(Contribution from the Zoological Laboratory of the University of Michigan, Ann Arbor, Michigan, U. S. A.)

DURATION OF LIGHT AND THE WINGS OF THE APHID MACROSIPHUM SOLANIFOLII.

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The cycles of aphids commonly involve two principal features: (1) the periodic or occasional occurrence of gamic individuals (males, and females whose eggs require fertilization and are laid), the remainder of the cycle being characterized by parthenogenetic and usually viviparous reproduction, and (2) the alternative possibility that most females of the parthenogenetic phase may be winged or wingless.

Although these cyclical changes have been the subject of speculation for over a century, and of experiment for several decades, it is only within the last few years that light has been seriously considered one of the possible causes of such changes. The first investigator to use light in attempts to alter the cycle experimentally, so far as I can discover, was MARCOVITCH (1923). Stimulated, no doubt, by the important work of GARNER and ALLARD (1920, 1921) on the effects of duration of light on plants, he subjected *Aphis forbesi* to $7\,^1/_2$ or 8 hours of sunlight daily, keeping the insects in darkness in an outdoor ventilated chamber the remainder of the time. No record of the temperature in the light and in darkness is given, but MARCOVITCH apparently assumes that the difference would not have been more than 2^0 or 3^0 F. as in GARNER and ALLARD's experiments. After experiencing this treatment from February to May, the aphids began to produce gamic females, which laid eggs, though the normal time for such females in Tennessee, where the work was done, is November. No controls designed to show what would have occurred in normal length of day, or in light periods of other lengths, are mentioned. No males occurred in May in this experiment, but in June, in three (other?) species males were produced in experiments using a $7\,^1/_2$-hour day, though again controls showing the effect of other periods of light were lacking.

With respect to wings, MARCOVITCH obtained the following results. In June, when males appeared in three species under $7\,^1/_2$-hour illumina-

tion, the winged sexuparae (mothers of the gamic females) were also produced. For June, $7^1/_2$ hours represents a considerable shortening of the day. Nevertheless, the spring migrants of *Aphis sorbi* were held to have been produced as a result of lengthening of the day.

DAVIDSON (1924), using *Aphis rumicis*, exposed the aphids to 8 hours in addition to ordinary daylight, keeping other aphids as controls only in ordinary daylight. Sexual forms had appeared in this species in October, before the experiments began. However, during the experiment, which lasted from November until January, only wingless parthenogenetic females appeared, regardless of the duration of the light. The experiment was discontinued in January, the aphids where then kept in ordinary daylight and at a lower temperature than previously, and gamic forms were produced from February to June. No controls at the higher temperature were kept, to show that gamic forms would not have appeared any way, but DAVIDSON concludes that the lowering of the temperature was the cause of their occurrence.

DAVIDSON's own experiment from November to January would indicate no effect of duration of light. While he recognizes that probably sunlight, temperature and length of day govern gamic reproduction, his discussion of the work of MARCOVITCH calls attention to the possibility that duration of light affects the aphids indirectly, through its influence on the photosynthesis of the host plant, and that its effects on the aphids may be only nutritive.

With respect to wings, he appears to hold that in aphids in general light is of no influence whatever, for in a recent paper (DAVIDSON 1927b) he twice names temperature and nutrition as wing-producing agents, does not mention light at all, and states that intrinsic factors are primarily responsible for wings.

ACKERMAN (1926), in the course of experiments with temperature in relation to wings, mentions one experiment in which the plants used were grown in semi-darkness and, with the aphids on them, were put into a shaded chamber. All the aphids produced were wingless. ACKERMAN's experiments, however, were not designed to test the effect of light; that effect, if present, was incidental.

The above are, so far as I know, the only experiments or discussions which relate definitely to the effect of light as a wing-producing agent in aphids, aside from the preliminary statement of some of my own results (SHULL 1926). With ACKERMAN's experiments directed only toward temperature and physico-chemical properties of the body fluids, and DAVIDSON concluding that light has no effect on wing-production and only an indirect effect on gamic reproduction, the evidence that light is an important factor in the cycles of aphids so far comes chiefly from the experiments of MARCOVITCH. The absence of controls in his

experiments, the lack of certain knowledge of the temperatures involved, the possibility that normal periodicity of some sort resting on inherent factors exists, and the fact that as the experiments were conducted the differences in light must have been accompanied by differences in the aphids' nutrition, constitute weakness in this evidence which render the conclusions to be drawn from it somewhat uncertain. The experiments described in this paper were designed to exclude as many as possible of the uncertainties. Although both wings and the type of reproduction have been studied, this article includes only the experiments concerned with wing-production.

Apparatus.

The light employed in the experiments was furnished by electric lamps usually of 200-watt size. The curtains of the room were drawn so that the amount of daylight was probably negligible. The aphids were reared on potato plants in pots. These were put into chambers five sides of which were of wood, the sixth side being a thin glass-walled water-cell, filled with running water, to exclude heat. The electric lamp was set before this water-cell. Whatever slight rise of temperature might occur as a result of light in these chambers notwithstanding the water-cell was largely prevented by constant ventilation from the compressed air system.

Darkness was obtained by setting the plants under a paste-board cover which was ventilated in the same manner as the lighted chambers. A fall in temperature in these darkened chambers at night was prevented by hanging a small electric lamp near them. The distance of the lamp from the chambers was determined empirically and was changed with the seasons.

The temperature obtained in the above ways were ascertained from maximum-minimum thermometers read morning and evening. Temperatures in all the lighted chambers were found to be practically identical at any one time, though they varied during the day and night. In like manner, the temperatures in all the dark chambers were nearly identical at any one time. The temperature in the dark chambers covered a daily range about 3° C. greater than did the temperatures in the lighted chambers, but the mean temperatures over a long period of time differed by only two-tenths of one degree.

Early Recognition of Wings.

There are four instars before the adult stage of *Macrosiphum solanifolii*. The wings can be recognized in the third instar as rounded prominences at the anterior corners of the thorax. To test the certainty of this recognition, over 300 aphids in the third instar showing these prominences were set aside in continuous light to attain maturity. All of them

proved to be winged. Over 100 aphids without such prominences in the third instar were set aside in 8-hour light and, at maturity, proved to be without exception wingless. The light periods used were designed, as shown below, to reverse the condition of wings already arrived at, but did not do so. While immature aphids with these wing prominences have been recorded as certainly winged as early as the third instar, no aphid has been adjudged wingless until it reached the fourth instar or the adult stage. Considerable time has been saved in the experiments by determining the nature of the aphids before maturity.

Crude Comparison of Eigth-Hour and Twenty-four-Hour Illumination.

The first tests of the effect of duration of light were made by subjecting one group of adult aphids to 8 hours of light and 16 hours of darkness, and a closely related group to continuous light. They were kept thus for 4 or 5 days and all offspring produced in that time were reared and the presence or absence of wings recorded. In these early experiments, the aphids used were taken sometimes from 8-hour stocks, sometimes from 24-hour stocks; and the plants were not previously subjected to the period of illumination to be employed in the experiment. However, both halves of the experiments began with equal material. If either the aphids or the plants required any length of time to become adjusted to the experimental conditions before effects were produced on wing-production, the results of the experiments would thus be much less sharply defined than they should be. That such a period of adjustment is required by the aphids is shown by later experiments.

