209-227-6000-L180

TEXAS AGRICULTURAL EXPERIMENT STATION

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COLLEGE STATION, BRAZOS COUNTY, TEXAS

BULLETIN No. 353 APRIL, 1927

DIVISION OF ENTOMOLOGY

THE INFLUENCE OF PARENTAGE, NUTRITION, TEMPERATURE, AND CROWDING ON WING PRODUCTION IN *APHIS GOSSYPII*, GLOVER

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SYNOPSIS

There are two forms of the cotton louse, Aphis gossypii. One form has fully developed wings and the other form is wingless. This is a technical Bulletin and contains the results obtained from the studies on the influence of parentage, nutrition, temperature, and crowding on the production of the winged forms. It was found that the normal tendency for this insect is to be wingless. The production of wings is dependent entirely upon environmental influences. Starvation produces an increased number of winged individuals in the progeny of wingless mothers but has little or no effect in stimulating wing development in the offspring of winged mothers. Temperatures ranging from 70° F. to 90° F. do not affect the proportion of forms produced in this species. When these insects are crowded during development an increased number of winged forms occur. Crowding was found to be the dominant if not the controlling factor in stimulating the production of wings. No correlation was found to exist between the prevailing relative humidity in which the insects were reared and the ratio of winged to wingless forms produced.

TABLE OF CONTENTS

BULLETIN No. 353 APRIL, 1927

THE INFLUENCE OF PARENTAGE, NUTRITION, TEMPERATURE, AND CROWDING ON WING PRODUCTION IN *APHIS GOSSYPII*, GLOVER

H. J. REINHARD

Incidental to the life history studies of *Aphis gossypii* by Paddock (6), some observations on factors affecting dimorphism in this species were made. These preliminary observations resulted in a more complete study of the effect of parentage, nutrition, temperature, and crowding on the ratio of alate to apterous forms produced in this species. The work was begun in March 1924 and continued with interruptions until October 1926. The results of these studies are given in this paper.

REVIEW OF LITERATURE

The influence of parentage, nutrition, and temperature as factors affecting the proportion of alate and apterous forms of aphids has been noted by a number of investigators. The results of experiments conducted by Ewing (3), Gregory (5), Shull (7), Wadley (8), and Ewing (4), are extremely interesting and significant contributions to the subject. Ewing (3), working with the apple-grain aphid, then known as *Aphis avenae* Fab., found that temperature changes alone were capable of affecting dimorphism, and that fewer winged aphids were produced in a moderate temperature than in lower or higher temperatures. Gregory (5) found that the green pea-aphid, *Microsiphum destructor* John., when starved during development produced winged progeny and assigned nutrition as the primary factor in determining the development of wings in the offspring of wingless mothers. Shull (7), working with *Macrosiphum solanifolii* Ashm., noted that winged aphids produced largely apterous progeny, and that wingless individuals produced many alate progeny, and concluded that parentage was the dominant factor in wing development. Wadley (8), experimenting with *Rhopalosiphum prunifoliae* Fitch, showed that all three factors, viz., temperature, nutrition, and parentage, affected the proportion of alate and apterous forms produced and concluded that definite relations existed among them in their effect on wing development. Ewing (4) confirms this opinion in the following words:

"Among the outstanding factors that have been demonstrated experimentally as affecting the ratio between the two agamic forms of aphids are inheritance, temperature and nutrition, and the relative importance of each of these appears to depend on the conditions imposed by the combination of all other factors. Either inheritance, temperature or nutrition may under certain conditions become the dominant or even the controlling factor."

This previous work was used as a guide in arranging experiments to study the influence of parentage, nutrition, temperature, and crowding on wing development in *Aphis gossypii* Glover, commonly known as the cotton or melon aphid. The data obtained from these experiments with certain conclusions are presented in this paper as a contribution to our present knowledge of this apparently elusive yet popular and interesting subject.

THE EFFECT OF PARENTAGE

A study of the influence of parentage and ancestry on the production of alate and apterous forms of *Aphis gossypii* was begun on October 10, 1925, and continued without interruption for one year. During this time 59 complete generations were produced in the laboratory and insectary on young succulent cotton plants grown in pots and protected by street-lamp globes.

Beginning with an isolation of an apterous agamic individual, this form was selected as the parent of each succeeding generation. The progeny of each parent was transferred to an uninfested plant and reared to maturity. Temperature and humidity conditions were recorded by a hygrothermograph. The data obtained in this experiment are presented in Table 1.

