	14 7.4	2 4.2	0 1.4	1 0.4					0.01
18	33	1 3.6	8 6.4	8 5.4	3 3.0	0 1.2	0 0.4				0.15
19	12	10 10.8	8 6.8	2 2.0	0 0.4						0.60
20	10	10 12.0	10 6.4	0 1.4	0 0.2						–[3])
21	11	12 11.4	5 6.6	3 1.8	0 0.2						–[3])

TABLE 23 continued

No.	Total no. of eggs	No. of nymphs with									P[2])
		0 eggs	1 egg	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	7 eggs	8 eggs	
22	13	11	6	2	1						0.70
		10.2	7.0	2.2	0.4						
23	43	1	4	7	7	1	0	0			0.20
		2.2	5.0	5.6	4.0	2.0	0.8	0.2			
24	29	0	12	7	1	0	0				0.01
		4.6	6.8	5.0	2.4	0.8	0.2				
25	44	3	4	5	4	2	2	0			0.95
		2.0	4.8	5.4	4.0	2.2	1.0	0.4			
26	28	2	8	10	0	0	0				0.01
		4.8	7.0	5.0	2.2	0.8	0.2				
27	14	9	8	3	0						0.70
		9.8	7.2	2.4	0.6						
28	18	8	8	2	2	0					0.75
		8.0	7.6	3.4	1.0	0.2					
29	38	1	4	11	4	0	0	0			0.02
		2.8	5.6	5.6	3.6	1.6	0.6	0.2			
30	20	8	5	6	1	0					0.20
		7.2	7.6	3.8	1.2	0.2					
31	24	3	11	5	1	0	0				0.15
		5.8	7.4	4.4	1.8	0.4	0.2				
32	21	6	10	1	3	0					0.25
		6.8	7.6	4.0	1.4	0.4					
33	81	0	3	1	4	3	3	5	1	0	0.70
		0.3	1.4	2.9	4.0	4.1	3.3	2.2	1.2	0.6	
34	30	8	5	1	3	2	0	1			0.02
		4.2	6.8	5.2	2.6	1.0	0.2	0.0			
35	23	8	4	5	3	0					0.15
		6.2	7.4	4.4	1.6	0.4					
36	14	10	6	4	0						0.45
		9.8	7.2	2.4	0.6						
37	14	13	5	0	0	1	1				0.17
		9.8	7.2	2.4	0.6	0.0	0.0				

[1]) In each pair of frequency distributions, the first line represents the actual distribution observed in the experiment and the second line represents the expected values as calculated from a binomial distribution.

[2]) P is the probability to obtain the observed egg distribution over the twenty host nymphs, or an equally or less probable distribution, assuming that the null-hypothesis: "Oviposition occurs at random" is true. The obtained values of P are based on X^2-tests for goodness of fit of the observed distribution with the best fitting binomial distribution. In case of low frequencies, several classes had to be combined before the test could be used.

[3]) In these cases X^2-tests could not be used; after the necessary combination of classes, the number of degrees of freedom (= K-2) was zero.

ber of parasite eggs deposited. Since it has been shown before that females of *A. rapae* deposit only one egg per insertion, so the total number of eggs indicates the total number of ovipositions. Only cases in which a total number of 10 or more eggs were deposited by one female in one day were used to test the fitness of their egg distribution with a random distribution. Under these conditions, a binomial distribution was taken as the most appropriate approximation for a random distribution. The results of 37 cases are shown in table 23.

These results show that it was not possible to reject the hypothesis that, within the exposed twenty host individuals, the number of eggs per host followed a binomial distribution. This means that, given the choice to deposit in any of the exposed 20 individuals, the females did not discriminate between parasitized and non-parasitized hosts. If the parasites completely discriminated, all the parasitized hosts would have fallen into one class only; hosts with *one* parasite egg. Furthermore, if the parasites even partly discriminated, there would have been a tendency for a higher number of hosts with one parasite egg than is expressed by the binomial distribution. Both cases were found not to be true in *A. rapae*.

This conclusion is further supported by the data obtained from the fecundity of 25 female parasites described above (page 491). In that experiment a total of 977 nymphs of *B. brassicae* were parasitized and the number of eggs per host were distributed as shown in table 24.

TABLE 24. Frequencies of numbers of parasite eggs per nymph of *B. brassicae*. Result of 25 female parasites each given 10 host nymphs per day

Number of parasite eggs per host individual	Frequency	Total eggs deposited	Eggs deposited in unparasitized hosts	Eggs deposited in parasitized hosts
1	436	436	436	0
2	279	558	279	279
3	125	375	125	250
4	67	268	67	201
5	33	165	33	132
6	15	90	15	75
7	8	56	8	48
8	8	64	8	56
9	2	18	2	16
10	2	20	2	18
11	1	11	1	10
13	1	13	1	12
Total	977	2074	977	1097

It is shown that a total of 2074 eggs were deposited, out of which 1097 eggs were deposited in already parasitized hosts.

When only one host individual was exposed to one female parasite for 24 hours, superparasitism was inevitably accelerated and a maximum of 28 eggs were found in one host.

All above mentioned data were collected under laboratory conditions and with only one female parasite depositing at a time. Superparasitism also occurs in the field either by the same parasite or by several parasites. By dissecting

several thousand individuals of *B. brassicae* collected in the field, a maximum of 13 first instar larvae of the parasite (one alive and 12 dead) were found in the same host individual.

All this superparasitism is a waste for the parasite since, as has been mentioned before, only one parasite larva can survive.

B. Preference of the parasite to different stages of the host

Since normally the cabbage aphid lives in colonies, all the stages of the aphid are as a rule exposed simultaneously to the parasite throughout the main part of the season. Therefore a study was made of the parasite preference for oviposition in different stages of the host.

1. Method: Since the parasite oviposits in a moving host, in contrast to other species of parasites which oviposit in stationary hosts such as eggs or pupae, and since the preliminary trials to glue the host individuals to render them immobile did not succeed, a method had to be devised to obtain the information from a group of host individuals rather than from single individuals.

The bottom of a petri dish was covered with a cauliflower leaf on which ten apterous adults of *B. brassicae* plus ten individuals of another stage were placed simultaneously. The aphids were left for a few minutes till they settled down in an approximately random distribution. Then one female of *A. rapae*, about one day old, that had been fed on honey droplets, was introduced into the dish. Contacts of the female with any of the aphids of either stages were recorded for half an hour and classified into three categories: Mere encounters, encounters followed by oviposition attempts and encounters followed by oviposition attempts resulting in actual oviposition as revealed by dissection.

Due to the fact that the parasite deposits only one egg per insertion (see p. 502), the number of successful attempts can be determined from the number of eggs present in the host.

Ten replicas were made in each case. The apterous females were taken in all cases as a standard for comparison and so the following combinations were made for testing the preference of the parasite:

A. Apterous females and young nymphs
B. Apterous females and half-grown nymphs
C. Apterous females and advanced nymphs
D. Apterous females and alate females

2. Results and discussion: The results are summarized in tables 25 and 26.

The first point to be considered is the difference in encounters. It has been stated (p. 502) that searching parasites make random movements on the substrata. Hence, the encounter with a host is merely a matter of chance. Nevertheless, there were significant differences between the various stages of the host encountered by the parasite. This phenomenon is presumably due to the fact that the hosts exposed simultaneously differ in size. The most pronounced difference was observed between young nymphs and apterous adults. The distinction disappears when the various stages were of equal size such as between apterous and alate adults. When these stages were exposed to parasite attack, the probability of being encountered proved to be the same (table 26).

TABLE 25. Preference of the parasite *A. rapae* to different stages of *B. brassicae*

	Combination A			Combination B			Combination C			Combination D		
	Apterous adults	Young nymphs	Total	Apterous adults	Half-grown nymphs	Total	Apterous adults	Advanced nymphs	Total	Apterous adults	Alate adults	Total
Number of encounters	256	154	410	291	271	562	233	180	413	217	215	432
Number of encounters with another host with oviposition attempt	146	87	233	120	133	253	110	95	205	111	90	201
Number of eggs deposited . .	50	63	113	45	95	140	45	52	97	40	19	59
Number of exposed hosts parasitized	37	51	88	34	64	98	34	39	73	33	7	40

TABLE 26. Preference of the parasite *A. rapae* to different stages of *B. brassicae*

	Combination A		Combination B		Combination C		Combination D	
	Apterous adults	Young nymphs	Apterous adults	Half-grown nymphs	Apterous adults	Advanced nymphs	Apterous adults	Alate adults
Percentage of total encounters	62.4	37.6**	51.2	48.8	56.4	43.6**	50.2	49.8
Percentage of effectiveness of encounters	8.7	34.1**	8.6	25.8**	11.4	16.9*	11.5	7.5
Percentage of effectiveness of oviposition attempts	10.7	53.4**	12.9	41.3**	16.6	23.3+	16.5	14.8
Percentage of exposed hosts parasitized	37	51	34	64**	34	39	33	7*
Percentage of total eggs deposited . . .	44.2	55.8	32.1	67.9**	46.4	53.6	67.8	32.2**

** Difference is highly significant ($P < .001–.01$)
* Difference is significant ($P < .05$)
+ Difference is nearly significant ($.05 < P < .10$)

However, under field conditions in most cases the different stages occur together in colonies and, consequently, if a colony is encountered by a parasite, the individual hosts within the colony will have more chance to be encountered regardless of their stage.

The second point to be studied deals with the fact that once the parasite has contacted a host individual, there might be a difference in the reaction of the parasite to the various stages of the host. Having encountered the host, the parasite may either start its oviposition attempts or reject the host without trying to oviposit. The latter phenomenon occurred in 43%–59% of the cases regardless of the stage of the host. There were no significant differences between the various stages. This indicates that rejection of the host without any attempt to oviposit is caused by some factor intrinsic to the parasite.

The host may also be rejected after oviposition attempts have been made. In this respect considerable differences between the various stages of the host proved to exist. To illustrate this phenomenon the effectiveness of encounters has been calculated. This term is defined as:

$$\frac{\text{Total number of actual ovipositions}}{\text{Total number of encounters}} \times 100\% = \frac{\text{Total number of eggs deposited}}{\text{Total number of encounters}} \times 100\%$$

The values of this index have been given in table 26. For apterous adults the index ranged from 8.6% to 11.5%; alate adults were even less infected (7.5%). The nymphs, however, were significantly more succesfully parasitized; the fractions of encounters resulting in oviposition were 34.1% for the young nymphs, 25.8% for the half-grown nymphs and 16.9% for the advanced nymphs.

These facts may be explained by assuming a preference of the parasite to oviposit in earlier stages of the host. However, the observations made on the females during the process of oviposition showed that the attacked hosts made frantic movements to scare off the parasite. The effect of these movements increased with the development of the host stage. This means that an oviposition in a more advanced stage of the host requires a higher number of oviposition attempts. This phenomenon has been expressed in terms of the effectiveness of oviposition attempts, which is an index defined as:

$$\frac{\text{Total number of actual ovipositions}}{\text{Total number of oviposition attempts}} \times 100\% = \frac{\text{Total number of eggs deposited}}{\text{Total number of oviposition attempts}} \times 100\%$$

The values of this index have also been given in table 26. It decreased from a high value, 53.4%, for young nymphs to 10.7%–16.6% for apterous adults.

The results strongly support the view that the movements made by the adult hosts attacked are more effective as to scaring off the attacking parasite. Another possible explanation, however, is the ability of the parasite to pierce the thin cuticle of a young host more easily than the thicker cuticle of a more advanced host.

To sum up, the experiments show that, proceeding from small to large host

stages, the probability of being encountered increases, but the chance of being parasitized, once being encountered, decreases. Due to these opposite effects the half-grown nymphs run the highest risk of being parasitized. An index of the comparative number of hosts parasitized and number of eggs deposited in each of the five aphid stages was calculated from the data obtained in these experiments and is shown in table 27.

TABLE 27. Index of parasitized host individuals and parasite eggs deposited in five different stages of *B. brassicae*

Stage	No. of parasitized host individuals	No. of parasite eggs deposited
Half-grown nymphs	100	100
Young nymphs	73	60
Advanced nymphs.	61	55
Apterous adults.	53	47
Alate adults	11	22

The experiments also show that, even if the hosts are encountered at random, the final process of oviposition and parasitism is not accomplished at random. The deliberate actions of both host and parasite interfere with that process so that some stages of the same host species would have more parasitism and recieve more parasite eggs than some other stages.

It is also shown that the alate adult is the stage which is less preferred for parasitism; less individuals are parasitized and less parasite eggs are deposited in them. This conclusion is of practical importance because of its relation to the dispersal of the parasite (see p. 517).

3. EFFECT OF PARASITISM IN DIFFERENT STAGES OF HOST ON BOTH HOST AND PARASITE

Since it had been shown that there is a decisive tendency for some stages of the host to be parasitized more than other stages, the next logic step was to study the effects of parasitism in different host stages on both host and parasite.

A. Methods

In case of the series of experiments concerning the apterous forms, a group of newly born first instar nymphs of *B. brassicae* or newly moulted individuals of second, third, and fourth nymphal instars and apterous adults, were exposed individually to the parasite and kept under observation until each individual was definitely parasitized. Fourty of these parasitized aphids of each instar were confined in 8 glass dishes (plate 1, B) so as to have a group of five individuals per dish. However, 80 first instar nymphs were used because they are normally more delicate to handle. The same number of non-parasitized aphids of the same age of the five developmental stages were also confined in similar dishes for control. It was ascertained that the newly moulted apterous adults, either parasitized or non-parasitized, had not deposited any nymphs before they were included into the experiment. The aphids were reared on cauliflower leaves as described on p. 456. The dishes were kept under room conditions starting 21-VII-'60.