The combined results of these experiments, many times repeated, are shown in Table 1. There is a strong tendency for the offspring to be winged when the parents are reared in 8 hours light per day, and a very strong tendency to be wingless when the parents are continuously lighted. Later experiments show this tendency to be even stronger than is apparent in Table 1.

Table 1. The effect of 8 hours of light per day compared with continuous illumination of winged and wingless aphids upon wing-production in their offspring.

Parents	8 Hours of Light		24 Hours of Light	
	Wingless	Winged	Wingless	Winged
Wingless .	594	1282	2017	231
Winged .	69	44	263	23

Effects of Other Periods of Light.

The plants used in this experiment were alternated between light and darkness, 24 hours of each. One lot of wingless aphids was removed from one to the other of two such plants, and back again, so that the

aphids were continuously in darkness, except 5 or 10 minutes each day when the transfer was being made. A second lot of aphids was alternated between two other such plants at times which gave the aphids 2 hours of light and 22 hours of darkness. A third lot of aphids was similarly alternated between two plants so as to be in the light 5 hours, in darkness 19 hours. Other lots of aphids were alternated in like manner so as to be illuminated 8, 12, and 24 hours, respectively. The period of light for the aphids was in each case the last part of the 24 hour period of light to which the plant was subjected. Thus, aphids to be illuminated 8 hours were put on a plant which had already been in the light 16 hours, and 8 hours later the plant with the aphids on it was set in darkness. Each lot of aphids remained on each plant 24 hours, and therefore experienced every phase of any nutritive cycle that the plants passed through during that time. If the decrease and increase of nutrition during darkness and light, respectively, are uniformly spread over the entire period, the average nutrition of all the aphids should be identical. The various lots of aphids differed only (1) in the number of hours they were exposed to light and to darkness, (2) the time in the 24-hour cycle at which they were transferred from plant to plant, and (3) the possible total amount of nutrition if the nutritive changes in the plant are not evenly distributed over the periods of light and darkness. Experiments described later appear to show that the last two of these differences were of little, if any, consequence. Hence the results, which are shown in Table 2, are attributed to the duration of light.

Table 2. Showing the effects of various periods of illumination of the parent aphids upon wing-production in their offspring.

Hours of Illumination on Parents	Offspring Produced, in Hours After Beginning of Experiment							
	0—42 hours		42—114 hours		114—210 hours		210—306 hours	
	Wingless	Winged	Wingless	Winged	Wingless	Winged	Wingless	Winged
0	8	0	33	6	37	7	11	0
2	11	0	15	40	24	61	7	23
5	3	0	12	50	0	53	0	46
8	20	0	5	47	0	81	0	44
12	15	0	10	33	2	75	0	45
24	11	0	37	0	50	0	26	3

The output of the first 42 hours of this experiment, as indicated by later experiments, must probably be discarded because it shows only the effect of the previous illumination of the parents, which was 24 hours daily. Probably also a portion of the output of the second period (42—114 hours) was also produced under the influence of this same previous illumination. The last two periods (114—306 hours), however, should show only the effects of the experimental periods of light. The

offspring produced by parents lighted 5 hours or 8 hours were all winged, offspring of those lighted 12 hours were nearly all winged, while in continuous light the offspring were nearly all wingless. Two hours of light made nearly three-fourths of the offspring winged, while practically continuous darkness made nearly seven-eights of them wingless. It is probably also significant that, in the second period (42—114 hours), there is a greater proportion of winged aphids at 8-hour light than at either 5 or 12 hours, and that the longer or shorter the period of illumination is, above or below 8 hours, the lower the proportion of winged females is in that period. This no doubt means an earlier effect of 8-hour light, than of any other period, even when the ultimate effect is just as great, as it is with 5-hour and perhaps 12-hour illumination. The maximum of wing-production is therefore probably effected by about 8 hours of light, both longer and shorter periods produce a smaller effect, while continuous light and continuous darkness mostly result in winglessness.

Stage at Which Wings are Determined by Light.

The section of this paper entitled "Early recognition of wings" contains evidence that, once wings begin to appear in the third instar, it is probably too late to stop their development, and that if the third instar is reached without signs of wings, it is probably too late to acquire them. Whether, by beginning at an earlier age, it is possible to control wing-production in the lifetime of an individual is shown by the following test. Young aphids from wingless parents kept continuously lighted, within 8 to 14 hours after birth and hence at ages averaging not over 6 hours, were divided into two lots, one lot being reared in 8 hour light, the other in 24-hour light. The nature of the aphids at maturity, together with control groups showing what should be expected of 8-hour and 24-hour illumination, is shown in Table 3.

Table 3. Showing effect of altering duration of light shortly after birth, upon production of wings.

	Light Hours of Parents	Light Hours of Offspring	Nature of Offspring	
			Wingless	Winged
Experiment	24	8	75	3
		24	69	1
Controls	8	8	1	147
	24	24	108	1

The controls in the lower lines of Table 3 confirm the conclusion reached above that 8-hour light applied to the parents causes the offspring to be nearly all winged, while 24-hour illumination of the parents

causes nearly all of the offspring to be wingless. The excess of winged aphids in the first line of the same table over the number of winged individuals in the second line is so slight, compared with the great difference between the controls, that it must be regarded as probably accidental. Duration of light does not, therefore, modify wing-production in these aphids after they are 6 hours old. Moreover, since about one-eleventh of the 78 aphids recorded in the first line of Table 3 must have been changed to 8-hour light within their first hour after birth, any immediate effect of the change of light ought to have disturbed the ratio of winged to wingless very appreciably. To indicate such an effect accurately, about 7 of the offspring in the first line should have been winged. It is conceivable that the slight excess of winged offspring in the first line (3 in 78 as against 1 in 70) was due to an early effect of the change of light; and if a calculation on this basis were justified, it would indicate that a change of light could not be effective later than about 20 minutes after birth. Such a calculation with the small numbers of winged individuals involved is presumably not warranted.

To ascertain whether wings are determined at some time before birth, 10 wingless females which had been kept for 8 days in continuous light, and during that time had produced 126 wingless offspring (no others), were divided into two lots of 5 each, one lot being continued in 24-hour light, the other changed to 8-hour light. The offspring were isolated at frequent intervals and reared in separate groups. Table 4 shows their nature with respect to wings.

Table 4. Showing the nature of the progeny of wingless aphids first kept in 24-hour light and then changed to 8-hour light, together with controls which were continued in 24-hour light. The offspring were isolated at frequent intervals, as indicated, and separately reared.

Hours After Change of Light	Progeny of Parents Changed to 8-hour Light		Progeny of Parents Continued in 24-hour Light	
	Wingless	Winged	Wingless	Winged
0—22	14	0	16	0
22—34	8	0	16	0
34—46	10	0	14	0
46—58	7	6	12	0
58—70	1	6	6	0
70—81	0	6	7	0
81—153	0	42	45	0
153-end of life	0	8	30	0

The transition from wingless to winged offspring did not occur at the same time in all parents, since one wingless daughter was produced after six winged ones. Ignoring this irregularity, the change must have

come about the middle of the fourth period, or about 52 hours after the change to 8-hour light. Four other experiments of the same kind yielded approximately 46 to 48 hours as the time that must elapse after the change of duration of light before offspring are born whose wing-determination is affected by the change. Three of these experiments involved wingless, the fourth one winged, parents, and in two of the experiments one lot was changed from 8-hour to 24-hour illumination, another lot changed from 24-hour to 8-hour illumination. The time required to bring about a change in wing-production was about the same, that is, approximately 46 to 48 hours, for both winged and wingless parents and for both increase and decrease of the period of light.