Table 1.—Apterous Generation Series

Generation	Date Born	Date Matured	Number Reared	Apterous	Alate
1	Oct. 10, 1925	Oct. 19, 1925	9	9	0
2	Oct. 20, 1925	Oct. 26, 1925	25	25	0
3	Oct. 27, 1925	Nov. 2, 1925	31	31	0
4	Nov. 3, 1925	Nov. 8, 1925	21	21	0
5	Nov. 9, 1925	Nov. 15, 1925	17	17	0
6	Nov. 16, 1925	Nov. 23, 1925	14	14	0
7	Nov. 24, 1925	Nov. 30, 1925	17	17	0
8	Dec. 1, 1925	Dec. 7, 1925	11	11	0
9	Dec. 7, 1925	Dec. 13, 1925	25	25	0
10	Dec. 14, 1925	Dec. 19, 1925	19	19	0
11	Dec. 20, 1925	Dec. 27, 1925	19	19	0
12	Dec. 28, 1925	Jan. 2, 1926	14	14	0
13	Jan. 3, 1926	Jan. 9, 1926	13	13	0
14	Jan. 10, 1926	Jan. 15, 1926	36	32	4
15	Jan. 16, 1926	Jan. 22, 1926	13	13	0
16	Jan. 23, 1926	Jan. 28, 1926	31	31	0
17	Jan. 29, 1926	Feb. 3, 1926	7	7	0
18	Feb. 3, 1926	Feb. 8, 1926	27	27	0
19	Feb. 9, 1926	Feb. 14, 1926	81	75	6
20	Feb. 15, 1926	Feb. 20, 1926	16	16	0
21	Feb. 21, 1926	Feb. 26, 1926	19	19	0
22	Feb. 26, 1926	Mar. 3, 1926	19	19	0
23	Mar. 4, 1926	Mar. 9, 1926	27	27	0
24	Mar. 10, 1926	Mar. 15, 1926	29	22	7
25	Mar. 16, 1926	Mar. 21, 1926	17	17	0
26	Mar. 22, 1926	Mar. 28, 1926	25	25	0
27	Mar. 29, 1926	April 3, 1926	21	21	0
28	April 4, 1926	April 9, 1926	9	9	0
29	April 10, 1926	April 15, 1926	22	22	0
30	April 16, 1926	April 21, 1926	11	11	0
31	April 22, 1926	April 26, 1926	10	10	0
32	April 27, 1926	May 2, 1926	18	18	0
33	May 2, 1926	May 7, 1926	17	17	0
34	May 7, 1926	May 12, 1926	17	17	0
35	May 12, 1926	May 17, 1926	15	15	0
36	May 17, 1926	Nay 22, 1926	12	12	0
37	May 22, 1926	May 27, 1926	15	15	0
38	May 27, 1926	June 1, 1926	13	13	0

Table 1.—Apterous Generation Series—Continued

Generation	Date Born	Date Matured	Number Reared	Apterous	Alate
39	June 2, 1926	June 8, 1926	14	14	0
40	June 8, 1926	June 13, 1926	13	13	0
41	June 14, 1926	June 20, 1926	15	15	0
42	June 20, 1926	June 25, 1926	13	13	0
43	June 26, 1926	July 1, 1926	14	14	0
44	July 2, 1926	July 8, 1926	15	15	0
45	July 9, 1926	July 14, 1926	14	14	0
46	July 15, 1926	July 20, 1926	13	13	0
47	July 20, 1926	July 25, 1926	15	15	0
48	July 26, 1926	July 31, 1926	16	16	0
49	July 31, 1926	Aug. 5, 1926	17	17	0
50	Aug. 6, 1926	Aug. 11, 1926	13	13	0
51	Aug. 12, 1926	Aug. 17, 1926	12	12	0
52	Aug. 18, 1926	Aug. 25, 1926	12	12	0
53	Aug. 26, 1926	Aug. 31, 1926	14	14	0
54	Aug. 31, 1926	Sept. 6, 1926	13	13	0
55	Sept. 7, 1926	Sept. 14, 1926	16	16	0
56	Sept. 14, 1926	Sept. 20, 1926	11	11	0
57	Sept. 21, 1926	Sept. 26, 1926	15	15	0
58	Sept. 26, 1926	Oct. 2, 1926	13	13	0
59	Oct. 2, 1926	Oct. 8, 1926	9	9	0

The continued selection of the apterous agamic form, it will be noted, reproduced a like form throughout the entire generation series except in three instances. In each of these cases the winged form appeared evidently in response to another factor, viz., crowding, which unintentionally was permitted to occur for a period of time sufficient to produce its effect. A more complete discussion of crowding as a factor affecting wing production will be given elsewhere in this paper.

An attempt was made to run a parallel series of alate generations under conditions identical with those in the experiment described above. However, it was found to be impossible to maintain consecutive generations of the alate agamic form. The progeny of winged mothers invariably were wingless and their offspring continued to reproduce the wingless form as long as crowding was not permitted to occur. This experiment was therefore discontinued after the fifth-generation descendants of an alate stem mother had reached maturity. The results of this experiment are given in Table 2.