The same procedure as is mentioned with the apterous forms was followed with the alate forms, but with the following minor differences:

1. Because the alate nymphs could not be distinguished before the third nymphal instar, only third instar nymphs, fourth instar nymphs and alate adults were used.

2. Because the alate forms were found to have a higher mortality under the conditions of the experiment than the apterous ones, 50 nymphs in 10 dishes, instead of 40 in 8 dishes, were used in each case of the two nymphal instars.

3. Because the alate adults were known from previous experiments to have a rather high initial mortality, 40 adults were used in each case (parasitized and non-parasitized); they were isolated individually in dishes and so it was possible to exclude from the experiments all the adults, whether parasitized or non-parasitized, which died within the first three days.

4. This series was also kept under room conditions but as it started rather late (on 26-X-'60) a period of 16 hours of day light was given.

All dishes of both series were checked daily for moulting of the aphids, number of nymphs deposited and mummification. The mummies were removed, kept individually in glass vials and checked daily for emergence. The body length of emerging adult parasites was measured. The emerging females were fed on honey droplets and water for three days after which they were dissected to determine the number of ovarian eggs. This number was used as an index for the reproductive capacity.

B. Results and discussion

The results of these series of experiments are summarized in tables 28 to 31 and fig. 16 and 17.

These results show that the stage parasitized has important effects on both host and emerging parasite.

1. Effects on the host: It has been found that a parasitized *B. brassicae* still developed and moulted till it attained the fourth nymphal instar or the adult stage before it mummified. If the host was parasitized as first or second instar nymph, all mummification took place in the fourth nymphal instar (with the exception of only one individual in each case which mummified as an adult). If the host was parasitized as third or fourth instar nymph or as adult, the mummification took place in the adult stage. The same holds true in the winged forms, because all the mummies obtained from hosts parasitized in the third and fourth nymphal instars and in the adult stage were mummified alate adults with fully developed wings (plate 2 B, d). This means that the mummies collected in the field with abortive wing pads (plate 2 B, b and c) must have originated from nymphs destined to develop to alatae but were parasitized in the first and second nymphal instars. Hence, any parasitized *B. brassicae*, alate or apterous, mummifies in the fourth nymphal instar or as an adult.

Another effect of parasitism on the host was a general increase of the duration of development as compared to a non-parasitized aphid (fig. 16). This was especially true in case of hosts parasitized early in their immature stages because hosts parasitized in the third and fourth nymphal instars attained the adult stage before the parasite reached a stage that can seriously influence them. In such cases there was no significant differences in the duration of the nymphal

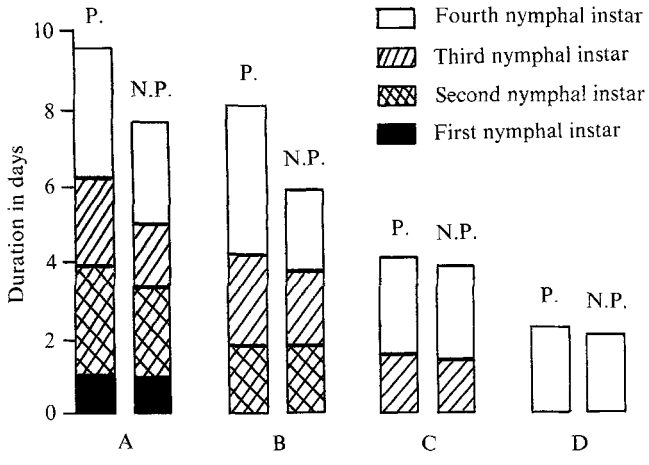


FIG. 16. Effect of parasitism in different stages on rate of development of *B. brassicae*. P, parasitized; N. P, non parasitized for control; A, parasitized in the first nymphal instar; B, parasitized in the second nymphal instar; C, parasitized in the third nymphal instar; D, parasitized in the fourth nymphal instar

TABLE 28. Effect of parasitism in different stages of *B. brassicae* (apterous forms) on its rate of development

Host stage	Mean rate of development of host (days)							
	parasitized in first instar	non-parasitized	parasitized in second instar	non-parasitized	parasitized in third instar	non-parasitized	parasitized in fourth instar	non-parasitized
First instar . .	1.17	1.06						
Second instar .	2.74	2.29	1.87	1.85				
Third instar .	2.28	1.67	2.26	1.92	1.56	1.44		
Fourth instar .	3.29	2.63	3.92	2.05	2.48	2.40	2.22	2.03
Total rate of development up to adult	9.48[1])	7.65	7.05[1])	5.82	4.04	3.84	2.22	2.03

[1]) Up to mummification because they mummified in the fourth instar.

TABLE 29. Total number of nymphs deposited per parasitized and non-parasitized adult of *B. brassicae* (Apterous and alate forms)

Stage of host when parasitized	Average no. of nymphs deposited per adult	
	Parasitized	Non-parasitized
Early third nymphal apterous instar	0.0	34.9
Early fourth nymphal apterous instar	3.3	
Early apterous viviparae	10.3	
Early third nymphal alate instar	0.7	23.4
Early fourth nymphal alate instar	3.2	
Early alate viviparae	8.2	

TABLE 30. Effect of stage of parasitized *B. brassicae* (apterous forms) on the parasite *A. rapae*

Stage of host when parasitized	Rate of development of parasite females (days)			Aver. body length of emerging female in mm	Aver. no. of eggs in ovaries of emerging female
	From oviposition to mummification	From mummification to emergence of adult	Total rate of development from oviposition to emergence of adult		
Early first nymphal instar	9.5	4.7	14.2	2.33	176
Early second nymphal instar . .	8.3	4.8	13.1	2.33	173
Early third nymphal apterous instar	7.6	4.7	12.3	2.39	197
Early fourth nymphal apterous instar	7.5	4.3	11.8	2.40	203
Newly moulted apterous adult . .	7.5	4.5	12.0	2.43	213

TABLE 31. Effect of stage of parasitized *B. brassicae* (alate forms) on the parasite *A. rapae*

Stage of host when parasitized	Rate of development of parasite females (days)			Aver. body length of emerging female in mm	Aver. no. of eggs in ovaries of emerging female
	From oviposition to mummification	From mummification to emergence of adult	Total rate of development from oviposition to emergence of adult		
Early third nymphal alate instar .	12.4	7.7	20.1	2.2	216
Early fourth nymphal alate instar	11.5	7.4	18.9	2.1	195
Newly moulted alate adult . . .	12.2	8.2	20.4	2.1	163

stage between a parasitized and a non-parasitized aphid. In the case of apterous forms, a nymph parasitized early in the first instar took an average of about 9.5 days before it finally mummified late in the fourth instar (see table 28), whereas a similar non-parasitized nymph took only about 7.5 days to reach the adult stage. The difference between the duration of development in each nymphal instar of parasitized and non-parasitized nymphs persisted in each instar with increasing magnitude, due to the gradual development of the larva of the parasite. The difference in duration of the first instar was nearly significant ($0.05 < P < 0.10$) whereas it was highly significant ($P < 0.001$) in later instars.

Nymphs parasitized early in the second instar showed no significant difference in the average duration of the second instar compared with non-parasitized nymphs whereas the difference was significant ($P < 0.05$) in later instars (see table 28 and fig. 16).

Thus it could be concluded that, if first or second nymphal instars of *B. brassicae* are parasitized, the duration of development increases in comparison to the non-parasitized nymphs.

Parasitism had also an important effect on the rate of reproduction of the host. As has been mentioned before, a nymph parasitized in the first or second instar will mummify before it reaches the adult stage and so its power of increase will be entirely eliminated. A nymph parasitized in the third instar will develop into an adult before it mummifies. However, the ovaries of these adults would have been destroyed by the parasite to such an extent that their reproductive capacity can be considered as being practically eliminated. In case of the apterous adults parasitized early in the third nymphal instar no reproduction occurred while in case of alate adults they deposited an average of 0.7 nymphs before they mummified (table 29).

Nymphs parasitized in the fourth instar moulted into adults and started depositing some of their progeny before they finally succumbed. However, the number of nymphs deposited was very low as compared with normal reproduction (table 29). It was observed during the experiment that such parasitized apterous adults could deposit till a minimum of 3 days before mummification, whereas in case of alatae the adult succumbed earlier and the last nymph was deposited six days before mummification.

The hosts parasitized as early adults had more capacity to deposit nymphs before they mummified. Thus on the average both parasitized apterous and alate adults were able to deposit about one third of the normal number of nymphs deposited by the non-parasitized controls (table 29). Though in some cases deposition of nymphs continued till 3 or 4 days before mummification, it was observed that in most cases parasitized adults stopped deposition some time earlier, while the parasite was still in an early stage and did not grow old enough to consume or injure all the embryos or the internal organs of the mother. Presumably the young parasite larva can exert an inhibiting influence on the reproduction of the host. The daily rates of reproduction of both parasitized and non-parasitized adults are shown in fig. 17.

The above discussion concerns the early moulting adults. However, since the host is readily parasitized in the adult stage, it is most probable that parasitism can take place indiscriminately regardless of the age of the parasitized adult and thus all age groups have the same chance to be parasitized. Hence, it might be possible that some adults, if parasitized late enough, escape the effect of

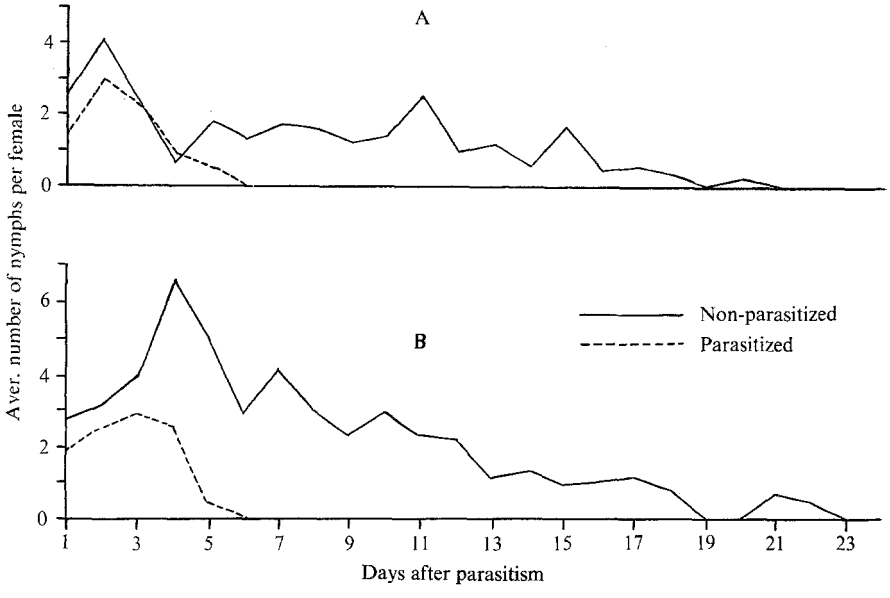


FIG. 17. Daily rate of reproduction of parasitized and non-parasitized *B.brassicae*; parasitized as early adults. A, alate virginoparae; B, apterous virginoparae

parasitism since they would have deposited most of their offspring before the inhibiting effect of the parasite was felt. This "escape" should be even more conspicuous in the alatae because their reproduction is more concentrated in the initial part of the adult life than that of the apterae (see fig. 4 and 5).

The capacity of a parasitized host to reproduce has a bearing on the economic importance of the parasite and should be taken into consideration in any mathematical model of host-parasite interactions.

2. Effects on the parasite: The three main properties of the parasite which are probably affected by the stage of the host are:

1. Size of the emerging parasite (as indicated by the body length).
2. Rate of development of the immature stages; i.e. the period between oviposition and emergence of adult.
3. Fecundity of the emerging female. This property was indicated by the number of eggs present in the ovaries of the female three days after its emergence and without any access to hosts.

Because the effect on the female of the parasite is most relevant and because the results have shown that there is no significant difference in the duration of development between males and females, only the effects on females are discussed here.

As for the size of the female parasites, no significant differences were found as a result of the stage of host parasitized (tables 30 and 31).

Concerning the rate of development, the results show that the duration of the immature forms took longer when parasitism started in the first nymphal instar

and that it gradually decreased with significant differences between the stages parasitized (tables 30 and 31). The shortest duration of development of the parasite was reached when the aphid was parasitized in the fourth nymphal instar. Further, when the apterous or alate adult was parasitized, most probably the duration of the parasite development increased again. Compared with parasite development in the fourth nymphal instar, the increase of the mean rate of development is nearly significant ($0.05 < P < 0.10$) in case of the apterous and significant ($P \leqslant 0.05$) in case of the alate adults.

It is of importance to note that when the duration of parasite development is divided into two successive periods, *viz.* from oviposition to mummification (a feeding stage occurring inside the living host) and from mummification to emergence (a non-feeding stage occurring inside the mummy), the latter period proved to be independent of the host stage parasitized. The former period, however, was longest when parasitism started in the first instar and gradually decreased with the development of the host when parasitized till the fourth nymphal instar. Further, when the host was parasitized in the adult stage, the duration of the former period of the parasite either remained as it was in the fourth instar (in apterae) or slightly increased again (in alatae) (tables 30 and 31).

It might be suggested that, other factors being equal, the duration of the immature stages of the parasite inside their hosts depends on a combination of the quantity and quality of the available food. The quality of food, increasing with the development of the host, may lead to an increase in the rate of development of the parasite. This holds true till the last nymphal instar of the host. After this, though the quantity of food may increase still further, at least early in the adult stage, its quality might become so different (especially in case of the alate hosts) that the result would be a decrease in the rate of development of the parasite.