A further repetition of this test was made later (in summer) and the time required for wing-production to be affected was approximately 68 hours. Whether the greater length of time required was due to the higher temperature which prevailed then is being investigated as part of the problem of temperature effects in general.

The above facts indicate that wings are determined in the embryo sometime within the last 46—68 hours before birth. If the action of the light on wings is immediate, then determination occurs at the beginning of that 46-hour or 68-hour period. If, after the light is changed, there must be a period of adjustment of the parent, or the embryo, or the plant, or any combination of two or more of these, to the new conditions before the wings are affected, then actual final wing-determination occurs just so much nearer the time of birth. If any such adjustment takes place, and some condition or set of conditions can be found that hastens the adjustment, then wing-production may be affected in less than the two days required in the above experiments. In experiments described later, combining light and starvation, the time required to alter wing-production has been decreased to 24 hours or even less.

In two of the experiments described above, in which some parents were changed from 24-hour to 8-hour light, others changed from 8-hour to 24-hour light, each female produced 5 or 6 offspring before an alteration of the wings took place. A number of very similar adult females (of the same age as the parents) were killed at the time the light was changed, and were dissected. In each one the oldest five or six young were advanced enough to have pigment in the eyes, while all younger ones were without pigment. At this time the appendages are fully formed, and the body is very similar to that of the young aphid at birth. This appears to show that wings are not determined until body, legs and eyes are well formed. A study of the histology of the wing-bud region at this stage has been commenced.

Is Nutritive Condition of Plant a Wing-Producing Factor?

The experiments described in the preceding sections do not show whether the effect of light upon wing-production is a direct effect upon the aphids, or whether the aphids respond to changes in nutrition due to action of the light upon the plants. If the action of light is upon the plant first, it might be supposed that the two days (more or less) which must elapse after a change of light, before young are born whose wings show a response to that light, is the time required for the plant to become sufficiently adjusted to the changed condition to be able to modify the wings of aphids whose parents feed upon it. Or a portion of that time, at least, might be required by the plant for some change within itself, and the balance of the two days be necessary for adjustment within the aphids. In either case, if the duration of light is changed for the aphids, and they are put upon plants which have already been subjected to the new period of illumination for some time, the response of the aphids in wing-production ought to occur more quickly than if the insects are put an plants that have not been subjected to the new period of light and must therefore still undergo their adjustment to it.

Advantage was taken of this presumptive effect in the following experiment. Two lots of aphids from the same source, which was a line that had been in continuous light for ten days, were put in 8-hour light, one lot on a plant that had been in 8-hour light for some time, the other lot on a plant which had been in continuous light for an equal length of time. Another experiment was performed in which the aphids were changed from 8-hour to 24-hour light, one group being put on a plant accustomed to 8-hour light, another lot on a plant previously grown in 24-hour light. Table 5 gives the results of both experiments.

In the first of these experiments, the change from wingless to winged offspring on the plant which was previously in continuous light (upper right quarter of Table 5) occurred presumably at about the middle of the second period, and may therefore be estimated to have taken place about 49 hours after the change to 8-hour illumination. The time of change from wingless to winged offspring on the plant previously in 8-hour light (upper left quarter of Table 5) can not be so easily computed because two wingless offspring were born in the second period after 11 winged ones in the first period. If these two late wingless aphids be ignored, and the computation be based only on the aphids of the first period, the change to wings must be regarded as occurring about 31 hours after the change of light. If the first two periods be combined and the computation be based on the total numbers of winged and wingless offspring, the beginning of wing-production would appear to have happened about 29 hours after the change of light-duration. This first experiment

Table 5. The change from wingless to winged offspring, or *vice versa*, as influenced by previous illumination of the plants on which the aphids are raised. If the action of the light is on the plants first, and only indirectly on the aphids, the left side of the upper part of the table and the right side of the lower part should show an acceleration of the change in wing-production.

Change of Light on Parents	Hours After Change of Light	Nature of Offspring			
		On plant previously in 8-hour light		On plant previously in 24-hour light	
		Wingless	Winged	Wingless	Winged
24-hour to 8-hour	0—44	26	11	39	0
	44—54	2	3	5	5
	54—264	0	94	0	112
8-hour to 24-hour	0—44	36	30	30	32
	44—55	16	0	17	1
	55—68	14	0	12	0
	68—96	45	0	27	5
	96—121	24	0	17	0
	121—192	6	0	5	2

by itself, therefore, would appear to favor the conclusion that rearing the aphids on a plant which had had an opportunity to become adjusted to 8-hour illumination before the experiment began had hastened the development of wings by about 18 or 20 hours.

The second experiment, however, shows a smaller difference and in the opposite direction. On the plant previously kept in 8-hour light (lower left quarter of Table 5) only 20 hours appear to have elapsed until wing-production ceased. On the plant already presumably adjusted to the 24-hour light (lower right quarter) it is difficult to calculate the time of cessation of wing-production because wings never did entirely cease to be produced, even to the end of the experiment. If the small number of winged individuals that were scattered along through the whole latter part of this experiment be ignored as probably due to some condition not connected with the light or the condition of the plant, and the calculation be based only on the output of the first 44 hours, then about 22.7 hours would appear to be the time necessary for wing-production to stop. If any of the later groups be combined with the first, and the time of change to winglessness be computed from their combined numbers, the time required for the change to be produced is in every such combination more than the 22.7 hours based on the first group alone. In whatever manner the period required for cessation of wing-production be calculated, therefore, it was longer on the plant previously adjusted to the new condition (24-hour light) than it was on the plant which presumably had to undergo this adjustment after the experiment began.

A third test of this sort was made, by changing aphids from 24-hour

to 8-hour light, later (in summer) when the temperature was higher, and the period required for wing-production to be affected was, as previously stated, considerably longer, but this period was almost exactly the same (about 68 hours) on the plant previously adjusted to 8-hour light as on that which had previously been kept in continuous light.

The irregular and contradictory results of these tests are interpreted to mean that the alteration of nutritive conditions within the plant is not the agent directly affecting wing-production, or is at most only a minor agent easily counteracted by other influences. This inference is greatly strengthened by other results described below.

Action of Light Directly on Aphids.

Direct action of light upon the aphids was largely separated from indirect influence through the plant in the following several experiments.

Two lots of wingless aphids, previously in 8-hour light, were kept, beginning less than two days after emergence as adults, in continuous darkness for 7 days, except for about 5 minutes three times a day. One of these lots was shifted from one to another of three plants which were being lighted 8 hours and darkened 16 hours daily. The aphids were on each plant during the first 8 of its 16 hours of darkness. The second lot of aphids was transferred from one to another of three similar 8-hour plants, but at such times that the aphids were on each plant during the last 8 of its 16 hours of darkness. The latter lot of aphids should have had less abundant nutrition than the former.