Table 2.—Alate Generation Series

Generation	Date Born	Date Matured	Number Reared	Apterous	Alate
1	May 13, 1926	May 19, 1926	5	5	0
2	May 19, 1926	May 24, 1926	9	9	0
3	May 25, 1926	May 31, 1926	10	10	0
4	May 31, 1926	June 6, 1926	12	12	0
5	June 6, 1926	June 11, 1926	23	23	0

Paddock (6) reared 51 complete generations of *Aphis gossypii* using practically the same methods in rearing the insects as those described above. The primary object of this experiment was to determine the maximum number of generations of this species that were possible during one year at College Station. For this reason only the first-born 2 or 3 young of each mother were transferred to an uninfested plant, which precluded any possibility of crowding. By selecting the apterous form as the parent of each succeeding generation only one alate individual was obtained during the course of the entire generation series.

The results of these two generation series experiments with *Aphis gossypii* appear to be in exact accord with regard to the effect of parentage and ancestry on the ratio of forms produced. These observations, which include the careful rearing of 110 generations, fail to give any indication that there is a tendency, in this species at least, for the wingless parent to produce winged offspring when reared under conditions of ample food and no crowding.

Further significant results of an experiment pertinent in this connection are reported by Comstock (2) page 417, who states:

"In an experiment conducted under my direction by Mr. Slingerland, in the insectary at Cornell University, we reared 98 generations of the wingless agamic form without the appearance of any other form. The experiment was carried on for four years and three months without any apparent change in the fecundity of the aphids, and was discontinued owing to the press of other duties. As the aphids were kept in a hothouse throughout the winters, seasonal influences were practically eliminated; and as members of each generation were placed singly on aphid-free plants and their young removed as soon as born, there was no crowding."

Summary of the Effect of Parentage

During the period of twelve months 59 complete generations of the wingless agamic form of *Aphis gossypii* were reared in the laboratory and insectary without the appearance of any winged forms except in three generations in which the aphids were allowed to become crowded during development. The offspring of winged parents matured wholly wingless forms throughout 5 complete generations counting from the winged stem mothers. In the light of these results, which are in exact accord with those of a similar experiment with the same species, it appears logical to conclude: (a) that the normal tendency for this species is to be wingless; (b) that the production of wings is dependent entirely upon environment influences.

THE EFFECT OF NUTRITION

Nutrition as a factor affecting the forms of aphids produced has been emphasized by several investigators. In fact, poor nutrition has been assigned as the primary factor in determining the development of wings in at least one species.

To determine the influence of starvation on the development of wings in *Aphis gossypii*, several series of starvation experiments were conducted in which both young and adult aphids were used. The daily period of starvation in all tests was 6 to 8 hours. In case of the young this was applied soon after birth for varying periods ranging from 2 days to all through the time required for development.

Before referring to the data obtained in these experiments it should be stated that no precautions were taken in any of the tests to prevent crowding. The extreme importance of this factor in affecting the forms produced was not fully appreciated at the time some of these experiments were performed. While this may have affected the results of some of the tests, however, this source of error should be practically negligible since only small numbers of aphids were used in each individual test.

A summary of the data obtained by starving young aphids for varying periods during development is given in Table 3.

Table 3.—Effect of Starvation for Varying Periods During Development

Parent	No. of Tests	Period Starved	Progeny		Check Progeny	
			Apterous	Alate	Apterous	Alate
Apterous. .	10	First two days after birth.	88	10	75	0
Alate.	5	First two days after birth.	34	4	21	0
Apterous. .	12	First three days after birth.	74	10	98	0
Alate.	3	First three days after birth.	28	0	27	0
Apterous. .	15	First four days after birth.	155	38	171	1
Alate.	5	First four days after birth.	48	0	66	0
Apterous. .	19	All through development.	160	16	195	2
Alate.	8	All through development.	55	0	91	0
Apterous. .	6	After third day to maturity.	74	8	90	0

The influence of starvation on the forms produced is quite apparent in the progeny of apterous mothers. Out of a total of 633 starved young reared to maturity, 82 or 12.9 per cent were winged as compared with 3 or 0.4 per cent of the 632 young reared as checks which were not starved. However, when the progeny of alate parents was starved during development the effect on the ratio of forms was not so pronounced. In fact, in only one case did the winged form appear in response to the imposed condition of starvation.

The data in Table 4 are presented to show the effect of poor nutrition on the progeny of parents starved throughout the reproductive period. The progeny produced in each test was well nourished from birth to maturity.