The effect of parasitism of the different host stages on the fecundity of the parasite was also studied. In the apterous series (table 30), the average number of ovarian eggs per female amounted to 176 when the first nymphal instar was parasitized and to 213 eggs when the apterous adult was infested. Though there was no significant difference between each two successive stages, the difference between the two extremes, *viz.* parasitized as first instar and as adult, was highly significant.

In the alate series (table 31), the fecundity of the parasite seemed to decrease – rather than to increase – when the host was parasitized in a later stage, at least from the alate third nymphal instar to the alate adult. Though the difference in fecundity between parasites started in the alate third and fourth nymphal instars was not significant, they both contained a significantly higher number of eggs than parasites started in the alate adults.

It should be noted here that on the average a female parasite that had started in an apterous adult had 213 eggs in its ovaries whereas it had 163 eggs when started in an alate adult. These figures, however, are not conclusive because several factors, other than the morph of the host, might have contributed to it, since the experiments on alatae and on apterae were not conducted simultaneously.

It can be concluded, both from the effects on rate of development and on fecundity of the parasite, that there is a difference between the apterous nymphs

and adults on the one hand and the alate nymphs and adults on the other. The alate adults seem to be comparatively less suitable for parasite development than the advanced alate nymphs while this is not the case in the apterae.

To conclude, both host and parasite are influenced by the stage of host parasitized. The most important properties affected in both host and parasite are fecundity and rate of development.

4. EFFECT OF PARASITISM ON ALATE FORMATION

Winged aphids are generally considered to be the main instrument of dispersion of their parasites. After being parasitized, they may take to the wing while carrying early stages of the parasite within them and fly for a long distance to a new locality (ULLYETT, 1938; VEVAI, 1942; SCHLINGER & HALL, 1960).

It has been shown earlier in this chapter (p. 510) that if the cabbage aphid is parasitized in the first or second nymphal instar, it will mummify before reaching the adult stage. An aphid parasitized in the third nymphal instar or later will develop into an adult before it mummifies. Furthermore, it has also been shown (p. 509) that an alate adult runs a lower risk of being parasitized than any of the other stages. Hence, the preference of the parasite to deposit in alate or apterous advanced nymphs remained to be tested and the following experiment was conducted for this purpose.

In each of 11 glass dishes 10 apterous and 10 alate advanced nymphs of *B. brassicae* were confined simultaneously on a cauliflower leaf. Five females of *A. rapae* were introduced into each dish and left for 24 hours to deposit eggs in any of the nymphs. The nymphs were then dissected and the results of egg deposition are given in table 32.

TABLE 32. Parasite eggs deposited in apterous and alate advanced nymphs of *B. brassicae* exposed simultaneously to the parasite

Dish	Total no. of eggs deposited	No. of eggs deposited in the apterous nymphs	No. of eggs deposited in the alate nymphs	Percentage of total eggs deposited in the alate nymphs
1	92	59	33	35.9
2	22	9	13	59.1
3	9	8	1	11.1
4	3	3	0	00
5	40	31	9	22.5
6	39	20	19	48.7
7	9	8	1	11.1
8	47	34	13	27.7
9	28	19	9	32.1
10	5	2	3	60.0
11	20	15	5	25.0
Total . .	314	208	106	33.8

More eggs are deposited in apterous nymphs, $P = 0.01$

These results show that the apterous nymphs had significantly more parasite

eggs than the alate nymphs. As the number of eggs deposited is taken as an indication for the preference of the parasite for oviposition in a certain host, so it can be concluded that the apterous nymphs are preferred by the parasite over the alate nymphs. When both forms of nymphs were offered simultaneously, only about one third of the eggs were deposited in the alatae.

In the field where a variety of stages of the host is present this preference will be even more pronounced. A total of 4042 mummies of *B. brassicae* collected at random in the field during 1960 were classified into: apterous mummies, mummies with fully developed wings and mummies with reduced wing pads (plate 2, B). The results show that less than 0.5% of the mummies had fully developed wings and about 2.2% had reduced wing pads while 97.3% were totally apterous mummies. The ratio of alate mummies was far less than the ratio of the alatae in the aphid population.

This high percentage of apterous mummies was, at least partly, attributed to the fact that the parasite prefers to deposit its eggs in apterous forms. However, another factor that can contribute to a high proportion of apterous mummies is a functional response of the host to the parasite, leading to a suppression of the alate characters and to the formation of an apterous mummy even if an individual destined to be an alate was parasitized. JOHNSON (1958 and 1959) has shown such a suppression of the alate characters in *Aphis craccivora* Koch. when parasitized by *Aphidius platensis* Bréthes.

An experiment was carried out to test the occurrence of such a suppressing effect in *B. brassicae* after being parasitized by *A. rapae*.

A number of first instar nymphs, collected from one leaf of a cauliflower plant, were divided at random into two groups. The nymphs of one group were parasitized. Fifty nymphs out of each group (so 50 parasitized plus 50 non-parasitized) were reared on a cauliflower plant in a sealed cage. Two replicas were used and when the non-parasitized nymphs developed into adults and the parasitized ones developed into mummies each group was classified into alate and apterous. The results are shown in table 33. (Plate 2, B; a, shows the apterous mummies; b and c, show the type of alate mummies obtained in this experiment).

TABLE 33. Effect of parasitism on alate formation

	Non-parasitized; no. of adult aphids			Parasitized; no. of mummies		
	Alate	Apterous	Total	Alate	Apterous	Total
Cage I	10	36	46	6	29	35
Cage II	11	34	45	3	29	32

From these results it was not possible to conclude that there was a significant difference in the proportion of alate and apterous forms caused by the effect of parasitism.

More work should be carried out on the physiological suppression of the alate characters by the parasite before definite conclusions about the causes of the scarcity of alate mummies in the field can be drawn. However, this type of study is beyond the scope of the present work and the fact remains that under natural conditions the proportion of alate mummies is extremely low. More-

over, it was possible to prove that at least one reason for this phenomenon is the preference of the parasite for deposition in apterous adults and advanced nymphs more than in alate ones. It may be concluded that the role of parasitized alatae in the dispersion of the parasite is not very important. The proportion of alatae in nature may not be taken as the index to estimate their role in dispersion of the parasite.

5. EFFECT OF HOST DENSITY ON RATE OF PARASITISM

It has often been stated that parasites play an important role in the regulation of insect numbers (NICHOLSON, 1933; VARLEY, 1947). This statement is based on the assumption that the actual rate of reproduction of the parasite is proportional to host density. Theoretically, assuming that the parasite encounters its host at random and that it has an unlimited supply of eggs to deposit, the relation between host density and the number of eggs deposited per parasite would be linear. In practice, however, it is logic to suppose that, if this linear relation can apply to lower host densities, undoubtedly the parasite fecundity has its limit and the linear relation will inevitably reach a certain maximum with increasing host density. When this density is exceeded, the number of eggs deposited per parasite remains constant.

It has been pointed out by TINBERGEN & KLOMP (1960) that the activity of parasites may be slowed down temporarily after each successful egg deposition. This means that the parasite can be more active at low than at intermediate densities of the host.

Due to the combined effect of limited egg supply and inhibition of activity after oviposition, the relation between host density and number of eggs deposited per female tends to be curvilinear, approaching asymptotically the value indicating the maximum egg production of the parasite.

This curvilinear relation has been demonstrated before in several species of parasites: *Trichogramma sp.* on *Sitotroga cerealella* Oliv. (FLANDERS, 1935), *Mormoniella vitripennis* Wlk. and *Muscidifurax raptor* Gir. on *Musca domestica* L. (DE BACH & SMITH, 1941), *Chelonus texanus* Cress. on *Ephestia kühniella* Zell. (ULLYETT, 1949), *Dahlbominus fuscipennis* (Zett.) on *Neodiprion sertifer* (Geoffr.) (BURNETT, 1951), and *Encarsia formosa* Gahan on *Trialeurodes vaporariorum* Westw. (BURNETT, 1958).

It has been demonstrated earlier in this work (p. 500) that the parasite *A. rapae* has long periods of rest after some successful ovipositions. Therefore an experiment was conducted to study the combined effect of this behaviour and the reproductive capacity of the parasite on the relation between host density and number of eggs deposited.

A. Methods

In the set-up of the experiment, the following three main points were taken into consideration:

1. The area over which the parasite searched for the hosts was kept constant, i.e. a glass dish as was used in earlier experiments (plate 1, B).
2. In order to eliminate any interference of the searching parasites, only one female parasite was used per dish.

3. The experiment was carried out during the whole life-time of the adult parasite.

Each dish was provided with a small leaf of brussels sprouts inserted in a small glass vial full of water. Half-grown apterous nymphs of *B. brassicae* were placed on the sprout leaves. Four different densities of the hosts were used; 1, 5, 10 and 20 nymphs per dish. A newly emerged female parasite was introduced into each dish and provided with honey droplets for food. Every day the female parasites were transferred to a new dish containing the same number of hosts as before. To facilitate the detection of the number of parasite eggs deposited, the dishes with the exposed nymphs were kept under about 25 °C for 2 to 3 days before dissection (see p. 491). During this period, the nymphs were checked daily and any nymph that seemed weak or moribund was dissected to record the number of parasite eggs within it. In order to determine the proportion of eggs deposited, the female parasites were also dissected after dying to count the number of eggs retained in their ovaries.

Ten replicas of each treatment were carried out. Since it was practically impossible to handle all fourty dishes at one time, whole series of the four different treatments of host densities were set up on a given day to minimise as much as possible the effect of variation in environmental conditions.

B. Results and discussion

The results of the experiment are summarized in table 34 and shown in fig. 18.

TABLE 34. Effect of host density on rate of parasitism and fecundity of the parasite, *A. rapae*

	Number of host nymphs given daily to each parasite female			
	1	5	10	20
Total number of nymphs exposed per female parasite	7.7	57	110	172
Total number of nymphs parasitized per female parasite	3.8	25	53.1	62.3
Percentage of exposed nymphs parasitized per female parasite	49.6%	43.9%	48.3%	36.2%
Total number of eggs deposited per female parasite	26.2	63.9	106	104
Number of eggs retained in the ovaries after death of the female parasite	135.3	52.8	52.8	82.4
Total number of eggs (deposited + retained in ovaries) per female parasite	161.5	116.7	158.8	186.4
Percentage of total eggs deposited per female parasite	14.6%	58.6%	68.7%	67.0%
Number of eggs deposited per female per day	3.6	5.6	10.6	12.4

These results show that host density affected both the number of eggs deposited per parasite and the fraction of hosts parasitized.

The number of eggs deposited during the whole life of the female parasite gradually increased from an average of about 26 eggs per female when it had access to one host individual per day, to an average of 106 eggs when 10 host individuals were available per day. A highly significant difference ($P < 0.01$)

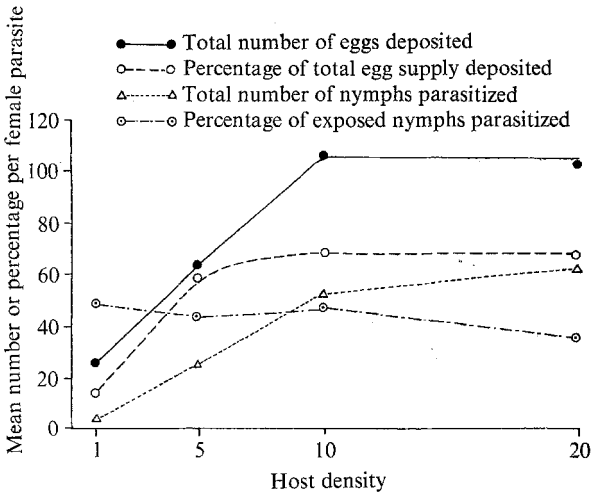


FIG. 18.
Effect of host density on rate of parasitism

occurred between means when 1 or 5 nymphs were exposed and a significant difference ($0.01 < P < 0.05$) when 5 or 10 nymphs were given. Apparently 106 eggs deposited per female at a host density of 10 nymphs per day was the highest value that could be obtained under these experimental conditions. This value remained almost constant with a further increase of host density from 10 to 20 nymphs.

The dissection of dead females made it possible to compare the number of eggs deposited with the total number of eggs produced. It was shown that on the average the total egg supply of the female was in no case exhausted. The mean fraction deposited was very low (14.6%) when one host individual was available per day, while it increased gradually to a maximum of 68.7% when 10 host nymphs were available. At a higher density it remained almost constant. The difference between the value obtained at the lowest density (14.6%) and the other values was highly significant, whereas no significant differences were obtained between the three higher values. Comparing the female parasites within each group, it was found that in the first treatment (1 host per day) the total number of eggs per female was never in short supply. In the extreme case, one female had a maximum of 70% of the eggs deposited. In each of the three other treatments (5, 10, and 20 hosts per day) 3 out of 10 females were able to deposit more than 90% of their eggs. In a few cases; 1 at density 5, 1 at 10 and 2 at 20 nymphs per day, the potential reproductive capacity was actually reached. On dissection, the ovaries were entirely devoid of eggs.

These results show that the relation between host density and number of eggs deposited is curvilinear rather than linear. A linear relation can be illustrated, if it is presumed that the parasite searches at random and that it is neither affected by egg limitation nor by periods of rest. Thus, starting from the mean number of 26.2 eggs deposited at the lowest density, theoretical numbers were calculated for the higher host densities as shown in table 35.