As controls, two other similar groups of aphids were reared, one continuously on 8-hour plants, the other continuously on 24-hour plants. Table 6 shows the results.

Table 6. Showing the effect of nearly continuous darkness on wing-production in aphids, fed on plants that have just been removed from the light, and on plants that have been darkened for some hours, as compared with one another and with aphids in 8-hour and 24-hour light.

Illumination in Hours		Period in Which Aphids Were on Plants	Offspring			
			First 2 days		Next 5 days	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged
8	0	First half of dark period	0	72	44	41
8	0	Last half of dark period	3	77	28	22
8	8	Continuously on plant . .	0	60	3	92
24	24	Continuously on plant . .	0	51	39	47

Presumably only the offspring of the last 5 days are to be used in judging of these results. Comparison of the first two lines of the table indicates that the plants which were darkened 8 hours before aphids were put on them bore a somewhat smaller percentage of winged offspring than did the plants which were illuminated up to the time when aphids were put to them. Since the latter plants must have furnished better food than did the former, and since, if the plants are supposed to affect wing-production by modifying the food of the aphids, reduced nutrition must be held to favor wings, the above experiment would indicate that the plants have no influence upon wing-production. The very slightly earlier occurrence of wingless individuals in the second line of Table 6 could be interpreted as due to the previous 8-hour preparation of the host plant in darkness before the aphids were put on it, but to take advantage of that possible interpretation it would be necessary to assume that lowered nutrition in the plant favors winglessness. Since 8-hour illumination produces more wings than does 24-hour illumination, such a relation between nutrition and wings as has just been suggested for Table 6 can not be assumed.

Incidentally this experiment (Table 6) also shows that continuous darkness is as effective in preventing the production of wings as is continuous light (cf. lines 1, 2, and 4 in table 6), a corroboration of line 1 of Table 2.

A second experiment designed to distinguish direct action of light upon the aphids from indirect action through the plants was the following. A group of wingless aphids which had been all their lives in 8-hour light were divided into four lots. One lot was kept constantly in the light by transferring them three times a day from one to another of three plants each of which was lighted only 8 hours a day. The second lot was kept in continuous light on three plants that were also in continuous light, but the aphids were transferred from one plant to another three times a day. The third lot was in 8-hour light, but was changed three times a day from one 8-hour plant to another, being on one plant during its lighted period, and on the other two plants during different parts of their 16-hour period of darkness. The fourth lot was kept in continuous darkness (except about 15 minutes a day while transfers were being made) on 8-hour plants, the aphids being on each of three plants during its second 8 hours of darkness. The offspring of the four lots are recorded in Table 7.

Comparison of the first two lines shows that the period of illumination of the plant makes little difference in the percentage of winged offspring produced on it. Indeed, what difference there is in the direction opposite to that which would be expected from other experiments, since continuous light in those experiments greatly reduces or even ex-

cludes winged offspring. Line 3, as compared with line 1, shows that duration of the illumination of the aphids affects very considerably the production of wings in their offspring, though the effect is not so great in this experiment as in most others.

Continuous darkness is again shown, in line 4 as compared with line 1 or line 2 of Table 7, to reduce wing-production about as much as does continuous light, just as in Tables 2 and 6.

Table 7. Showing the effect of 8-hour and 24-hour illumination of aphids and the plants on which they feed, and of continuous darkness, upon wing-production in the aphids' offspring.

Illumination, in Hours		Aphids Were on Each Plant During	Offspring			
			0–52 hours		52–174 hours	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged
8	24	8-hour lighted period	19	17	64	3
24	24	$^1/_3$ of lighted period	23	15	61	6
8	8	8-hour lighted period of one plant, different parts of dark period of other two	1	26	26	19
8	0	Second half of dark period	5	29	29	2

The only marked evidence that the period of illumination of the plant had an effect on wing-production is derived from the following experiment. Wingless aphids previously in continuous light were divided into two groups. One group was kept in continuous light, but on plants that were illuminated only 8-hours daily, by shifting them from plant to plant every 8 hours. The second group was put on a plant that was continuously lighted, but the aphids were lifted from this plant and set back on it every eight hours. The latter precaution was taken in order that both groups might be mechanically disturbed to the same degree. Table 8 records the offspring.

Table 8. Showing the effect of different periods of illumination of plants upon wing-production of aphids borne on them.

Illumination, in Hours		Offspring			
		Of first two days		Of next six days	
Of plants	Of aphids	Wingless	Winged	Wingless	Winged
8	24	44	9	76	76
24	24	58	0	151	0

Only the last two columns presumably show the results of the experimental treatment, and these appear to indicate a striking increase

of winged offspring on the 8-hour plants (first line). Since the other experiments bearing on this point all show that the duration of illumination of the plant has little or no effect on wing-production, the differences involved in this experiment should be carefully stated. The only possible difference in treatment between the two lots of aphids seem to be these: (1) one lot was reared on plants lighted 8 hours, the other on plants lighted 24 hours daily; (2) the 24-hour plant was the more crowded, since approximately as many offspring were produced on one plant as upon the three 8-hour plants combined; and (3) changing the aphids of the first lot from one plant to another may have been a greater disturbance than lifting them from one plant and returning them to the same plant. How much effect the second and third differences might have has not been determined. Crowding on the plant has usually been held by other students of aphids (see ACKERMAN 1926, pp. 14—20, for his own experiments and citations of other articles) to cause wings to be produced, though here the effect is in the opposite direction. Tests of mere mechanical disturbance have so far shown no effect, though it is possible that, in combination with certain other conditions not present in these separate experiments, mechanical or nutritive disturbance may increase wing-production. At present, therefore, the experiment of Table 8 is not in harmony with the remaining experiments bearing on the effect of the plant on wing-production.

Starvation and Light, Separately and Combined.

Two equivalent lots of wingless aphids which had been all their lives in continuous light were removed, as soon as they became adult, to plants that had been in 8-hour light. Both plants were continued in 8-hour light, but the aphids were removed from the plants during the latter's 16-hour period of darkness, put into cotton-stopped vials, and then returned to the plants when these were set in the light again. One of the vials with the aphids in it was kept dark during the 16 hours, the other was put in the light. The former lot of aphids was subjected, therefore, to 8-hour illumination, the latter lot to continuous light. The two lots were treated alike in that both were starved 16 hours and fed 8 hours, and that both were fed on plants that were illuminated only 8 hours daily; they differed only in that one lot was in the light 24 hours, the other lot only 8 hours. The experiment was performed twice, with the results shown in Table 9.

There is a very large majority of winged offspring in the 8-hour light, and a considerable majority of wingless aphids in 24-hour light. Since only the period of illumination of the aphids differed, and there was no difference in the illumination of the plants, it is clear that a very large part of the influence exerted by duration of light on wing-production is

Table 9. Showing the offspring of two lots of aphids, both starved 16 hours and fed 8 hours daily, both fed on plants that were illuminated 8 hours daily, but one lot being in the light 8 hours, the other 24 hours, each day.