Table 4.—Effect on Well Nourished Progeny of Starved Parents

Parents Starved During Reproductive Period	Number of Tests	Progeny Well Nourished		Check Progeny	
		Apterous	Alate	Apterous	Alate
Apterous.	28	64	31	79	0
Apterous.	15	26	3	49	1
Apterous.	15	47	4	55	5
Apterous.	10	31	12	90	0
Alate.	28	64	2	64	0
Alate.	15	41	0	44	0

It will be noted that the offspring of apterous parents though well nourished were influenced considerably by starving the parents. Out of a total of 218 young reared, 50 or 22.9 per cent were alate; whereas among the individuals in the check experiments only 6 or 2.1 per cent were alate out of a total of 279 young reared to maturity. Starving alate parents, however, had very little influence in regard to the development of alate progeny. Only 2 winged individuals appeared in the 107 young reared in these experiments.

The influence of nutrition as a factor affecting the proportion of winged and wingless forms in the well nourished progeny of parents starved during development and supplied with ample food after reaching maturity is shown in Table 5.

Table 5.—Effect on Well Nourished Progeny of Parents Starved During Development and Well Nourished After Maturity

Parents Starved Through Development, Well Nourished Throughout Reproduction Period	Number of Tests	Progeny Reared Well Nourished		Progeny Reared Check	
		Apterous	Alate	Apterous	Alate
Apterous	10	69	64	60	0
Apterous	18	45	22	34	0
Apterous	10	56	8	71	1
Apterous	11	19	3	47	1
Alate	15	69	0	90	0
Alate	13	34	0	29	1

These results are especially interesting because they give some indication of the influence of nutrition, under the most adverse conditions, on the ratio of forms produced. It will be noted in the data presented above, that the effect of starvation during development is reflected by the appearance of many winged forms in the progeny of apterous parents even though the parents and young are well fed. Thus it is apparent that the lack of sufficient nourishment during development produces a hold-over effect which becomes manifest by an increased number of winged forms in the offspring of wingless parents. Similar tests with the progeny of alate parents produced negative results.

Summary of the Effect of Nutrition

From the data obtained in the starvation experiments with *Aphis gossypii,* it is obvious that nutrition may or may not affect the ratio of forms produced, depending on the parent form. The results obtained in this connection appear to warrant the following conclusions: (a) that starvation increases the number of alate individuals in the progeny produced by apterous parents; (b) that starvation does not appear to have any influence on the production of alate forms in the progeny produced by alate parents; in other words the offspring of alate parents revert to the normal tendency of the species, viz., the apterous form, with such puissance, that the effect produced by starvation in stimulating wing development is practically if not entirely counteracted.

THE EFFECT OF TEMPERATURE

Ewing (3) studying the effect of protracted parthenogenetic reproduction in *Aphis avenae* made some incidental observations regarding the influence of temperature on dimorphism in this species. In rearing aphids under constant-temperature conditions he noted that at 60° F. all the individuals produced wings; at 65° F. or slightly above, only the wingless forms were produced; at 70° F. 15.1 per cent were winged; at 80° F. 69.6 per cent were winged.

This demonstration of the effect of temperature on wing production in this species is indeed a remarkable fact when considered in the light of the complete inverse ratio of forms produced in a temperature variation from 60° F. to 65° F. or slightly above. Unless it is assumed that the imposed condition of a constant temperature is too unnatural, the question immediately arises, will similar slight fluctuations in temperature under natural conditions produce like or even approximating results? This subject will be considered in detail with reference to *Aphis gossypii* elsewhere in this paper.

Wadley (8) working with the same species used by Ewing, obtained more or less conforming results in his experiments on the effect of temperature, although the data presented are much less impressive than Ewing's. At 62° F. only 15.1 per cent were winged; at 65° F. 1.3 per cent were winged; at 70° F. 2.3 per cent produced wings; at 80° F. only 6.5 per cent produced wings.

Ewing (4) discussing the factors of inheritance and parentage as affecting aphid forms produced, elaborated the conclusions presented in his earlier paper on the effect of temperature, in the light of Wadley's results. He notes that there is a summation effect of parentage on the offspring of a generation of aphids, depending upon the number and nearness of the ancestors of either form. This is suggested as the explanation for the apparent differences occuring between the results of the temperature experiments cited above. In other words he concludes that the effect of temperature on the ratio of the agamic forms produced is more precisive in aphids having an apterous monomorphic parentage of 16 or more generations.

For the purpose of studying the effect of temperature on wing development in *Aphis gossypii* a Freas Electric Oven with a constant temperature regulator was procured. This oven, which contains a large compartment (34″x24″x17″) lighted by four small windows, and in which temperature and humidity conditions could be controlled within certain limits, seemed ideally suited for this purpose.