It is shown in table 35 that an increasing deviation is obtained between the theoretical and the actual number of eggs deposited per parasite. The exhaustion of the egg supply of some of the ovipositing females could account for this

TABLE 35. Effect of host density on actual oviposition in comparison to calculated theoretical oviposition in *A. rapae*

No. of hosts given daily to one parasite female	Observed mean no. of eggs deposited	Calculated no. of eggs deposited	Percentage observed to calculated
1 nymph	26.2	26.2 × 1 = 26.2	100
5 nymphs	63.9	26.2 × 5 = 131	49
10 nymphs	106	26.2 × 10 = 262	40
20 nymphs	104	26.2 × 20 = 524	20

trend. However, it could not be the only reason because it has been shown that actually most of the female parasites did not deposit all their eggs, even at higher host densities. Another factor which presumably contributed to this trend was the behaviour of the parasite during oviposition which may be responsible for its inefficiency at the higher host densities. It was shown before (p. 500) that the parasite took periods of rest after some eggs were deposited. These periods gradually increased in magnitude as more hosts were parasitized. This fact leads to the assumption that in most cases the parasite was hindered in its searching for hosts by the limited time available within its life span rather than by the exhaustion of its egg supply.

As a consequence of the observed phenomena, the number of hosts encountered and parasitized showed the same curvilinear trend with the increase of host density. It is of importance to note that at lower host densities (1 to 10 nymphs) the parasite was able to parasitize an average of about 44 to 50% of the exposed nymphs, while this rate declined to only 36% when the host density increased to 20 nymphs per day.

The number of eggs deposited per day per female have more or less the same trend as the total number of eggs deposited and the same explanations can be applied here.

From the practical point of view, the observed phenomena of a curvilinear relation between host density and number of parasite eggs deposited is of importance under field conditions. Aphid densities comparable to 10 hosts per dish can readily occur in the field. During the two years of investigation, large areas of the leaves and sprouts of most of the brussels sprout plants were almost covered with aphids early in the season of 1959 and 1960 and in autumn of 1959. With such host densities the parasite would reproduce at its maximum rate. However, when the net rate of increase of the host at these densities is higher than that of the parasite, the latter would not be able to regulate the numbers of the aphid. Consequently the percentage of parasitism would decrease when the host density increases. Actually this proved to be the case under field conditions (see fig. 19, chapter VII).

CHAPTER VII

HOST – PARASITE INTERACTIONS IN THE FIELD

In CHAPTER III, the course of population changes of the cabbage aphid in the field was studied throughout the seasons of 1959 and 1960. Some of the mortality factors which influence the changes were discussed in CHAPTER IV. *A. rapae*

was found to be the only primary parasite infesting this aphid in The Netherlands. In the present chapter an assessment of this parasite as a mortality factor in the field is made in an effort to evaluate its role in the observed changes in host density.

1. PARASITISM DURING THE SEASON

A. Estimation of parasitism by dissection of nymphs

1. Method: The immature stages of related species of the family Aphidiidae cannot be easily separated. However, because *A. rapae* was found in this work to be the only primary parasite of *B. brassicae* in The Netherlands, any immature stages of primary parasite within the aphid indicate parasitism by this species. Parasitism was estimated by weekly dissection of advanced nymphs of the cabbage aphid collected at random from each of the three sampled brussels sprout fields during the summer and autumn of 1959 and 1960. Normally about 100 nymphs were dissected, but in three cases in 1960 the infestation was so low that it was practically impossible to secure that number. During three other weeks in 1960 it was possible to dissect 400 nymphs, instead of 100, per sample. Advanced nymphs were selected for the dissections because they provide the maximum chance of an aphid individual to be parasitized without being mummified. Therefore, the fraction of advanced nymphs parasitized was taken as an index for the rate of parasitism, but it could not be used to calculate the absolute quantities of parasitism of the whole aphid population.

2. Results and discussion: The results of the dissections of nymphs collected in each of the three fields are given in table 36 and shown in fig. 19.

When the trend of parasitism, as revealed in this way, is compared with the population changes of the host, it could be shown that the rate of parasitism was not governed by the population density of the host alone. If it was governed in this way, the delayed effect of host density on the rate of parasitism would have formed a curve of parasitism oscillating more or less in the same manner as host density, but slightly lagging behind it. This was not the case and there are indications that other factors, in addition to host density, affected the rate of parasitism.

Probably, early in the season the rate of parasitism was more closely correlated with host density because the other factors are not yet strongly operating. With the increase in host populations in July, in general the trend of the fraction of hosts parasitized declined. Two main factors are presumably responsible for this decline:

1. The limited egg supply and the relative decrease of activity of the parasite at high host densities, discussed in chapter VI.
2. The effect of hyperparasitism causing high mortality of the parasite. This factor will be discussed in the next chapter.

A clear influence of the first factor can be seen in the case of the sudden increase of host density during a certain week, followed by a decline in the next week (20-VII-'59 in field B and 20-VII-'60 in field C). These changes of host density were accompanied by a sudden decline, followed by an increase again, in the percentage of parasitism.

In spite of the high proportion of hyperparasitism during the main part of

TABLE 36. Percentage of parasitism of *B. brassicae* (advanced nymphs) by *A. rapae* in the field. (Based on dissections of about 100 nymphs in most cases)

Field A (1959)			Field B (1959)			Field C (1960)		
Date	No. dissected	Percentage parasitized	Date	No. dissected	Percentage parasitized	Date	No. dissected	Percentage parasitized
10-VII	100	42	6-VII	100	26	22-VI	100	34
17-VII	109	24	13-VII	100	39	28-VI	100	78
24-VII	100	21	20-VII	113	10	6-VII	100	47
31-VII	100	8	27-VII	100	33	13-VII	400	27
7-VIII	100	21	3-VIII	100	26	20-VII	400	15
14-VIII	100	55	10-VIII	105	56	26-VII	400	32
21-VIII	102	45	17-VIII	100	59	3-VIII	147	46
28-VIII	100	34	24-VIII	100	22	10-VIII	38	39
4-IX	100	22	31-VIII	100	26	17-VIII	100	36
11-IX	100	4	7-IX	100	12	24-VIII	56	30
18-IX	100	2	14-IX	100	7	1-IX	100	1
26-IX	100	11	21-IX	103	13	8-IX	100	1
2-X	100	24	28-IX	100	12	15-IX	100	28
9-X	100	12	5-X	100	34	22-IX	100	12
16-X	100	12	12-X	100	17	28-IX	100	00
23-X	100	9	20-X	100	18	5-X	100	7
31-X	100	8	26-X	100	11	13-X	100	14
6-XI	100	11	2-XI	100	15	20-X	100	23
13-XI	100	12	10-XI	106	13	27-X	57	4
20-XI	100	9	16-XI	101	8			
27-XI	100	18	24-XI	100	18			
4-XII	100	13	30-XI	100	15			
11-XII	100	12	7-XII	100	9			
18-XII	107	7	14-XII	100	9			
			21-XII	100	7			

the season, the mid-season decline in host population was accompanied by an increase of the rate of parasitism, reaching a maximum of 55% and 59% in fields A and B respectively. During that period, the host populations were at their mid-season minimum.

When the parasites reproduce at their maximum rate at a high host density, the percentage of parasitism will increase after a decrease of the host density, so long as the decline in host density is not too drastic to influence the reproduction rate of the parasite to a large extent. It is very unlikely, however, that this phenomenon is the only factor responsible for the high percentage of parasitism during the mid-season decline. Probably, another factor is that the absolute number of parasites during the host minimum is very high due to the peak numbers of the host in the foregoing weeks.

In 1960, probably because the mid-season decline of the aphid population was very severe (down to a minimum of 3 aphids per plant on 8-IX-'60 in field C), the trend of parasitism was different. Presumably, the host density was so low that the actual reproductive rate of the parasite was seriously affected. Moreover, the parasite density must have been much lower than the foregoing year. These factors led to a minimum parasitism of only 1% during the period when the host was at its mid-season minimum.

Later in the season, several other factors besides host density affected the rate of parasitism. The hyperparasites enter diapause earlier than the parasites. This reduced the effect of an important mortality factor of the parasite. Further-

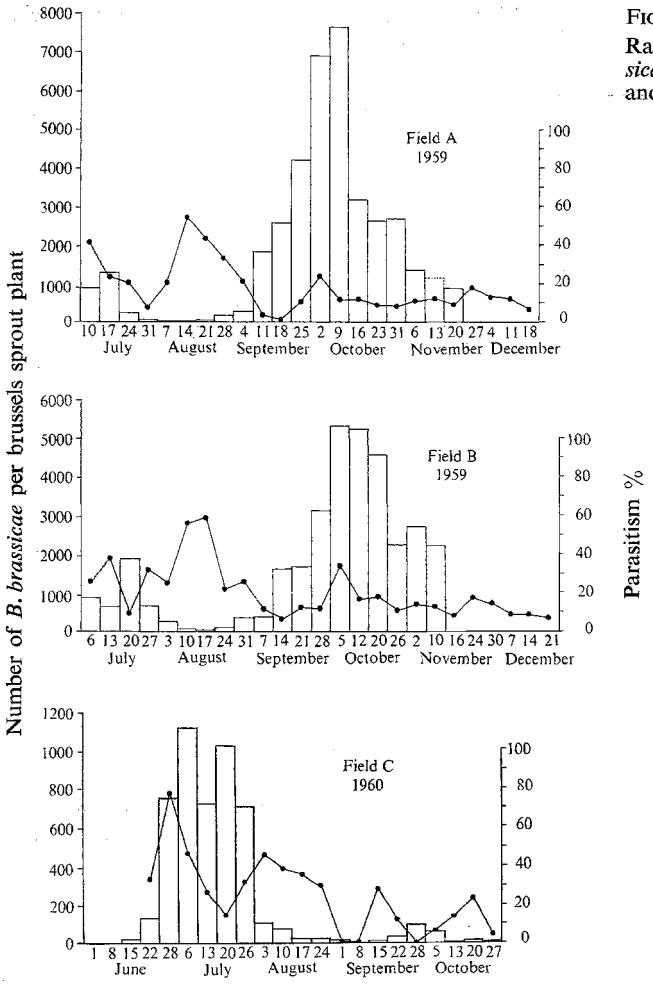


FIG. 19.
Rate of parasitism of *B. brassicae* in fields A and B (1959) and C (1960)

more, physical factors (such as temperature, rainfall and photoperiod) might unfavourably affect the host, the primary parasite and the hyperparasites. The interactions of all these factors in autumn and early winter have led to a trend of parasitism that fluctuated around a comparatively low mean.

At any rate, parasitism in the late season is not of great practical importance because normally the parasite larva which does not reach at least the last larval instar and change the host into a mummy before winter, will perish together with its host during winter due to physical factors.

B. Estimation of parasitism by counting the proportion of mummies

1. Method. It was shown in chapter VI that regardless of the stage parasitized, the host develops into an advanced nymph or an adult before it mummifies. Thus, within a given population with all age groups, the proportion of mummies to the sum of adults, advanced nymphs and mummies would give an

idea of the fraction of aphids parasitized. If this proportion is measured periodically, the seasonal trend of parasitism can be obtained.

To collect the necessary data for such an estimation, the mummies were counted when sampling the three fields of brussels sprouts as described in CHAPTER III. Only unemerged and intact mummies were counted.

2. Results and discussion: The results obtained by this method are given in table 37.

For evaluating the results of this method, the following points should be considered:

1. When the counts were started very early in the season, as was the case in field C in 1960, the number of mummies could not be a correct indication of the actual rate of parasitism. In such periods all, or most, of the parasitized aphids would still be in an early stage of parasitism. Thus, the rate of parasitism could not be measured by the number of mummies.

2. Also late in the season, starting about early September, the rate of parasitism as indicated by the proportion of mummies included a certain error because by that time the parasite starts to hibernate as last instar larva inside the mummy. This would lead to an increasing accumulation of the number of mummies. Thus, the percentage of mummies would be biased if it was taken as an indication for parasitism.

3. If other mortality factors, such as climate or predators, would eliminate different proportions of parasitized and non-parasitized aphids, the proportion of mummies would also be biased. It is very unlikely that this is the case in *B. brassicae* at least up till the time of mummification.

4. Only the apparent sound mummies were considered, while empty mummies from which parasites had emerged were not included in the data. Also mummies that were injured and dead were not counted. This prevented recounting the same mummy repeatedly on successive weeks. An error would be introduced by counting the apparently sound mummies which in fact have a dead parasite but which, because of lack of any external symptoms would be counted again for several weeks. This class of mummies will not exceed about 20% of all the mummies. In 1959 out of 5798 non-hibernating mummies kept in glass tubes under outdoor conditions 22% failed to emerge while in 1960 out of 4456 mummies 21% failed to emerge.

5. There is a difference in the way aphids and mummies hold to the substratum. An aphid clings to it with its legs and proboscis whereas a mummy is cemented to the surface by the threads of the cocoon spun by the last instar larva of the parasite. Consequently when a mortality factor kills an aphid, it will either drop to the soil, remain on the plant as a dead individual or be removed away by the factor. In all these cases the dead aphid will not be counted as a living individual. On the other hand a mummy that succumbs to the same mortality factor may still be cemented to the plant enclosing a dead parasite, and so it will still be counted as a mummy. This difference could also lead to an error in favour of a higher rate of parasitism than is actually the case.

6. The mummies, advanced nymphs and apterous adults are stationary whereas the alate adults are mobile. Therefore, these latter were not included in the calculations. Since their numbers per plant were generally negligible, this procedure could not have an important influence on the results.