Experiment No.	Days After Change of Light	Offspring			
		8-hour light		24-hour light	
		Wingless	Winged	Wingless	Winged
1	0—4	2	50	27	29
	4—7	0	37	12	7
2	0—2	21	3	19	8
	2—6	5	43	20	2
	Total	28	133	78	46

exerted *directly* on the insects. A new factor, starvation, was introduced into this experiment, and there was no simultaneous test of starvation alone — a defect remedied in the next experiments; but this additional factor does not in the least vitiate the conclusion that light acts directly on the insects and produces a very large effect in this way.

The effects of light and starvation, separately and in combination with one another, were discovered from the following experiment. Four lots of wingless aphids, reared all their lives in continuous light, were put on four plants. Two of the plants were illuminated 8 hours, two of them 24 hours, each day. The aphids were kept on the plants only 8 hours daily during or within the period of illumination of the plant, and in vials stopped with cotton plugs the other 16 hours. One of the lots fed on 8-hour plants was kept in darkness while in the vial, the other lot in the light. One of the lots fed on 24-hour plants was kept dark while in the vial, the other lot was in the light. All aphids were thus starved 16 hours and fed 8 hours; but the feeding of two of the lots was on 8-hour plants, that of the other two lots was on 24-hour plants, and some of the aphids were in the light only 8 hours, others 24 hours a day. Simultaneously a group of equivalent aphids was raised in continuous light and with continuous feeding, and produced only wingless offspring. A group fed continuously in 8-hour light was unfortunately not kept in this experiment. The results of the experiment appear in Table 10.

If one discards the offspring produced in the first 51 hours as being determined by the treatment which the parents received before the experiment began, it is apparent that the amount of wing-production chiefly depends on the illumination of the aphids themselves. Comparison of line 2 with line 4, which differed only in the illumination of the plants, shows that nearly identical results were produced in them (last two columns of Table 10). Lines 1 and 3, which likewise differed only in the light-period of the plant, diverged somewhat in that the

Table 10. Showing effect of starvation (16 hours daily) and of 8- or 24-hour illumination of plants and aphids, upon wing-production in their offspring.

Illumination, in Hours		Offspring Produced, in Hours After Beginning of Experiment			
		0—51		51—159	
Of plants	Of aphids	Wingless	Winged	Wingless	Winged
8	8	28	0	2	46
8	24	17	9	23	3
24	8	27	0	7	26
24	24	15	10	11	1

24-hour plant bore a larger percentage of wingless aphids. Nevertheless, this percentage is far below that (100%) which the control experiment mentioned in text produced, in which the aphids remained undisturbed on the plant in 24-hour light.

Lines 1 and 2 of Table 10 show what a difference of illumination of the aphids alone accomplishes. The great excess of winged offspring in the former, and of wingless ones in the latter, fall only a little short of the results of 8-hour and 24-hour illumination of aphids on plants which also are lighted 8 and 24 hours, respectively. Comparison of lines 3 and 4 leads to the same conclusion, only a little less strikingly. It is clear that the effect of light on the aphids directly is much greater than its influence on them indirectly through the plant.

There may be some doubt, indeed, whether any influence indirectly through the plant is demonstrated in Table 10. The aphids there recorded were being starved two-thirds of the time, and this may have had an effect on wing-production. In the discussion of Table 10, the output of the first 51 hours has so far been rejected. It is worthy of note, however, that in lines 2 and 4 more than one-third of the offspring produced in this period were winged. The parents were being subjected to 24-hour light which, in all other experiments so far, excluded winged offspring almost completely. Here (Table 10) it is precisely those aphids which were thus continuously lighted that produced these winged offspring soon after the change of light. It appears as if continuous light combined with starvation[1] produces wings quickly, though, if so, it is an effect that is greatly diminished or completely lost later.

[1] Although in this description starvation has been constantly referred to as the agent which, if occurring in the light or in conjunction with continuous light, causes wings to appear quickly, I am not at all convinced that starvation is the real agent. Starvation was not sought in the experiments; it was merely incidental to one method of giving the aphids a period of illumination different from that of their host plants. In ignorance of what feature of this treatment hastened wing-production I have, for brevity, named the obvious feature of starvation. Other possibilities are being tested in the continuation of the work.

If the winged offspring in lines 2 and 4, in the first 51 hours, are due to the change of light or to starvation, or to both, and not merely to accident or to some unknown agent operating earlier, then the effect of these changes is produced in much less time than the approximately 48—68 hours which the earlier experiments indicated was necessary. In line 2 it would appear that only 34 hours, and in line 4 only about 31 hours was necessary. This would mean that wings are determined not earlier than 31 or 34 hours before birth.

The production of winged aphids in so short a time as a result of applying starvation and continuous light to their parents seemed so likely to give ultimate evidence regarding the fundamental nature of the process involved, that it was deemed desirable to repeat the test still further. For the greater safety of the aphids in these tests, the period of illumination was 12 hours, so that the period of starvation could be reduced to 12 hours. A group of wingless aphids which had been in continuous light for some days was divided into six lots. One lot was put on a plant and set in the light for 12 hours, after which the plant was put in darkness for 12 hours and the aphids removed to a cotton-stopped vial in darkness for 12 hours. At the end of this second 12-hour period the aphids were returned to the plant and both were set in the light. The second lot was put on a plant in the light for 12 hours, and then removed to a vial and continued in the light for 12 hours while the plant was kept dark. The third lot was put on a plant for 12 hours in the light, then removed to a vial which was kept dark for 12 hours while the plant was continued in the light. The fourth lot was put on a plant in the light for 12 hours, then removed to a vial and both plant and aphids continued in the light for the next 12 hours. These four lots were, consequently, being starved 12 hours daily, some of them being in the light and others in darkness during the starvation, and some of them being fed on 12-hour plants, others on 24-hour plants, during the remaining 12 hours.

The other two lots of aphids were fed continuously on their respective plants, one in 12-hour, the other in 24-hour light, these aphids being merely lifted with a brush and set back on the plant again whenever the other four lots of aphids were handled.

The experiment described above was performed three times. The results are given in Tables 11, 12, and 13.

In interpreting these experiments, attention may be first called to those aphids which were allowed to remain on their plants all the time, recorded in the last two lines of each table. These unstarved aphids, if in continuous light, produced, with a single exception, wingless offspring; if in only 12-hour light, they produced, after the lapse of two or three days (at most), almost exclusively winged offspring. These results are in harmony with all other simple tests of the effect of duration

Table 11. Showing the effect, upon wing-production, of different periods of illumination of aphids and plants, with and without starvation.

Illumination, in Hours		Aphids Were on Plant During	Offspring, in Hours After Beginning of Experiment							
			0—24		24—48		48—168		168—264	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged	Wingless	Winged	Wingless	Winged
12	12	12-hr. lighted period, in vial in darkness other 12 hrs.	0	0	17	3	1	59	0	22
12	24	12-hr. lighted period, in vial in light other 12 hrs.	0	0	8	2	19	9	9	5
24	12	1/2 of lighted period, in vial in darkness other 12 hrs.	2	0	17	0	2	45	1	20
24	24	1/2 of lighted period, in vial in light other 12 hrs.	2	1	6	4	9	15	4	1
			0—60		60—180		180—264			
			Wingless	Winged	Wingless	Winged	Wingless	Winged		
12	12	All the time	6	2	0	47	0	9		
24	24	All the time	12	0	57	0	20	0		

Table 12. Showing the effect, upon wing-production, of different periods of illumination of aphids and plants, with and without starvation.