Such did not prove to be the case, however, for it was found impossible to rear even a single generation of aphids under optimum conditions of temperature and humidity. For some unknown reason this species was found unable to tolerate confinement within the oven and invariably succumbed before any effects of temperature could be noted. Very likely the greatly subdued light proved to be a condition too unnatural for the insects to withstand for any extended period of time.

After numerous attempts to rear the insects within the oven had failed the studies were confined to the laboratory and insectary.

The generation series experiment referred to above was in reality a compound experiment in that all the factors herein discussed as affecting the ratio of aphid forms produced were considered and controlled within reasonable limits for part of or the entire duration of the experiment.

From October 10, 1925, to May 20, 1926, the experiment was conducted in a large well lighted laboratory. During this time the temperatures were fairly well controlled; at least the aphids for the most part were not subjected to any sudden or very great changes in temperature. Frequently the daily variation was not more than 3° or 4° F. and within the limits of 8° or 10° F. during the period of a week or more. Thus it was often possible to rear a complete generation of aphids under these conditions.

The effect of temperature on the ratio of forms produced in the laboratory is shown in Table 6. In this connection it is important to note that these data refer to aphids of a known apterous monomorphic parentage of 16 to 35 generations reared under conditions of ample food and practically no crowding. The maximum and minimum temperatures given are those occurring during the entire period required for the development of each generation and the mean temperature given is the average of the bi-hourly readings taken during the same period of time.

Table 6.—Effect of Temperature on the Ratio of Forms Produced in the Laboratory

Isolation No.	Apterous Monomorphic Parentage	Period of Development	Temperature			Number Reared	Ratio of Forms	
			Max.	Min.	Mean		Alate	Apterous
		1926						
1	16 generations	Jan. 29-Feb. 3.....	91	70	78.8	7	0	7
2	17 generations	Feb. 3-Feb. 8......	86	70	77.7	27	0	27
3	18 generations	Feb. 9-Feb. 14.....	77	65	72.9	81	6	75
4	19 generations	Feb. 15-Feb. 20....	75	64	71.1	16	0	16
5	20 generations	Feb. 21-Feb. 26....	78	66	74.2	19	0	19
6	21 generations	Feb. 26-Mar. 3.....	85	67	75.3	19	0	19
7	22 generations	Mar. 4-Mar. 9......	78	68	73.4	27	0	27
8	23 generations	Mar. 10-Mar. 15...	80	63	71.3	29	7	22
9	24 generations	Mar. 16-Mar. 21...	81	68	75.6	17	0	17
10	25 generations	Mar. 22-Mar. 28...	80	61	72.0	25	0	25
11	26 generations	Mar. 29-April 3....	80	63	71.2	21	0	21
12	27 generations	April 4-April 9.....	84	65	75.3	9	0	9
13	28 generations	April 10-April 15...	75	65	70.9	22	0	22
14	29 generations	April 16-April 21...	77	68	73.1	11	0	11
15	30 generations	April 22-April 26...	78	71	74.7	10	0	10
16	31 generations	April 27-May 2....	77	72	76.0	18	0	18
17	32 generations	May 2-May 7......	79	74	77.8	17	0	17
18	33 generations	May 7-May-12.....	85	76	81.3	17	0	17
19	34 generations	May 12-May 17....	82	73	77.5	15	0	15
*20	35 generations	May 17-May 22....	85	60	75.8	12	0	12

*In insectary on May 20, 1926.

From these data it will be observed that there is no correlation between temperature and the ratio of forms produced in this species. In mean temperatures ranging from 70.9° F. to 81.3° F. with extremes fluctuating between 5° F. and 21° F., the apterous forms continued to predominate. In fact, the winged forms appeared in but two isolations and these, as has already been explained, were attributable to crowding and certainly not to any influence of temperature, since the aphids reared under approximately the same temperature conditions in all other isolations were wholly apterous.

From May 20, 1926, to October 10, 1926, the generation series experiment was conducted in the insectary, where temperatures approximated natural conditions. The aphids reared during this time were thus exposed to considerable daily fluctuations of temperatures all through development. The range between the daily maximum temperature and the daily minimum temperature often extended from 15° F. to 20° F. or more, and these environmental conditions appeared extremely favorable for making observations on the effect produced by approximately natural variations in temperatures, with respect to the development of wings in this species.

The data obtained from this portion of the experiment are presented in Table 7. It should be noted that the aphids referred to in these data had an apterous monomorphic ancestry of 36 to 58 generations and that all were reared under conditions of ample food and no crowding. The maximum and minimum temperatures given in each case represent the extremes to which the individuals of each isolation were subjected, and the mean temperature is the average of bi-hourly readings taken during the time required for development of the aphids in the corresponding isolation.