TABLE 37. Percentage of parasitism of *B. brassicae* by *A. rapae* in the field (based on the proportion of mummies to total of advanced nymphs + apterous adults + mummies)

Field A (1959)				Field B (1959)				Field C (1960)			
Date	No. of advanced nymphs + apterous adults per plant	No. of mummies per plant	% mummies to total (ad. + apt. + mum.)	Date	No. of advanced nymphs + apterous adults per plant	No. of mummies per plant	% mummies to total (ad. + apt. + mum.)	Date	No. of advanced nymphs + apterous adults per plant	No. of mummies per plant	% mummies to total (ad. + apt. + mum.)
10-VII	111	10	8	6-VII	154	19	11	15-VI	3	0.4	12
17-VII	256	31	11	13-VII	174	24	12	22-VI	19	2	10
24-VII	60	29	33	20-VII	461	41	8	28-VI	56	7	11
31-VII	16	14	47	27-VII	156	17	10	6-VII	134	39	23
7-VIII	10	8	44	3-VIII	63	10	14	13-VII	384	61	14
14-VIII	7	3	30	10-VIII	9	5	36	20-VII	187	83	31
21-VIII	15	7	32	17-VIII	6.5	7	52	26-VII	294	120	29
28-VIII	37	13	26	24-VIII	18	8	31	3-VIII	59	57	49
4-IX	82	13	14	31-VIII	53	13	20	10-VIII	18	20	53
11-IX	488	31	6	7-IX	62	6	9	17-VIII	11	13	54
18-IX	672	41	6	14-IX	226	30	12				
26-IX	910	48	5	21-IX	211	11	5				
2-X	2006	101	5	28-IX	552	23	4				
9-X	3751	187	5	5-X	1630	68	4				
16-X	2097	263	11	12-X	2773	357	11				
23-X	1781	246	12	20-X	2802	498	15				
31-X	1778	235	12	26-X	1387	294	17				
6-XI	945	210	18	2-XI	1880	267	12				
20-XI	715	209	23	10-XI	1797	355	16				

The sources of error mentioned above lead to a higher estimation of the fraction of parasitized hosts than actually occurs. This error is obviously more emphasized when the host densities are low. This bias towards a high degree of parasitism should be taken into account when considering the mortality due to parasitism as a fraction of the total mortality suffered by the aphid.

The figures obtained by the two methods of estimation look different. However, the rate of parasitism as indicated by them have a rather similar trend, especially during the main part of the season.

C. Role of parasitism as a mortality factor of the cabbage aphid

The population changes of the cabbage aphid have been shown before (CHAPTER III) and it is rather obvious that a high mortality occurred within the populations of the aphid especially during the mid-season decline.

Judging from the percentage of parasitism as obtained by the two above mentioned methods, it was evident that during almost all the season the mortality due to parasitism accounted for a rather small fraction of the total aphid mortality. It might be safe to conclude that parasitism is not the main factor affecting the population changes of the cabbage aphid. In all three fields it was clear that parasitism could not be the mortality factor responsible for the sudden mid-season decline in the cabbage aphid population.

2. PARASITISM ON THE OVERWINTERED PLANTS EARLY IN THE SEASON

It has been mentioned before that *B. brassicae* overwinters in The Netherlands as eggs. These hatch early in spring during varying periods according to the type of weather prevailing in each season. In 1960 most hatching occurred in the three last weeks of March. In the same year the emergence of overwintering parasites increased rather gradually to a first peak in the second week of April and a second peak in the second week of May (see fig. 21). No reliable data could be obtained for the spring of 1961 owing to the scarcity of aphid eggs and mummies during the winter of 1960–1961.

The fundatrices which hatch in the spring on Brassica plants kept over winter for seed production are considered in The Netherlands to be the main source of infestation for the new crops. Consequently, the application of insecticides is recommended in spring on the seed plants to reduce, or to eliminate, this early source of infestation. Since the occurrence of the host and the parasite almost coincided early in 1960, it was important to determine the effect of parasitism on the early generations of *B. brassicae.*

A. Rate of parasitism early in the season

Weekly dissections of 100 individuals of *B. brassicae* taken at random from the overwintered brussels sprout plants kept for seed in the experimental farm near Wageningen were carried out from 1-IV-'60 to 11-VII-'60, inclusive. The material taken on 1-IV-'60 consisted almost exclusively of first instar fundatrices (with very few second instar ones), while the material taken on 8-IV-'60 consisted mostly of second and third instar fundatrices (with very few first instar nymphs). During the period from 15-IV until 11-VII only advanced nymphs were

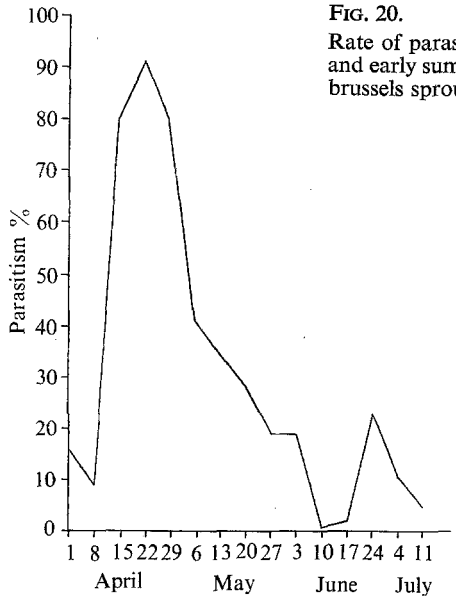


FIG. 20.
Rate of parasitism of *B. brassicae* in spring and early summer of 1960, on overwintered brussels sprout plants

dissected. By the end (11-VII-'60) the plants were senescent and most of the aphids had developed to alate adults and dispersed to the newly cultivated sprout plants. The results of the dissections are shown in fig. 20.

Though these results were obtained during one season only, they seemed to indicate that the right coincidence of emergence of overwintered host and parasite in early spring (together with the delayed emergence of hyperparasites as will be shown later) led to a very high peak of parasitism early in the season. Throughout the second half of April 1960 the dissected nymphs have shown a high degree of parasitism ranging from about 80% to 90%. Starting in May, however, this rate of parasitism declined very sharply to almost negligible values in June.

The following factors might have contributed to the high parasitism early in the spring:

1. The high rate of emergence of the parasites from overwintering mummies, which accumulated throughout autumn and early winter, leading to a high parasite density.
2. The hosts did not increase in numbers. On one hand the winter eggs have hatched and on the other hand the reproducing adults were not yet present. At the same time the parasite was still increasing in number by emergence, both from overwintering mummies and from early mummies of the first generation in spring.
3. Emergence of the hyperparasites from the overwintering mummies started later than that of the primary parasite.

The decline of the rate of parasitism in May, could be attributed to the emergence of increasing proportions of hyperparasites and the decline in rate of emergence of the primary parasite.

B. Economic importance of the early parasitism

The high rate of parasitism of the fundatrices on the overwintered seed plants may be an important factor in a program which integrates chemical and biological control of the cabbage aphid. More studies should be made as to the type of insecticide to be applied on the seed plants, its dosage, method and right time for application. Probably it would be possible to reduce the number of aphids before they develop to alatae and without seriously affecting the parasite population.

Furthermore, the different periods of emergence of overwintering parasites and hyperparasites may be of use in finding out the right time for destroying the overwintering host plants so that a large number of the parasites will be already emerged while a large number of the hyperparasites will be still within the mummies on the destroyed plants.

CHAPTER VIII

HYPERPARASITES AS MORTALITY FACTORS OF *A. RAPAE*

1. INTRODUCTION AND HISTORICAL REVIEW

Earlier in this paper the hyperparasites were occasionally mentioned as factors of possible importance in influencing the numbers of the primary parasite *A. rapae*. In the present chapter some details about the role of hyperparasites in decimating the numbers of *A. rapae* will be discussed.

The complex of Hymenopterous parasites emerging from mummified aphids has long caused some confusion as to their true status. An illustration of such a confusion is provided by the statement of PICARD (1919) about the interrelations of the Aphidiid *Trioxys sp.*, the Cynipid *Alloxysta kiefferi* Picard and the Pteromalid *Asaphes vulgaris* Wlk. He stated that the interrelations of these Hymenoptera are not definitely known, because many authors have considered the Cynipids to be true parasites of aphids, others consider them to be hyperparasites while a third possibility is that the Aphidiids are hyperparasites of the Cynipids. As for the Pteromalid *Asaphes vulgaris*, PICARD thought that it is a hyperparasite but he stated that there is no definite proof for that. A similar contradiction as to Hymenopterous parasites associated with the cabbage aphid pertained till rather recently, though it was generally accepted that the Aphidiid parasites are the only primary parasites while the others are secondary or tertiary parasites.

MELANDER & YOTHERS (1915, 1917) mentioned that in Washington State, U.S.A., the commonest parasites of *B. brassicae* were *Aphidius piceus* (Cress.) and *Charips brassicae* (Ashm.) while *Pachyneuron micans* How. and *Asaphes rufipes* Brues were hyperparasites. GOURLEY (1930) and TODD (1957) stated that in New Zealand *A. rapae* is parasitized by *Charips brassicae* (Ashm.) and *Lygocerus niger* How., and that though considerable numbers of *B. brassicae* were attacked by the parasite, this latter is nevertheless of little value in checking the population of the aphid, partly owing to hyperparasitism. BARNES (1931) found that out of a single brussels sprout plant heavily infested with *B. bras-*

sicae, 4366 mummies gave emergence to parasites; 12% primary parasites, 78% *Charips sp.* and 10% *Asaphes sp.* NEWTON (1934) reported that in England brussels sprouts were attacked by the cabbage aphid of which 15% were parasitized by *A. rapae*, 8% by *Asaphes vulgaris* and 1% by *Charips brassicae*. PETHERBRIDGE & MELLOR (1936) mentioned that in England the Hymenopterous parasites were active from April till October on the cabbage aphid. Beside the real primary parasite *A. rapae*, they mentioned as primary parasites *Asaphes vulgaris* and *Lygocerus testaceimanus* Kieff. They also mentioned *Charips victrix* Westw. var. *infuscata* Kieff. as hyperparasite. BILANOVS'KII (1938) collected 125 mummies of *B. brassicae* in Crimea (U.S.S.R.) out of which 25% gave the primary parasite *A. rapae* while 53% yielded *Charips minuta* Htg., 11% *Pachyneuron aphidis* Bch., 5% *Asaphes vulgaris* and 2% *Tetrastichus rapo* Wlk. His conclusion is that the hyperparasites destroyed 60% of the primary parasites.

ULLYETT (1938), in a study of parasitism in the genus *Aphidius* in South Africa, mentioned that *Charips spp.* contributed by far the largest number of species which parasitized *Aphidius spp.* Towards the end of the summer they became so numerous that as many as 80% of the *Aphidius* larvae dissected from the aphids contained *Charips.* ULLYETT correctly placed all the groups of parasites concerned in their right positions and so *Charips spp.* were mentioned as hyperparasites ovipositing in the early larvae of *Aphidius spp.* However, he recorded that at times, probably by accident, a *Charips* larva may be found free in the body cavity of an otherwise healthy aphid, acting as a primary parasite. *Charips spp.* have frequently been mentioned in the literature as primary parasites but it is obvious that these statements are erroneous, because they were based only on data taken from emergence from mummies. ULLYETT's statement was based on dissections and, though he admitted that it was comparatively rare, still it was such a drastic deviation from the normal position of *Charips spp.* as a secondary parasite, that it needs further confirmation. In this respect, it has to be stated that out of thousands of cabbage aphids dissected by the present writer in The Netherlands, larvae of *Charips sp.* were never encountered except as secondary parasites on *A. rapae.*

GEORGE (1957) mentioned *Charips sp.*, *Asaphes vulgaris* and *Lygocerus sp.* as hyperparasites on the cabbage aphid in England, but he stated that, within the material he worked with, the proportion of primary parasites exceeded those of any of the hyperparasites. SEDLAG (1958b) found in Germany that out of 4417 emerging parasites from mummies of *B. brassicae*, about 66% were the primary parasite *A. rapae*, while 34% were hyperparasites; 22% Charipinae, 11% *Asaphes sp.* and less than 1% for each of *Pachyneuron sp.* and *Lygocerus sp.*

Thus it is seen that, when the actual position of the hyperparasites was finally ascertained, in most cases they were supposed to play an important role in hindering the biological control of the cabbage aphid. In The Netherlands, the identity of the species of hyperparasites involved and their importance as a mortality factor of the primary parasite *A. rapae* have not been studied before.

2. SPECIES OF THE HYPERPARASITES OF *B. brassicae* IN THE NETHERLANDS

It has been mentioned above that *A. rapae* is the only primary parasite of the cabbage aphid that has been encountered during the present work. In ad-

dition out of about 25,000 mummies of *B. brassicae* collected in The Netherlands in 1959 and 1960, the following hyperparasites emerged:

A. Charips ancylocera Cam. *(Fam. Cynipidae)*

This species was determined by J. QUINLAN, who stated with some reserve that it is possibly *C. ancylocera.* The female approaches a parasitized aphid, mounts its back and slowly and with little reaction on the part of the aphid, deposits an egg internally inside the larva of *A. rapae* within the aphid. Normally the young larvae of the primary parasite, first and second instar larvae, appeared to be preferred for oviposition. Both larvae of the primary and secondary parasites develop till the former attains its mature instar and thus the host aphid will be mummified. When the larva of the secondary parasite is full-grown, it emerges out of the primary parasite larva, but still remains inside the mummy. The larva of *Charips* subsequently acts as an external parasite by consuming the remains of the primary parasite larva. Pupation takes place also within the mummy and eventually the adult hyperparasite bores its way out of the mummy through a characteristic hole. In 1960 under outdoor conditions 4 to 7 generations took place. The minimum duration from egg to adult was 19 days, in July, and the maximum duration was 37 days, in May and early June. In the overwintering generation, the maximum duration was 259 days, 16-IX-'60 to 2-VI-'61. Overwintering takes place in the prepupal stage inside the mummy. Only one adult emerges from each mummy.