Illumination, in Hours		Aphids Were on Plant During	Offspring, in Hours After Beginning of Experiment							
			0—24		24—48		48—120		120—216	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged	Wingless	Winged	Wingless	Winged
12	12	12-hr. lighted period, in vial in darkness other 12 hrs.	2	0	3	0	0	1	0	0
12	24	12-hr. lighted period in vial in light other 12 hrs.	2	6	6	2	8	5	12	3
24	12	$^1/_2$ of lighted period, in vial in darkness other 12 hrs.	6	0	6	0	1	13	3	11
24	24	$^1/_2$ of lighted period, in vial in light other 12 hrs.	5	0	0	1	3	4	3	0
12	12	All the time	9	0	10	0	1	10	0	8
24	24	All the time	0	0	2	0	2	0	0	0

of light. Any wide divergence from them in the other parts of these experiments may therefore be safely attributed to starvation, to the illumination, or to a combination of these factors.

Comparison of lines 1 and 2 of each table shows the effect of starvation combined with 12-hour and 24-hour illumination, when the feeding is done on 12-hour plants. In Table 11 there is no obvious *early* difference between 12-hour and 24-hour illumination; and with respect to the later offspring, the striking feature is the production of so many winged offspring in line 2, many more than is usually done by parents that are illuminated continuously.

In lines 1 and 2 of Table 12, there is a striking occurrence of winged aphids in the output of the first 24 hours when the starvation occurred in the light, as against no winged offspring until after 48 hours

when starvation occurred in darkness. The 24 hours referred to in the first two columns of offspring in these tables includes the 12 hour period of starvation with which the experiment started, and the succeeding 12 hours in which the aphids were on the plants. With only half a dozen exceptions, all of which occurred late in the families of their respective parents, all births occurred on the plants, not in the vials during starvation. The 8 aphids born in the first 24 hours of line 2, Table 12, were therefore born in the period from 12—24 hours after starvation commenced, or 0—12 hours after the first period of starvation ended. If the 8 births were distributed uniformly over this 12-hour period, the first winged individual must have been born not later than about 4 hours after the end of the first starvation period, or not later than about 16 hours after the beginning

Table 13. Showing the effect, upon wing-production, of different periods of illumination of aphids and plants, with and without starvation.

Illumination, in Hours		Aphids Were on Plant During	Offspring, in Hours After Beginning of Experiment							
			0–36		36–48		48–144		144–190	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged	Wingless	Winged	Wingless	Winged
12	12	12-hr. lighted period, in vial in darkness other 12 hrs.	14	0	7	0	4	8	0	1
12	24	12-hr. lighted period, in vial in light other 12 hrs.	7	3	3	2	7	6	2	0
24	12	1/2 of lighted period, in vial in darkness other 12 hrs.	13	0	2	0	14	9	0	3
24	24	1/2 of lighted period, in vial in light other 12 hrs.	13	0	3	9	1	13	2	1
12	12	All the time	15	0	5	0	20	17	0	11
24	24	All the time	11	0	3	0	41	0	14	1

of starvation. If for some reason only one of the parents used in line 2 (there were only 2 parents in this experiment) produced winged offspring, it must have begun to produce them immediately.

In lines 1 and 2 of Table 13 is a similar comparison of starvation in the light with starvation in darkness. After starvation in darkness, no winged offspring are produced (line 1) until at least 48 hours have elapsed, and that is late enough to be accounted for by 12-hour illumination alone, without starvation, as discovered from earlier experiments. After starvation in the light (line 2), however, 3 of the 10 offspring born in the first 24 hours were winged. If the same calculation be made for these as for the 8 born in the first 24 hours in line 2 of Table 12, it appears that the first winged aphid was born not later than about 9 hours after the end of the first starvation period, or not later than about 21 hours after the beginning of starvation.

In the preceding comparisons, the aphids involved were all placed on 12-hour plants during their feeding period. Similar conclusions must be drawn from those experiments in which 24-hour plants were used. In lines 3 and 4 of Table 11, it is shown that one winged aphid was produced within the first 24-hour period when starvation occurred in the light, while no winged offspring occurred until after 48 hours when the starvation took place in darkness. In lines 3 and 4 of Table 12, one winged aphid is recorded as produced within 48 hours after starvation in the light, while no winged offspring appeared until after 48 hours when starvation occurred in darkness. The same difference is shown more strikingly in lines 3 and 4, Table 13.

That no hastening of the production of winged offspring in these starvation-light experiments was caused by starvation in darkness is indicated by comparing lines 1 and 5 of Table 11. The unstarved parents (line 5) produced winged offspring within the first 24 hours of the experiment, and only winged offspring after 24 hours: while parents starved in darkness (line 1) produced no winged offspring until after a (calculated) lapse of about 44 hours. In Tables 12 and 13, the first winged offspring are shown occurring at about the time in line 5 as in line 1. The contrasted parents in all these cases were alike in being in the light 12 hours and in being on 12-hour plants whenever they fed. They differed only in that some were starved 12 hours (in darkness) while others were fed during the same 12 hours (in darkness). No striking effect was produced by this starvation, certainly no acceleration of the production of winged offspring.

In addition to accelerating the production of winged offspring, starvation in the light also increased the total proportion of winged individuals. Wether these effects were due to starvation while in the light, or to a combination of starvation with continuous illumination can not

be ascertained from the experiments. The test necessary to discover this (starving the aphids in the light, then feeding them in darkness) was not made, but is now in progress.

One possible interpretation of Tables 10—13 that has not been mentioned is that starvation in the light may accelerate a change from whatever has been occurring previously, rather than that it accelerates wing-production. This possibility was tested by performing the same experiments as those in Tables 11, 12 and 13, but with a stock of aphids that had been in 8-hour light for some time. Eight hours of light and 16 hours of starvation were substituted for 12 of each as in the previous experiments. Such aphids would continue to produce winged offspring until the conditions of the experiment had had time to produce some other result. Table 14 contains the data from this experiment.

Lines 1, 3 and 5 of this table (14) exhibit little difference; perhaps there is a significantly larger percentage of winged offspring as a result of the starvation in darkness (lines 1 and 3), especially in line 3 where all the offspring are winged after the first 27 hours.

Comparison of lines 2 and 4 with line 6 almost certainly indicates a prolongation of the

Table 14. Showing the effect, upon wing-production, of different periods of illumination of aphids and plants, with and without starvation. The aphids used as parents had been in 8-hour light prior to the beginning of the experiment.