Table 7.—Effect of Temperature on the Ratio of Forms Produced in the Insectary

Isolation No.	Apterous Monomorphic Parentage	Period of Development	Temperature			Number Reared	Ratio of Forms	
			Max.	Min.	Mean		Alate	Apterous
		1926						
21	36 generations	May 22-May 27....	87	64	76.1	15	0	15
22	37 generations	May 27-June 1.....	90	67	78.7	13	0	13
23	38 generations	June 2-June 8......	92	62	77.1	14	0	14
24	39 generations	June 8-June 13.....	93	71	80.7	13	0	13
25	40 generations	June 14-June 20....	96	73	84.6	15	0	15
26	41 generations	June 20-June 25....	96	72	82.3	13	0	13
27	42 generations	June 26-July 1.....	93	70	80.9	14	0	14
28	43 generations	July 2-July 8......	97	70	83.7	15	0	15
29	44 generations	July 9-July 14.....	96	69	82.0	14	0	14
30	45 generations	July 15-July 20....	93	66	81.4	13	0	13
31	46 generations	July 20-July 25....	92	71	80.8	15	0	15
32	47 generations	July 26-July 31....	97	73	85.7	16	0	16
33	48 generations	July 31-Aug. 5.....	98	73	85.9	17	0	17
34	49 generations	Aug. 6-Aug. 11.....	102	73	87.2	13	0	13
35	50 generations	Aug. 12-Aug. 17....	98	74	84.5	12	0	12
36	51 generations	Aug. 18-Aug. 25....	101	69	85.9	12	0	12
37	52 generations	Aug. 26-Aug. 31....	94	67	80.0	14	0	14
38	53 generations	Aug. 31-Sept. 6....	99	79	86.5	13	0	13
39	54 generations	Sept. 7-Sept. 14....	100	79	88.8	16	0	16
40	55 generations	Sept. 14-Sept. 20...	99	77	87.8	11	0	11
41	56 generations	Sept. 21-Sept. 26...	99	64	88.1	15	0	15
42	57 generations	Sept. 26-Oct. 2.....	99	65	83.2	13	0	13
43	58 generations	Oct. 2-Oct. 8.......	98	61	82.1	9	0	9

In comparing the temperatures occuring during this experiment with those given in Table 6, it will be noted that the range between maximum and minimum is usually much greater, and that the mean temperature also is consistently higher, in fact, averaging well above the temperature reported as effective in regard to the stimulation of wing development. However, not a single alate form appeared among all the aphids, of a long apterous monomorphic parentage, which were reared in this experiment.

Summary of the Effect of Temperature

In the data presented above it has been shown that the ratio of forms was not affected by temperature among 20 generations, which included 432 individuals, reared in the laboratory from January 29, 1926, to May 22, 1926, during which time the average mean temperature was 74.8° F. Two isolations reared in a mean temperature of 76.0° F. and 77.8°F., respectively, with the fluctuations within the limits of 5° F., as well as many other isolations reared in comparable mean temperatures with the fluctuations ranging from 10° F. to 20° F. matured 100 per cent apterous forms.

Similarly, the forms produced were not affected by temperature in the 23 generations, which included 315 individuals, reared in the insectary from May 22, 1926, to October 8, 1926, during which time the average mean temperature was 83.2° F. The apterous form continued to predominate in mean temperatures as high as 88° F. regardless of daily or extreme fluctuations ranging from 20° F. to 35° F. during the developmental period of a generation.

In the light of these results it appears logical to conclude: that temperature within the limits of 70° F. to 90° F. does not affect the ratio of forms produced in this species.

THE EFFECT OF CROWDING

The influence of crowding as a factor affecting wing development in aphids has been studied by several investigators. Most frequently crowding is discussed in connection with poor nutrition, the assumption being that aphids crowded on plants obtain insufficient nourishment and that the winged form appears in response to this stimulus. The results of these studies, however, indicate a wide difference of opinion regarding the relative importance of crowding in affecting the proportion of aphid forms produced.

Baker and Turner (1) working with *Aphis pomi* found that poor nutrition as a result of heavy infestations of this species did not cause the alate form to appear. They state:

"The theory has been frequently advanced that the production of winged forms during the summer is due to a lack of sufficient nourishment for the insects. In some cases the wording of this theory is modified by the statement that winged forms appear on plants which are very heavily infested. The writers' results are a flat contradiction of this theory for this species. As has been stated previously, in handling the insects the writers always transferred the mothers to new plants, rather than the progeny. In this way several consecutive generations were reared on one plant. Thus the effect of poor or good food would be accentuated. Yet the winged forms were never obtained in series of small, poorly fed insects, but occurred frequently in well-nourished series."

Comstock (2) after rearing 59 consecutive generations of the agamic apterous forms states:

"In order to determine the influence of crowding, members of the sixtieth generation were placed on separate plants and their young not removed. At the end of three weeks the winged agamic forms appeared, evidently in response to need of migration to less densely populated plants; while in other cages where the young were removed promptly, no migrants appeared up to the end of the experiment."