B. Asaphes vulgaris Wlk. *and Pachyneuron minutissimum* Fö

These representatives of the Family Pteromalidae were identified by V. DELUCCHI. Both are external parasites which deposit their eggs through the integument of the aphid mummy on the cuticle of any stage that occurs inside it; last instar larva, prepupa or pupa of either *A. rapa* or *Charips ancylocera.* Sometimes eggs were seen to be deposited even on individuals of the same species inside the mummy. So actually this group consists of secondary parasites, tertiary parasites or even further. More than one egg may be deposited within the same mummy but eventually only one parasite emerges. Parasitism by the Pteromalids will in all cases surpass other parasites because in the process of oviposition the host is venomized and so its development is arrested. Venomization also affects the larva of *Charips* inside the larva of *Aphidius* when an egg is deposited on the latter larva. By the time the Pteromalid larva is fully developed, almost all the parasite material inside the mummy is consumed. Pupation takes place inside the mummy.

C. Lygocerus aphidovorus K. *(Fam. Ceraphronidae)*

This species was determined by G. E. J. NIXON. It is an external parasite with the same behaviour as has been described in the Pteromalids. It can parasitize *Aphidius sp., Charips sp.* and even the Pteromalids, but its occurrence is very scarce. As has been mentioned for the other parasites, one adult emerges per mummy.

3. EMERGENCE OF PRIMARY PARASITES AND HYPERPARASITES FROM MUMMIES OF *B. brassicae* COLLECTED IN THE FIELD IN 1959 AND 1960

As has been mentioned before, about 25,000 mummies of *B. brassicae* were

collected from different cruciferous plants in different parts of The Netherlands, but mostly from brussels sprouts near Wageningen. The mummies were carefully removed from the plants and each collection was confined in a separate large glass vial kept in an outdoor insectary. Emergence in each tube was checked daily; all the mummies were left to overwinter and checked for additional emergence the following spring and summer. In all collections an average of about 18% of the mummies failed to emerge. The results of these collections are summarized in table 38.

TABLE 38. Emergence from mummies of *B. brassicae* collected in 1959 and 1960

Month, mummies were collected	Total no. of mummies collected	Percentage of mummies giving emergence to			
		Aphidius rapae	*Charips ancylocera*	*Asaphes vulgaris* + *Pachyneuron minutissimum*	*Lygocerus aphidovorus*
June 1959	1701	35.3	42.6	4.7	0.2
July	2355	4.5	40.3	30.2	0.3
August	2094	8.2	45.9	20.7	–
September	1172	11.6	60.7	13.3	–
October	4368	26.6	50.9	7.9	–
November	3151	36.7	39.2	13.6	–
December	1827	54.7	23.7	11.2	–
January 1960	322	46.2	28.3	14.3	–
February	573	26.0	19.4	38.6	–
March	612	32.2	24.8	26.3	–
April	864	21.8	19.4	36.5	–
May	1132	9.6	42.9	23.3	0.4
June	1170	7.5	40.9	26.3	0.1
July	2625	15.9	48.9	14.2	1.7
August	849	2.8	37.1	32.0	–
September	78	11.5	64.1	12.8	–
October	102	12.7	50.0	3.9	–

Owing to the very low infestation of *B. brassicae* in autumn 1960, the mummies were very scarce in the field in that season. For this reason, the collections were stopped at the end of October 1960.

The following points should be mentioned:

1. When the mummies are collected in the field and confined in tubes, the proportion of emerged *Aphidius* and *Charips* will not be changed, assuming that the Pteromalids and *Lygocerus* sp. parasitize them indiscriminately, which seems to be a justifiable assumption.
2. Parasitism by *Lygocerus sp.* is very low, and so no important changes will occur as a result of confining the mummies in tubes.
3. Parasitism by Pteromalids is of importance and undoubtedly the percentage of parasitism as taken from the collected mummies would be less than the actual percentage if the mummies were left under natural conditions. However, even such a low percentage of parasitism suffices to demonstrate the high effect of hyperparasitism on the primary parasite *A. rapae*.
4. *A. rapae* suffers highly from its hyperparasites. Emergence of *A. rapae* from mummies collected in each month of the main part of the season (July

to September) in the two years under consideration did not exceed a maximum of about 16% of the collected mummies while it went as low as about 3%.

5. Towards the end of the 1959 season from September through the winter, the proportion of mummies yielding *A. rapae* gradually increased while the fraction of hyperparasites (especially *Charips*) gradually decreased. This indicated that the primary parasite enters diapause later than the hyperparasites.

6. Since it is shown that through the season the rate of emergence of *Charips sp.* surpasses by far the rate of emergence of *A. rapae*, and since it is assumed that the Pteromalid parasites attack mummies containing either *A. rapae* or *Charips sp.* indiscriminately, the Pteromalid parasites destroy more *Charips sp.* than *A. rapae.*

7. The proportions of different groups of parasites emerging from mummies of *B. brassicae* collected in the field in The Netherlands are illustrated by the following data:

In 1959 a total of 16568 mummies were collected, out of which 26% yielded *A. rapae*, 44% *Charips*, 14% *Pteromalids* and 0.07% *Lygocerus.*

In 1960 a total of 8338 mummies were collected, out of which 16% yielded *A. rapae*, 38% *Charips*, 24% *Pteromalids* and 0.6% *Lygocerus.*

4. EMERGENCE OF PRIMARY PARASITES AND HYPERPARASITES EARLY IN THE SEASON

Since a very high infestation of *B. brassicae* occurred in the autumn of 1959, it was possible to collect a large number of mummies in autumn and winter, September '59 until end of February '60.

These mummies were kept for emergence through winter, spring and early summer in tubes placed in an outdoor insectary. A total of 8574 parasites emerged between January and June 1960; about 39% *A. rapae*, 45% *Charips* and 16% Pteromalids. The timing of emergence of the different parasites is shown in fig. 21. Because the infestation of *B. brassicae* late in the season 1960 was very scarce, the overwintering mummies were also scarce, and consequently no reliable figures on parasite emergence could be obtained. Hence, the following discussion is based on results of one year only and admittedly different results might be obtained under different conditions. However, results obtained in spring of 1960 could be applied to seasons with different conditions, taking into consideration such factors as aphid populations in autumn, time and proportion of emergence of the different groups of parasites and type of weather prevailing in autumn, winter and spring.

As mentioned above, the high population density of the aphid late in the season 1959, together with the fact that the hyperparasites start diapause earlier than the primary parasites, led to the occurrence of a larger proportion of overwintering mummies with *A. rapae* than is normally the case in summer. It is seen from fig. 21 that *A. rapae*, but not the hyperparasites, can emerge even in winter time, though in small quantities. Such emerging parasites, however, are bound to die without reproducing because normally hosts are not available in the field in that period.

The important phase in emergence was the early and steady increase in the rate of emergence of the primary parasite in the second half of March, which

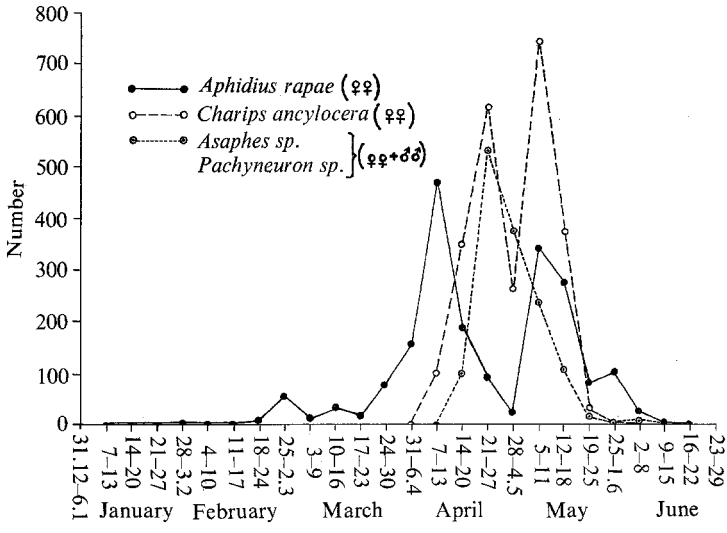


FIG. 21. Rate of emergence of *A.rapae, Charips ancylocera* and *Pteromalids* in 1960 from overwintered mummies

reached its peak in the second week of April. *Charips* started to emerge also in the second half of March, but only males emerged in that early period. The first females appeared in the second week of April, with the first peak of their emergence lagging two weeks behind that of the primary parasite. The Pteromalids started to emerge also late and reached their peak similarly two weeks behind that of *A. rapae*. This pattern of emergence of the different groups of parasites from the overwintering mummies gave the primary parasite a lead of about 2 to 3 weeks ahead of the hyperparasites.

The early emerging primary parasites would coincide with the first generation of *B. brassicae*. Most probably this is one of the causes for the early high rate of parasitism among the fundatrices (fig. 20).

In years with a low aphid infestation in the autumn (such as 1960) leading to a very low number of overwintering mummies, probably this difference in periods of emergence of the primary and hyperparasites would not be significant. However, in such years the number of overwintering aphid eggs will also be low leading to a very low number of hatching fundatrices in the following spring. In consequence, this first generation will not be of much practical importance.

As has been indicated before, from a practical point of view an annual estimation of the rate and time of emergence of the primary and secondary parasites of the cabbage aphid at various localities may be of importance in regard to the correct time to destroy the overwintered Brassica plants. Such timing should allow for emergence of as many as possible of the primary parasites and as few as possible of the hyperparasites.

CHAPTER IX

FACTORS LIMITING THE EFFECT OF *APHIDIUS RAPAE* CURT. AS A CONTROLLING AGENT OF *BREVICORYNE BRASSICAE* (L.)

In the previous chapters some bionomical features of the cabbage aphid, *B. brassicae*, some elements of the bionomics and behaviour of its parasite *A. rapae* and the interactions of the two insects both under laboratory and field conditions were discussed. The decrease of the rate of parasitism in the field when the host density increased gave evidence that the parasite is not a main factor in regulating the population density of the aphid. A summary of the factors which are believed to be responsible for the parasite being at a disadvantage in comparison to its host is given below.

1. Difference in sex ratio of both host and parasite: It was shown that, with the exception of the last part of the season when sexual forms appear and gradually increase in numbers, adults of the cabbage aphid are exclusively virginoparae. Hence, during the main part of the season, the host population consists of females only. As for the parasite, on the other hand, during the same period the ratio of females was about 60% only.

2. The host deposits its progeny on the food plant and so theoretically all progeny produced by an aphid female has the same chance to live, develop and reproduce. The parasite deposits its eggs indiscriminately in parasitized and non-parasitized hosts. Hence superparasitism was found to occur under laboratory and field conditions either by the same parasite female or by different females. Only one parasite individual emerges from one parasitized aphid, regardless of the number of eggs deposited in that host. This means that, in contrast to the host, the mere nature of deposition of the parasite eggs forms an additional obligatory mortality factor for the parasite, which inevitably leads to waste of progeny.

3. Under conditions of the open outdoor insectary in both 1959 and 1960, a maximum of 14 generations of the aphid occurred per year as compared to a maximum of 11 generations of the parasite. The shortest duration of a generation of the aphid was 8–10 days, while it was 14–16 days for the parasite. Consequently, the rate of development of the host is higher than that of the parasite.

4. The parasite has a higher reproductive potential than the host. However, because the host does not need to search for an appropriate place to deposit its progeny while the parasite does, it is more probable for the host to effectuate its reproductive potential than for the parasite.

5. A parasite which can regulate the population density of the host must have the ability to increase its pressure on the host population as the latter increases in number. It has been shown, from laboratory experiments and from evidence of the rate of parasitism in the field, that *A. rapae* does not have this ability. Under high host densities it was shown that the rate of parasitism decreases, instead of increases. This trend may be due partly to the exhaustion of the egg supply of some of the parasite females and partly to the behaviour of those females in searching and ovipositing. The periods of "inactivity" between successive periods of oviposition gradually increase when oviposition is inten-

sified. Hence, the rate of oviposition of a female parasite per unit of time does not increase in proportion to the increase of host density.

This means that the properties of the parasite do not allow it to regulate the numbers of the host when the population density of the host is very high.

6. Another factor related to the high host population density is of importance. It is well accepted by now that at least one of the factors responsible for the appearance of the alate forms is crowding and grouping (REINHARD, 1927; SCHAEFFER, 1938; BONNEMAISON, 1951; BROADBENT, 1953). Consequently a high population density of the aphid leads to a higher proportion of alates. It has been experimentally proven earlier in this paper that both alate advanced nymphs and adults are less preferred for oviposition by the parasite than apterae. It was also shown that even if the adult alatae are encountered by the parasite, they are generally rejected. This means that, other factors being equal, the rate of parasitism decreases with an increase of the proportion of alatae.

Since the occurrence of a high host density leads to the appearance of alate viviparae which in turn leads to a decrease of the rate of parasitism, this constitutes a case where the mortality factor is "inversely density dependent" (SOLOMON, 1949).

7. Parasitized hosts are not necessarily a total loss for the host population. It has been shown earlier that, depending on the host stage parasitized, a varying fraction of its reproductive capacity is lost. In an extreme case, when the host is parasitized late enough in the adult stage, it will be able to deposit all its nymphs.

8. The hyperparasites play a very important role in reducing the population of the primary parasite. In 1959 only about 26% of the collected mummified cabbage aphids yielded the primary parasite *A. rapae* whereas 58% yielded secondary (or tertiary) parasites. In 1960 only 16% of the mummies yielded the primary parasite, whereas about 63% yielded the secondary or tertiary parasites. The high intensity of hyperparasitism during the main season of the aphid infestation renders this factor even more injurious.

In conclusion, it may be stated that, according to the data obtained in the present study in The Netherlands, several factors greatly diminish the effectiveness of the parasite *Aphidius rapae* Curtis as a mortality factor able to regulate the populations of the cabbage aphid, *Brevicoryne brassicae* (L.).