Illumination, in Hours		Aphids Were on Plant During	Offspring, in Hours After Beginning of Experiment					
			0—27		27—51		51—247	
Of plants	Of aphids		Wingless	Winged	Wingless	Winged	Wingless	Winged
8	8	8-hr. lighted period, in darkness in vial other 16 hrs.	2	12	0	27	1	44
8	24	8-hr. lighted period, in light in vial other 16 hrs.	2	11	2	16	39	9
24	8	1/3 of lighted period, in darkness in vial other 16 hrs.	3	20	0	19	0	58
24	24	1/3 of lighted period, in light in vial other 16 hrs.	4	9	10	11	35	6
8	8	All the time	1	10	2	21	5	66
24	24	All the time	4	2	9	3	89	2

production of winged offspring by the parents starved in the light. In the second time-period of the experiment (27 to 51 hours) the majority of the offspring of parents starved in the light (lines 2 and 4) were still winged, while the offspring of the unstarved parents (line 6) were by this time already mostly wingless. Apparently, therefore, starvation in the light must be regarded as a factor favoring wing-production, not merely as provocative of change (especially, quick change). In addition, this experiment and the preceding ones show that starvation in the light does not merely accelerate whatever change is brought on by change of light, but that it definitely favors wing-production.

While it is clear that starvation in light does induce and accelerate wing-production, the foregoing analysis of the experiments which show that this in true should not be permitted to obscure the fact that, notwithstanding any effect of starvation, the effect of continuous light is to prevent wing-production. Even in those experiments where starvation in light most clearly induces wings, the offspring are still prevailingly wingless. This may be interpreted to mean that continuous illumination is a stronger influence than is starvation in combination with light.

It should also be remarked, in connection with the experiments with starvation and light that by means of them the period within which the actual determination of wings must occur has been considerably shortened. From the experiments with light-duration alone (Tables 3 and 4), it was inferred that wing-determination occurs not earlier than 46—68 hours before birth. With starvation and light combined, as shown in Tables 10—13, it has been possible to induce wings in offspring born in less than 24 hours — even as quickly as 16 hours — after the starvation began. It seems necessary, therefore, to conclude that wing-determination occurs within the last 16 hours before birth. All that such a statement can mean, of course, is that the agents so far discovered to be capable of inducing or preventing wing-development can not do so before or after the period named.

Discussion.

It is unnecessary to review the entire literature on wing-production in aphids, since that has been ably done up to very recent years by ACKERMAN (1926) in connection with his temperature experiments and physico-chemical tests, and by EWING (1926) in a general review of the subject. The papers bearing directly on the effect of light have been mentioned in the introductory paragraphs of this paper. There remain a few features of the cycle to which attention has been previously called by various writers, to which the new work with light may perhaps be related.

The aphid cycle is commonly described as involving winged migrants

in the spring, by which the species is transferred from its primary to its intermediate host, followed by generations of wingless females during the summer, and then winged return migrants in the late summer or fall. For species which respond to light as *Macrosiphum solanifolii* does, it is hardly necessary to assume any other factor than duration of light to explain these changes, since the days in spring and late summer are relatively short, those of early summer longer. It is not proposed, however, to regard light-duration as the sole factor; it is not unlikely that temperature will be found to operate to bring about precisely the same changes, thereby accentuating the changes, and other factors are not improbable.

The production of wings in response to short periods of illumination may also explain the progressive increase in the number of winged females appearing in successive generations during the summer, which occurred so strikingly, particularly in one season, in some of my former experiments (SHULL 1918). The progressive decrease in the duration of daylight from the latter part of June on through the season may well have been the reason for the increase in winged females. That is a result which would vary with the weather, since much cloudy weather might bring on many winged females out of season, and such progressive increase in wing-production would be expected to be clearly marked only when the cloudiness is somewhat regularly distributed.

It would be easy, of course, to overdo the environmental explanation of wings. DAVIDSON (1927b) is of the opinion that wings are due to intrinsic factors chiefly. That something else than the outside environment helps to produce them is shown by the fact (SHULL 1918) that when a winged and a wingless female *Macrosiphum* are raised under identical conditions, these conditions being such that some (not all) of the offspring of either or both of these females will be winged, the wingless female almost always produces more winged offspring than the winged female does. This difference can not be hereditary, in any strict sense, but is probably due to some physiological difference closely — perhaps absolutely — bound up with the presence or absence of wings. DAVIDSON no doubt uses "intrinsic" in some such sense as this.

Reference to the stage at which wings are determined is also made by DAVIDSON, when he states that conditions affecting the parents and the early development of the offspring are responsible for their appearance or non-appearance. To make his statement more accurate, in case my results with *Macrosiphum* are general, it should be specified that the "early development of the offspring" which is referred to is part of that which occurs before birth.

Discussions of the evolution of the cycle of the aphids should, in view of the effects of light, be conducted with caution. DAVIDSON (1927b)

because of the regularity with which winged females appear at certain seasons, concludes that "established intrinsic factors" insure their development at the times when migration should occur. A smaller burden will be put upon intrinsic factors if it is realized that short days in spring and late summer and longer days in early summer are thoroughly established. If temperature differences work in the same way, they too are in the long run established, subject to more variation than is length of day. Still more caution is required in explaining the differences in the cycles of the same species or closely related forms in different regions of the world. Such differences appear to be regarded as the results of evolution by SCHNEIDER-ORELLI and LEUZINGER (1926), MORDVILKO (1927), and DAVIDSON (1927b). Referring the form of the cycle to evolution, while no doubt partly justified, will only serve to delay discovery of the part played by the climatic differences of the regions involved. More progress in gaining an understanding even of the evolution of the cycle will be made by ascertaining first as accurately as possible the physiological conditions under which the cyclical changes occur.

There is little value in speculating now upon the nature of these physiological features in their relation to light, particularly since they are open to further experimental attack.

Summary.

Wingless aphids of the species *Macrosiphum solanifolii*, when reared in continuous electric light, produced almost exclusively wingless offspring. When reared in continuous darkness, with the exception of a few minutes daily, they produced relatively few winged offspring, the result being only a little less marked than in continuous light.

When the wingless parents were subjected to alternating light and darkness, the offspring included a varying percentage of winged individuals, depending on the length of the period of light. With only two hours of light, alternating daily with 22 hours of darkness, about three-fourths of the offspring were winged. With 5 hours of light, alternating with 19 hours of darkness, almost all the offspring were winged. Eight hours of light in every 24 also resulted in almost all winged offspring, while with 12 hour periods of light and of darkness there were a very few wingless daughters. There is some indication that the 8-hour period produced this result a little more quickly than did either the 5-hour or the 12-hour period of light.

Winged parents, when not in or near the gamic phase of the cycle, responded to alternating light and darkness in the same manner as did wingless parents, though there was a stronger tendency for their offspring to be wingless under any given conditions.

To produce winged aphids by means of alternating light and dark-

ness, it was necessary to subject their parents to the alternating conditions. Young aphids, an hour or two after birth, were incapable of being altered, but were winged or wingless, according to the conditions under which the parents lived.

Females that were kept first in continuous light, and then, at some time within their reproductive period, were changed to 8-hour light, continued to give birth to wingless offspring for a period varying in different experiments from 46 to 68 hours after the continuous illumination was interrupted. After that time, winged offspring were produced to as large an extent as was done by parents which had been in 8-hour light without change. The longest time (68 hours) required for the change from wingless to winged offspring was in an experiment performed in the summer when the temperature was distinctly higher than in the other tests; in all other experiments the time required was 46—52 hours.

When parents were changed from 8-hour light to 24-hour light, they continued to produce winged offspring for approximately two days after the change, wingless offspring thereafter.