Before referring to the results of any observations on the effect of crowding in this species it appears desirable to define the term as considered in this paper. Crowding is a relative condition which varies from a comparatively small colony of aphids situated in contiguous positions within a restricted area, to a maximum infestation in which the insects cover practically the entire stem, petiole or leaf of the food plant.

In these studies of *Aphis gossypii* it was noted that a high percentage of the alate form occurred invariably on plants which were heavily infested. Several series of experiments were conducted, therefore, to determine the influence of crowding on wing development in this species. It has already been noted above in the generation series experiment, Table 1, that the winged form failed to appear when crowding did not occur and that no difficulty was experienced in maintaining an apterous lineage for 59 generations under these conditions. Members of 10 separate generations of this series were isolated on uninfested plants and their progeny allowed to multiply without disturbance until a crowded condition occurred. It will be noted in Table 8, that the alate form appeared in every case.

Table 8.—Effect of Crowding Progeny on Wing Development

Generation	Parentage	Date Isolated	Number Isolated	First Young Observed Developing Wings	Winged Forms, After Progeny Well Crowded	Check, Progeny Not Crowded	
						Apterous	Alate
		1925		1926			
8	Apterous....	Dec. 9	9	Jan. 9........	Many.........	25	0
10	Apterous....	Dec. 20	17	Jan. 15........	Many.........	19	0
		1926					
13	Apterous....	Jan. 9	11	Jan. 20........	Few..........	32	4
18	Apterous....	Feb. 10	20	Feb. 16........	Many.........	75	6
19	Apterous....	Feb. 16	65	Feb. 24........	Predominate...	16	0
29	Apterous....	April 17	19	April 23........	Few..........	11	0
47	Apterous....	July 25	13	Aug. 9........	Few..........	16	0
48	Apterous....	July 28	10	Aug. 18........	Many.........	17	0
55	Apterous....	Sept. 15	9	Sept. 23........	Many.........	11	0
59	Apterous....	Oct. 3	9	Oct. 19........	Few..........	14	0

The individuals used in each check of these experiments were sisters to those isolated for observation in the corresponding generation. Hence they had the same parentage and ancestry, and their offspring were reared under comparable environmental conditions except as to crowding. In only two instances did the alate form appear in the checks, and it may be safely assumed that these were the direct result of crowding, since a considerably larger number of young were reared, making it more difficult to prevent the aphids, especially when very young, from feeding in contiguous situations.

In another experiment apterous individuals of an unknown parentage were placed on uninfested potted plants in the laboratory and allowed to reproduce for several generations. After these plants had become densely populated with aphids the adults and latter instar nymphs were removed daily and a record made of the number of winged and wingless forms. These data are presented in Table 9.

Table 9.—Effect of Crowding Parents and Progeny on Wing Development

Test	Date	Number Mature	Apterous	Alate	Check, Progeny Not Crowded	
					Apterous	Alate
	1924					
1.	Mar. 29	29	12	17	31	2
2.	Mar. 30	41	15	26	23	0
3.	Mar. 31	33	12	21	16	0
4.	April 1	27	21	6	19	0
5.	April 2	26	12	14	14	0
6.	April 3	18	15	3	9	0
7.	May 6	43	19	24	12	0
8.	May 7	28	11	17	21	0
9.	May 8	33	20	13	17	0
10.	May 9	41	16	25	14	0
11.	May 10	39	20	19	16	0
12.	May 11	21	16	5	27	3
13.	May 12	18	7	11	8	0
14.	May 13	41	21	20	12	0

The influence of crowding as a potent factor affecting the forms produced is shown by these data. Out of a total of 438 aphids noted, 221 or slightly more than 50 per cent were winged, while only 5 winged forms appeared among the 243 individuals reared in the checks in which crowding was practically eliminated.

To determine if crowding is likewise effective in altering the ratio of forms produced in the progeny of alate parents, 10 nymphs destined to become winged were isolated January 18, 1926, on a young cotton plant in the laboratory. These individuals were descendants of apterous parents for eight generations. Reproduction began on January 20, and the first-born young reached maturity by January 26, before a crowded condition occurred. There were no alate forms in the progeny of these alate mothers. In the succeeding generation, however, a crowded condition was apparent by January 30. Many nymphs with developing wings were visible on February 2, and two days later it was estimated that practically one-third of the entire population, which consisted of a hundred or more aphids, were winged or destined to become so.

In a parallel experiment to check these results, the progeny of alate mothers, which were sisters to those referred to in the experiment described above, continued to approach 100 per cent wingless forms in the succeeding generation when crowding was not permitted to take place. Out of a total of 79 aphids reared only 3 were winged.