SUMMARY

CHAPTER I. INTRODUCTION

In The Netherlands, it has been demonstrated before that, when certain insecticides were applied to control the cabbage aphid, *Brevicoryne brassicae* (L.), the infestation soon increased again after a sharp drop in aphid abundance. In the non-treated plots kept for check, the aphid infestation remained almost constant. On the basis of these results the present work was initiated mainly to contribute towards a better knowledge of:

1. The natural population densities of the cabbage aphid in The Netherlands.
2. The role played by natural mortality factors in limiting these densities.
3. The influence of the parasite *Aphidius* (*Diaeretiella*) *rapae* (Curt.) on the abundance of the aphid.

The study was made during the years 1959, 1960 and part of 1961.

CHAPTER II. SEASONAL HISTORY AND REPRODUCTIVE POTENTIAL OF THE CABBAGE APHID, *Brevicoryne brassicae* (L.)

Some elements of the bionomics and seasonal history of the aphid are given. The aphid overwinters as winter eggs on cruciferous plants kept for seed. In the experimental field near Wageningen there was an average of 5644 winter eggs per brussels sprout plant in 1959–1960, and of 2.3 eggs per plant in 1960–1961. Hatching of eggs started during the first week of March in 1959 and one week earlier in 1960. About 60% and 30% of the eggs failed to hatch in the two years, 1959 and 1960, respectively. High mortality occurred within the newly hatched fundatrices because of alternated periods of high and low temperatures (maximum 19 °C, minimum –6 °C). Generations overlapped; a minimum of 4 and a maximum of 14 generations occurred in each of the two years 1959 and 1960. Duration of generations ranged between a minimum of 8–10 days and a maximum of 37–56 days. Under different experimental conditions apterous virginoparae deposited an average of 26–29 nymphs whereas alate virginoparae deposited an average of 13–23 nymphs.

CHAPTER III. SEASONAL COURSE OF ABUNDANCE OF *Brevicoryne brassicae* (L.) IN THE FIELD

The seasonal trend of populations of aphids infesting four different crops in the temperate zone is reviewed. The general trend indicated an early increase in numbers followed by a rapid decline. Another increase may occur later if weather conditions are favourable. Several abiotic and biotic factors were presumed to cause the mid-season decline.

In 1959 and 1960, the seasonal abundance of the cabbage aphid in The Netherlands was studied. Two fields of brussels sprouts in 1959 and one field in 1960 were sampled each week in summer and autumn in order to determine the population densities of the various stages of the aphid. The three-leaf method was used for the sampling. The results showed a general pattern of aphid abundance which fitted a bimodal curve with one maximum in July and another maximum

in September or October separated by a minimum in August or September. No striking difference occurred between 1959 and 1960 in the first peak of aphid abundance. In the autumn peak, however, aphid populations were extremely larger in 1959 than in 1960.

CHAPTER IV: ANALYSIS OF THE SEASONAL FLUCTUATIONS IN POPULATION DENSITY OF *Brevicoryne brassicae* (L.)

Evidence indicated that the decline in population density of the aphid was mainly due to actual mortality factors rather than to effects on reproduction or migration. Some of these mortality factors are discussed.

A. *Abiotic factors*

1. Temperature: No drastic change in temperature occurred, that might account for the mid-season decline. A higher average temperature in September 1959 than in September 1960 might have partly contributed to the difference in aphid abundance in autumn of the two years.
2. Precipitation: The year 1959 was remarkably drier than 1960. Extensive rainfall in 1960 is thought to affect the aphid abundance in autumn by encouraging the outbreak of a fungous disease and by preventing the flight of alatae.

B. *Biotic factors*

1. Entomophagous fungi: Outbreaks of a fungous disease were not encountered in 1959. In 1960, the disease was very abundant in late July and early August and appeared to be responsible for the aphid decline in that period.
2. Predators: *Coccinella septempunctata* L., Syrphids, mainly *Epistrophe balteata* Deg., and *Phaenobremia aphidovora* Rübs. were the main predators in the brussels sprout fields. There was evidence that predators contributed towards the mid-season decline in both years.
3. Parasites: The only primary parasite on *B. brassicae* in The Netherlands was found to be *Aphidius rapae* Curt.

CHAPTER V. THE BIONOMICS OF THE PARASITE *Aphidius* (*Diaeretiella*) *rapae* (CURT.)

The nomenclature of the parasite is discussed, with the conclusion that it should be named *Aphidius* (*Diaeretiella*) *rapae* (Curtis). However, for simplicity, the name *Aphidius rapae* is used in this work. Besides *B. brassicae*, it also parasitized *Myzus persicae* (Sulz.), but it preferred the former species. It is an internal parasite, and only one adult emerges from each individual host. Females constituted 60% of the field populations of the parasite. Longevity of adults ranged between one and two weeks. Under laboratory conditions an average of 83 eggs were deposited per female. The parasite hibernated as a last instar larva inside the mummified host and started emerging in considerable numbers in spring. Two peaks of emergence, one in April and one in May, occurred in 1960. Number of generations per year ranged between 6 to 11 in 1959 and 5 to 11 in 1960. Minimum duration of a generation ranged between 14 to 16 days whereas an overwintering generation might take several months.

CHAPTER VI. HOST-PARASITE INTERRELATIONS

Newly emerged female parasites could start ovipositing a few minutes after emergence. Only one egg was deposited per insertion. Oviposition took place in previously parasitized and in non-parasitized hosts indiscriminately, hence superparasitism occurred. The parasite seemed to contact the aphid at random. Periods of oviposition alternated with increasing periods of rest which might extend for several hours. When the parasite had the chance to oviposit in any of the different stages of the aphid, it parasitized more half-grown nymphs than any other stage, whereas the alate adults were the least parasitized. The parasite also preferred apterous to alate advanced nymphs for parasitism. This behaviour was partly responsible for the scarcity of the alate mummies.

Parasitism in different stages of the host affected both host and parasite. If the aphid was parasitized in the first or second nymphal instar, it mummified in the last nymphal instar. If it was parasitized in a later stage, it would develop to an adult before mummifying. Parasitism caused an increase of the duration of development of the host. If the host was parasitized early enough, its reproductive capacity was eliminated. If, on the other hand, it was parasitized as a fourth instar nymph or an adult, reproductive capacity could be maintained partly or totally. Generally parasitism in more advanced stages resulted in shorter durations of development and higher reproductive capacity for the parasite.

The relation between host density and rate of parasitism was found to be curvilinear. This phenomenon is explained by the exhaustion of the egg supply of some parasites and by the increase of rest periods of the ovipositing female at high host densities. This mode of parasitism rendered the parasite inefficient in regulating the numbers of the host when they are high.

CHAPTER VII. HOST-PARASITE INTERACTIONS IN THE FIELD

The rate of parasitism of the cabbage aphid by *A. rapae* was estimated once each week during the main season of infestation in the three brussels sprout fields near Wageningen. Two methods were used for the estimation: (1) Dissection of advanced nymphs and (2) proportion of average number per plant of sound mummies to total of advanced nymphs, adults, and mummies.

The results showed that the rate of parasitism was not governed by the population density of the host alone. It also showed that mortality due to parasitism constituted a small fraction of the total mortality of the aphid and that parasitism was not the main factor affecting the population changes of the aphid. However, parasitism was very high, 80–90%, during the second half of April 1960 on the first generation of the fundatrices infesting the overwintered sprout plants kept for seed.

CHAPTER VIII. HYPERPARASITES AS MORTALITY FACTORS OF *A. rapae*

Hyperparasites were found to be very important in reducing the efficiency of the primary parasite. *Charips ancylocera* Cam. was found to be the most important species of the hyperparasites, followed by *Asaphes vulgaris* Wlk., *Pachyneuron minutissimum* Fö., and *Lygocerus aphidovorus* K. In 1959 out of

17,000 mummies of *B. brassicae* collected in the field, only 26% yielded *A. rapae*, whereas 58% yielded hyperparasites. In 1960, out of 8,000 mummies, 16% yielded *A. rapae* whereas 63% yielded hyperparasites.

Hyperparasites emerged in spring later than the primary parasite. This fact is one of the reasons for the high rate of parasitism early in the season.

CHAPTER IX. FACTORS LIMITING THE EFFECT OF *A. rapae* CURT. AS A CONTROLLING AGENT OF *B. brassicae* (L.)

It is concluded that the effectiveness of the parasite, as a factor regulating the populations of the cabbage aphid, was greatly diminished by several factors. Most important of these factors were: The behaviour of the parasite during parasitism (which renders it less efficient when population density of the host is high), the detrimental effect of hyperparasites, and the circumstance that the parasite develops more slowly than the host.

SAMENVATTING

HOOFDSTUK I. INLEIDING

In Nederland is geconstateerd, dat na het gebruik van bepaalde insecticiden tegen de koolbladluis, *Brevicoryne brassicae* (L.), een sterke daling in bladluisdichtheid spoedig gevolgd kan worden door een belangrijke toename. Dit is aanleiding geweest tot het instellen van een diepgaand onderzoek gedurende de jaren 1959 en 1960, alsmede tijdens de eerste helft van 1961. Het doel was een beter inzicht te verkrijgen in:

1. de mate van optreden van de koolbladluis in het veld.
2. de betekenis van de natuurlijke sterftefactoren voor de aantalsregulatie van de bladluis.
3. de invloed van *Aphidius rapae* Curt., de enige in Nederland voorkomende parasiet van de koolbladluis.

HOOFDSTUK II. ONTWIKKELINGS- EN VOORTPLANTINGSVERMOGEN VAN DE KOOLBLADLUIS

Er worden in dit hoofdstuk enige gegevens verstrekt over de bionomie en de ontwikkeling van de bladluis. *B. brassicae* overwintert in het ei-stadium op Cruciferen, die voor de zaadproductie worden doorgekweekt. Op een proefveld met spruitkool bij Wageningen waren in 1959–'60 gemiddeld 5644 eieren per plant aanwezig, in 1960–'61 bedroeg dit gemiddelde 2,3 per plant. In 1959 kwamen de eieren gedurende de eerste week van maart uit, in 1960 verschenen de jonge luizen één week vroeger. In die jaren bleek, dat zich uit respectievelijk ongeveer 60 en 30% van de eieren geen larve ontwikkelde. Bovendien trad er een hoge sterfte op onder de jonge bladluizen (fundatrices) als gevolg van het afwisselend voorkomen van dagen met hoge temperaturen (max. 19 °C) en met lage temperaturen (min. –6 °C).

De generaties overlapten elkaar. Zowel in 1959 als in 1960 verschenen een minimum van 4 en een maximum van 14 generaties. De duur van de verschillende generaties variëerde van minimaal 8–10 dagen tot maximaal 37–56 dagen. Onder proefomstandigheden werden door aptere virginopare wijfjes gemiddeld 26–29 nymphen geproduceerd; alate wijfjes gaven gemiddeld 13–23 nakomelingen.

HOOFDSTUK III. TALRIJKHEID VAN DE KOOLBLADLUIS IN VERBAND MET HET JAARGETIJDE

De seizoenschommelingen in de populatie van bladluizen op vier verschillende gewassen, die in de gematigde streken voorkomen, worden besproken. De algemene tendentie is een toename in dichtheid vroeg in het jaar, gevolgd door een snelle afname. Een nieuwe toename kan daarna onder gunstige weersomstandigheden plaats vinden. Verschillende milieufactoren kunnen het afnemen van de bladluisbevolking in het begin van de zomer veroorzaken.

Voor het eigen onderzoek werd gedurende de zomer en herfst van 1959 en

1960 in enige velden spruitkool wekelijks de populatiedichtheid van de koolbladluis bepaald. Telkens werden van 50 planten 3 blaadjes onderzocht. Het verloop van de dichtheid bleek bimodaal te zijn: een eerste maximum lag in juli, een tweede maximum werd in september of oktober aangetroffen. Het eerste maximum vertoonde voor beide jaren geen significante verschillen; het herfstmaximum van 1959 was evenwel opvallend hoger dan dat van 1960.

HOOFDSTUK IV. ANALYSE VAN DE SEIZOENSCHOMMELINGEN IN DE POPULATIEDICHTHEID VAN DE KOOLBLADLUIS

De daling van de dichtheid in de zomer werd voornamelijk veroorzaakt door sterfte. De invloed van verminderde voortplantingscapaciteit of van migratie was van veel minder belang.

De volgende mortaliteitsfactoren worden besproken:

A. Abiotische factoren

1. Temperatuur. De sterke afname van de bladluispopulatie midden in het seizoen kan niet veroorzaakt zijn door plotseling optredende ongunstige temperaturen; een opvallende temperatuursverandering deed zich in deze periode n.l. niet voor. Tot de grotere talrijkheid van de koolbladluis in de herfst van 1959 in vergelijking met de herfstperiode van 1960 kan daarentegen de hogere temperatuur van september 1959 wél hebben bijgedragen.
2. Regenval. Het jaar 1959 was opvallend droger dan 1960. De overvloedige regenval gedurende 1960 heeft de toename van de koolbladluis in sterke mate beperkt door het optreden van een schimmelziekte. Bovendien werden de alatae-vluchten door de regen sterk belemmerd.

B. Biotische factoren

1. Schimmelziekte. In 1959 werden geen door een schimmelziekte aangetaste bladluizen waargenomen. In 1960 daarentegen heerste er een schimmelziekte eind juli en begin augustus, die de bladluispopulatie sterk deed verminderen.
2. Roofvijanden. *Coccinella septempunctata* L., diverse Syrphidae, in hoofdzaak *Epistrophe balteata* Deg., en *Phaenobremia aphidovora* Rübs. vormden de voornaamste roofvijanden. Zij droegen zowel in 1959 als in 1960 bij tot de afname van de bladluispopulatie in het midden van het seizoen.
3. Parasieten. De enige tot nu toe gevonden parasiet van de koolbladluis in Nederland is *Aphidius rapae* Curt.

HOOFDSTUK V. DE BIONOMIE VAN DE PARASIET *Aphidius rapae* CURT.

De juiste benaming van deze tot de familie Aphidiidae behorende parasiet is *Aphidius* (*Diaeretiella*) *rapae* (Curtis). Kortheidshalve wordt echter in dit proefschrift de naam *Aphidius rapae* gebruikt.

Behalve *B. brassicae* wordt ook, zij het in mindere mate, *Myzus persicae* (Sulz.) door deze sluipwesp geparasiteerd. *A. rapae* is een endoparasiet; slechts één parasiet ontwikkelt zich volledig in een bladluis. Zestig procent van de sluipwespen in het veld bestond uit wijfjes. De levensduur van de volwassen dieren bedroeg 1–2 weken. Onder laboratoriumomstandigheden werden gemiddeld 83 eieren per wijfje afgezet. In het veld overwintert de parasiet in het larve-

stadium binnen de gemummificeerde bladluis om vervolgens in het voorjaar uit te vliegen. In 1960 vertoonde de verschijningsperiode van de sluipwespjes twee maxima, n.l. in april en in mei. In 1959 en 1960 varieerde het aantal generaties respectievelijk van 6–11 en van 5–11. De minimale ontwikkelingsduur van een generatie bedroeg 14–16 dagen; de ontwikkeling van de overwinterende generatie neemt enkele maanden in beslag.

HOOFDSTUK VI. WISSELWERKINGEN TUSSEN WAARD EN PARASIET

Pas uitgekomen sluipwesp-wijfjes kunnen reeds na enkele minuten een bladluis(waard) beparasiteren. Met behulp van een legbuis wordt een waard aangestoken, waarbij slechts één eitje wordt binnengebracht. Wel kan de eiafzetting plaats vinden in een bladluis, die reeds door een andere sluipwesp beparasiteerd was. In dit geval vindt superparasitisme plaats. De sluipwesp maakt geen onderscheid tussen reeds geparasiteerde en niet-geparasiteerde bladluizen. Perioden van eiafzetting wisselen af met steeds langer wordende rustperioden van soms enkele uren.

Half volwassen bladluisnymphen worden boven alle andere stadia geprefereerd, terwijl gevleugelde wijfjes het kleinste aantastingspercentage vertonen. Ongevleugelde, goed ontwikkelde nymphen blijken geprefereerd te worden boven gevleugelde nymphen. Dit gedrag was één van de oorzaken van het schaarse voorkomen van gevleugelde mummies.

Het stadium, waarin de waard wordt beparasiteerd, blijkt van belang te zijn zowel voor de ontwikkeling van de parasiet als voor de verdere ontwikkeling van de waard zelf. Indien koolbladluis-nymphen in het eerste of tweede stadium beparasiteerd worden, ontwikkelen zij zich nog tot het laatste nymphestadium. Wanneer de bladluis in een later stadium wordt aangestoken, ontwikkelt hij zich tot een volwassen dier alvorens te mummificeren.

Parasitisme veroorzaakt een verlenging van de ontwikkelingsduur van de waard. Indien de waard vóór het vierde nymphe-stadium wordt aangetast, gaat het voortplantingsvermogen verloren. Dit vermogen blijft geheel of gedeeltelijk aanwezig, indien de bladluis in het vierde nymphe-stadium of eerst in het volwassen stadium wordt beparasiteerd. In het algemeen blijkt de totale ontwikkelingsduur van de parasiet zelf korter te zijn en diens voortplantingscapaciteit groter naarmate de ontwikkeling van de waard, op het moment waarop het ei wordt afgezet, verder gevorderd is.

Naarmate de waard-dichtheid toeneemt, vertoont het aantal eieren dat een *Aphidius*-wijfje afzet, een toename, die asymptotisch tot een maximum nadert. De verklaring hiervan is, dat bij een hoge bladluisdichtheid een toename van de rustperioden van het eileggende sluipwespwijfje optreedt en het eiproductievermogen geleidelijk uitgeput raakt. Dit feit draagt ertoe bij, dat *A. rapae* niet bij machte is een regulerende werking uit te oefenen ten tijde van het optreden van grote koolbladluis-aantallen.

HOOFDSTUK VII. WEDERZIJDSE BEÏNVLOEDING VAN WAARD EN PARASIET IN HET VELD

De mate waarin de koolbladluis geparasiteerd werd, is wekelijks nagegaan in de drie bij Wageningen gelegen velden met spruitkool. Hiertoe werd sectie

verricht op bladluisnymphen in hun latere ontwikkelingsstadia, terwijl tevens per plant de verhouding bepaald werd van het aantal niet geparasiteerde nymphen en volwassen dieren tot het aantal gemummificeerde luizen.

Het bleek, dat de parasiteringsgraad slechts zeer ten dele bepaald werd door de populatiedichtheid van de waard. Bladluissterfte als gevolg van parasitisme vormde slechts een betrekkelijk kleine fractie van de totale sterfte over het gehele jaar. Wel kan deze aantasting door *A. rapae* in bepaalde perioden hoog zijn. Gedurende de tweede helft van april 1960 was b.v. op overwinterde koolplanten 80–90% van de fundatrices geparasiteerd.

HOOFDSTUK VIII. DE BETEKENIS VAN DE HYPERPARASIETEN VOOR DE MORTALITEIT VAN *A. rapae*

Hyperparasieten bleken in zeer belangrijke mate op te treden. De belangrijkste hyperparasiet is *Charips ancylocera* Cam. Andere hyperparasieten zijn *Asaphes vulgaris* Wlk., *Pachyneuron minutissimum* Fö. en *Lygocerus aphidovorus* K. Van 17,000 koolbladluis-mummies, verzameld in 1959, bleek 26% de primaire parasiet op te leveren, terwijl uit 58% van deze mummies hyperparasieten te voorschijn kwamen. In 1960, toen 8,000 mummies onderzocht werden, waren deze percentages respectievelijk 16% en 63%.

In het voorjaar verschijnen de hyperparasieten later dan *A. rapae*. Dit is één van de oorzaken voor de hoge graad van *A. rapae*-aantasting in deze periode.

HOOFDSTUK IX. FACTOREN DIE DE WAARDE VAN DE PRIMAIRE PARASIET *A. rapae* VERMINDEREN

Uit het onderzoek is duidelijk geworden, dat aan *A. rapae* als beperkende factor voor de koolbladluisontwikkeling geen grote waarde kan worden toegekend. Het gedrag van de parasiet bij hoge luisdichtheden (Hoofdstuk VI) is weinig efficiënt. De geringere ontwikkelingssnelheid van *A. rapae* in vergelijking met de koolbladluis vormt eveneens een nadeel. Hyperparasitisme (Hoofdstuk VIII) doet verder afbreuk aan de betekenis van de parasiet *A. rapae*.

ACKNOWLEDGMENTS

The present work was carried out in the Instituut voor Plantenziektenkundig Onderzoek (I.P.O.) in Wageningen, The Netherlands. The work was conducted under the supervision of Professor Dr. J. DE WILDE, Professor of Entomology, and Professor Dr. H. KLOMP, Professor of Zoology, in the Agricultural University of Wageningen. The writer wishes to express his deepest gratitude for their guidance, valuable advice and stimulating criticism throughout the work and for reading and correcting the manuscript.

The writer feels greatly indebted to Dr. J. G. TEN HOUTEN, Director of "I.P.O." for his sincere hospitality and for his unfailing enthusiasm throughout the course of this work. Dr. H. J. DE FLUITER, deputy-director of "I.P.O." and head of the Department of Entomology, is wholeheartedly thanked for his deep interest in the study, useful suggestions and for all the help and time he freely gave throughout the work and during the preparation of the manuscript. Thanks are also due to the staff members and personnel of "I.P.O." who never failed to help in every possible way.

The writer is much indebted to Prof. Dr. L. J. ALEXANDER, Ohio Agricultural Experiment Station and Ohio State University, U.S.A., for the very thorough reading and correcting of the English text. Special thanks are extended to Mr. D. HILLE RIS LAMBERS, Bennekom, for his valuable discussions, helpful suggestions and free access to his library. Dr. J. B. M. VAN DINTHER was very kind to prepare the Dutch summary and the writer is much obliged to him. Sincere gratitude is due to Mr. C. VAN DEN ANKER, Statistician, "I.P.O.", for his continuous help and advice in the design of the experiments and for the statistical analysis.

The writer also wishes to express his thanks to the artist Mr. M. P. VAN DER SCHELDE, for preparing the figures, to Mr. A. Th. B. RAST for his help during part of the work and for using some data of his unpublished report, and to Miss A. ZEEGERS for her assistance in some of the experiments.

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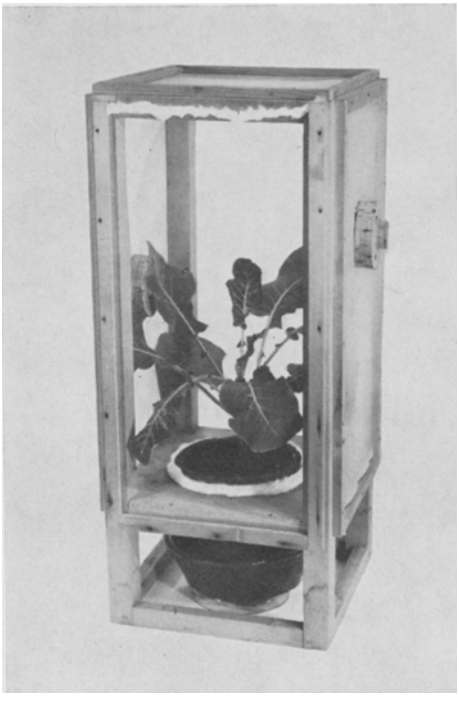


PLATE 1, A. Cage for rearing *B. brassicae* and *A. rapae* on a potted plant

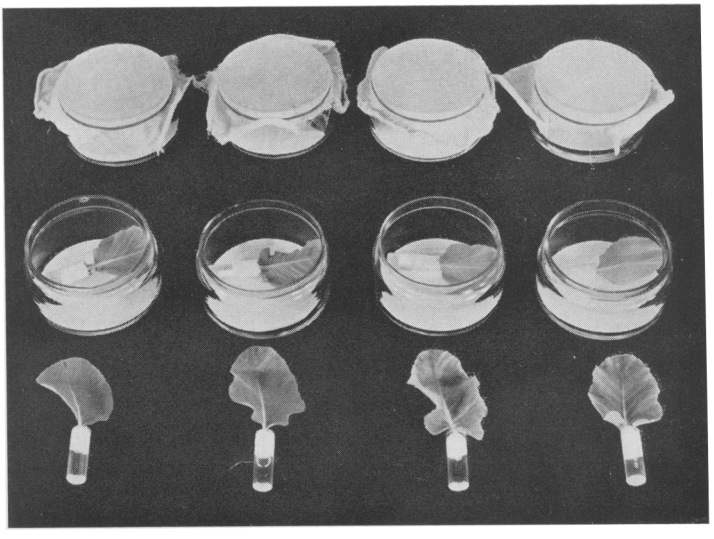


PLATE 1, B. Glass dishes for rearing *B. brassicae* and *A. rapae* on cut leaves

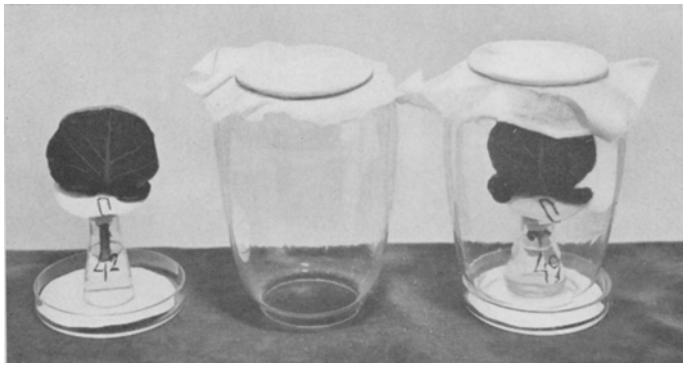
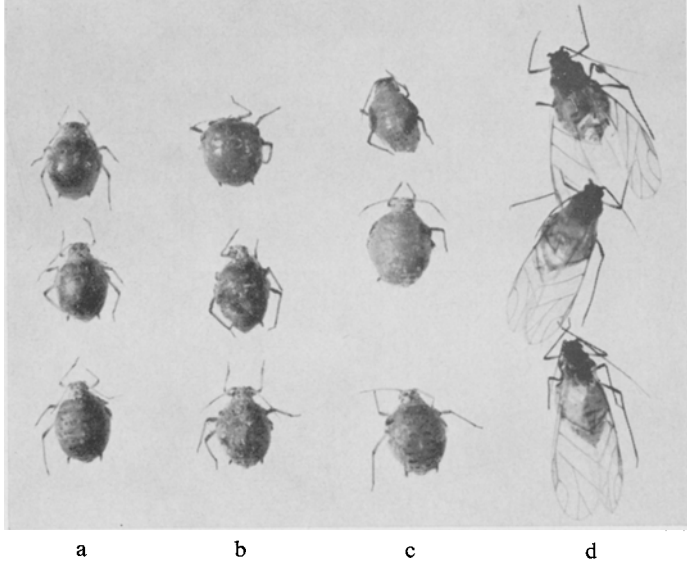


PLATE 2, A. Lamp glasses for rearing *B. brassicae* on cut leaves



a b c d

PLATE 2, B. Mummies of *B. brassicae*
a, apterous mummies; b & c, mummies with reduced wing pads;
d, mummies with fully developed wings