All efforts to determine the effect on the progeny of crowded alate parents proved unsuccessful. The winged forms of this species refused to tolerate any crowding and migrated from the plants to the sides of the cages, where they starved in preference to returning to the plants for food.

Some references to the effect of crowding on wing production in aphids embrace the theory that the insects located on heavily infested plants obtain insufficient nourishment, and that hence poor nutrition is the primary cause for the appearance of the alate forms. In these studies of *Aphis gossypii,* however, frequent observations were made which appeared at variance with this explanation. For instance, comparatively small colonies of aphids with the individuals situated closely together along the stem of a young succulent plant, on a leaf petiole, or even on a leaf, were found often to contain a high percentage of winged forms even though the infestation was not very heavy nor did the plants show any visible effects resulting from the feeding of the insects so far as wilting or any lack of vigorous appearance is concerned.

Several tests were made to ascertain if crowding becomes an effective factor in stimulating wing development in this species primarily because it results in a depletion of the food supply. In each of these tests two heavily infested leaves of a cotton plant attached to the same branch were selected and all the aphids carefully removed. Immediately after the leaves were freed from all the insects 4 or 5 apterous individuals of a known apterous parentage were placed on one leaf and 30 to 40 comparable individuals on the neighboring leaf. In the former case the progeny produced were not allowed to become crowded at any time during development, while in the latter case none of the progeny were removed and a crowded condition thereby encouraged.

The results of these tests proved to be in accord regarding the following points: (a) the progeny of apterous parents will approach 100 per cent apterous if not crowded during development, when reared on a leaf that has sustained a heavy prior infestation; (b) the offspring of apterous parents which were reared on a leaf previously infested will approach 100 per cent apterous if not crowded during development; (c) the time required for the appearance of the alate form in the crowded progeny of apterous parents reared on a leaf previously infested by many insects, is practically the same as in case of no prior infestation of the food supply.

From these observations it will be noted that any changes wrought by the feeding of a dense population of this species, either in the amount or chemical composition of the food, available to the aphids subsequently placed thereon, did not manifest itself by affecting the ratio of forms produced.

Since the metabolic processes of a plant in manufacturing and storing up food elements are rather slow processes, any changes in the amount or character of food in a leaf resulting from the feeding of many insects will remain present for an indefinite period of time. However, since the ratio of forms of aphids reared on a food supply which had sustained a prior heavy infestation of insects, was not affected to any appreciable degree, it appears that crowding embraces another factor or factors through which it may become effective in stimulating wing development.

Summary of the Effect of Crowding

In the data presented above it will be observed: that in rearing individuals of *Aphis gossypii* of a known apterous monomorphic parentage of 16 generations or more under conditions of ample food and either fairly uniform or widely fluctuating temperatures, crowding during development resulted in an increased number of winged forms in every case; that the first generation offspring of the progeny of alate parents when reared under similar conditions, also contained a higher percentage of winged forms. The very positive effect of crowding aphids during development, on the ratio of forms produced under practically any given set of conditions indicates the conclusion: that crowding is a very potential, if not the dominant or controlling factor, in stimulating wing development in this species.

OBSERVATIONS ON THE EFFECT OF HUMIDITY

During the entire extent of the generation series studies, i. e., from October 10, 1925, to October 10, 1926, relative humidity conditions were recorded in conjunction with the temperatures. While the degree of fluctuation of the relative humidity in the laboratory frequently was greater than in case of the temperatures for the same period of time, nevertheless, it was often fairly uniform for periods of three or four consecutive days. When the relative humidity dropped below 40 per cent the aphids developed more slowly, but no winged forms appeared in response to this condition. In the insectary, where the temperatures approximated natural conditions, the per cent of relative humidity often ranged from 88 to 41 per cent in a 24-hour period; averaging from 60 to 70 per cent for periods of more than a week. When aphids were reared under these conditions, no correlation was found to exist between the per cent of relative humidity and the ratio of alate to apterous forms produced.

CONCLUSIONS

1. The normal tendency in *Aphis gossypii* is to produce offspring which do not develop wings.
2. The production of wings is dependent entirely upon environmental influences.
3. Starvation increases the number of winged forms in the progeny produced by apterous parents.
4. The offspring of alate parents revert to the normal tendency of the species, viz., the apterous form, with such puissance, that the effect produced by starvation in stimulating wing development is practically if not entirely counteracted.
5. Temperature within the limits of 70° F. to 90° F. does not affect the ratio of forms produced in this species.
6. Crowding is a very potential, if not the dominant or controlling factor in stimulating wing development in *Aphis gossypii.*
7. There is no correlation between the prevailing relative humidity in which the aphids are reared and the ratio of alate to apterous forms produced.

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