It might be inferred from the above results that wing-determination occurs in young aphids at some time within the last two days before birth. At the beginning of this period the body and appendages are well-formed, and the eyes have just assumed pigmentation. If the young aphid or the parent requires considerable time to become adjusted to the changed conditions, actual determination of wings may occur at or only shortly before birth.

The effect of alternating light and darkness was produced on the whole no more quickly when the aphids were reared on plants that were subjected to the change of light earlier than the aphids were, than when the aphids and their host plants were changed at the same time. Moreover, when the aphids were lighted only 8-hours daily, while the plants on which they fed were in continuous light, the offspring produced were mostly winged; and when the aphids were in continuous light, but fed on plants illuminated only 8-hours daily, the offspring were mostly wingless. The offspring thus accorded with the light conditions applied to the parent aphids, not to the conditions to which the plants were subjected.

It is inferred from these results that the effect of the periodicity of light is directly upon the aphids, and not indirectly through any change in the photosynthesis of the host plant. (Only one experiment seemed to indicate any influence of the plant; its results can not for the present be harmonized with those of all the others.)

Aphids that were previously in continuous light, and then changed to 8- or 12-hour light, being starved 16 or 12 hours in darkness, produced winged offspring in about the same proportion as did aphids that were

fed continuously in the same periods of light. That is, starvation during the period of darkness did not appreciably increase or diminish wing-production. Moreover, the starvation of the parents in darkness neither hastened nor delayed the birth of the first winged offspring after the light-change and the starvation began. Aphids that were fed 8 or 12 hours daily in the light, and then starved 16 or 12 hours in the light, produced more winged offspring than did parents fed continuously in continuous light, but not so many as did parents fed continuously in 8- or 12-hour light. Moreover, the winged offspring produced by parents that were starved in the light, began to be produced sooner after the starvation began, than did the winged offspring of unstarved parents after the change of light. The winged offspring of parents starved in the light began to appear in 16—34 hours (in different experiments) after the starvation began, as against 44 hours for unstarved parents in 12-hour light. Starvation in light, therefore, or some factor incidental to starvation, not only caused the production of many winged offspring, but produced that effect very quickly.

From the above data it may be inferred that actual wing determination occurs within the last 16—34 hours before birth. How late in this period it takes place none of the experiments show.

When parents that had previously been in 8-hour light were changed to continuous light, and were starved during 16 hours of each day (in the light), more winged offspring were produced than by parents fed continuously in continuous light. Moreover, the expected production of a majority of wingless offspring after a certain period was somewhat delayed. Starvation in the light, therefore, is not merely provocative of change, and is not merely an accelerator of whatever change a change of light induces, but must be regarded as definitely favoring wing-production.

Zusammenfassung.

Flügellose Aphiden der Species *Macrosiphum solanifolii*, die ständig bei elektrischem Licht gehalten wurden, erzeugten fast ausschließlich flügellose Nachkommen. Wurden sie, mit Ausnahme weniger Minuten täglich, ständig im Dunkeln gehalten, so erzeugten sie verhältnismäßig wenig geflügelte Nachkommen, nur ist das Resultat etwas weniger scharf wie bei dem Versuch mit ständiger Beleuchtung.

Wurde die flügellose Elterngeneration abwechselnd Licht und Dunkelheit unterworfen, so enthielt die Nachkommenschaft einen wechselnden Prozentsatz von geflügelten Individuen, der von der Länge der Hellperiode abhing. Bei nur 2 Stunden Licht, die täglich mit 22 Stunden Dunkelheit abwechselten, waren ungefähr drei Viertel der Nachkommen geflügelt. Bei 5 Stunden Licht und 19 Stunden Dunkelheit waren fast alle Nachkommen geflügelt. Bei 8 Stunden Licht von je 24 resultierte

gleichfalls eine beinahe durchgehend geflügelte Nachkommenschaft, während bei 12stündigen Hell- und Dunkelperioden eine geringe Menge flügelloser Individuen dabei war. Manches spricht dafür, daß die 8-Stunden-Hellperiode dies Resultat ein wenig schneller zeitigte als sowohl die 5-Stunden- wie die 12-Stunden-Periode.

Geflügelte Eltern, die nicht in der geschlechtlichen Phase des Zyklus standen und auch nicht kurz davor, reagierten auf Wechsel von Licht und Dunkelheit wie flügellose, jedoch war unter allen gegebenen Bedingungen bei ihrer Nachkommenschaft eine stärkere Tendenz zur Flügellosigkeit zu beobachten.

Um durch Wechsel von Licht und Dunkelheit geflügelte Aphiden zu bekommen, war es nötig, ihre Elterngeneration den wechselnden Bedingungen auszusetzen. Junge Aphiden waren (1—2 Stunden nach der Geburt) nicht mehr zu beeinflussen, sondern wurden geflügelt oder flügellos entsprechend den Bedingungen, unter denen die Elterngeneration gelebt hatte.

Versetzte man solche Weibchen, die anfänglich bei ständiger Helligkeit gehalten worden waren, während ihrer Fortpflanzungszeit in eine 8-Stunden-Hellperiode, so fuhren sie zunächst fort, flügellose Nachkommen zu erzeugen, und zwar noch 46—68 Stunden lang (die Dauer wechselte in den verschiedenen Experimenten), nachdem die dauernde Helligkeit zuerst unterbrochen worden war. Nach dieser Zeit war der Prozentsatz geflügelter Nachkommen bei ihnen genau so groß wie bei einer Elterngeneration, die von Anfang an bei 8-Stunden-Belichtung gehalten worden war. Die längste Zeit (68 Stunden), die erforderlich war für den Übergang von flügellosen zu geflügelten Nachkommen, bezieht sich auf ein im Sommer ausgeführtes Experiment, bei dem die Temperatur deutlich höher war als bei den anderen Versuchen; in allen sonstigen Experimenten waren 46—52 Stunden nötig.

Wurden Elterntiere aus 8-Stunden-Helligkeit in 24-Stunden-Helligkeit versetzt, so produzierten sie noch etwa 2 Tage lang weiter geflügelte Nachkommen, danach flügellose.

Man könnte aus den obigen Resultaten schließen, daß die Determination der Flügel bei jungen Aphiden zu irgendeinem Zeitpunkt während der letzten 2 Tage vor der Geburt stattfindet. Am Anfang dieses Zeitraums sind Körper und Anhänge wohlausgebildet, die Augen haben gerade Pigment bekommen. Wenn die junge Aphide oder ihr Elter beträchtliche Zeit nötig hat, um sich den veränderten Bedingungen anzupassen, so wird die aktuelle Determination der Flügel zur Zeit der Geburt oder nur kurz vorher stattfinden.

Züchtete man Aphiden auf Pflanzen, die schon vorher dem Wechsel von Licht und Dunkelheit ausgesetzt worden waren, so wurde der Effekt dieses Wechsels im ganzen nicht schneller erreicht, als wenn Aphiden

und ihre Wirtspflanzen gleichzeitig der Veränderung unterworfen wurden. Noch mehr, wurden die Aphiden nur 8 Stunden täglich beleuchtet, während die Pflanzen, von denen sie fraßen, dauernd im Hellen standen, so war die erhaltene Nachkommenschaft meist geflügelt; und wenn die Aphiden ständig im Hellen waren, aber von Pflanzen fraßen, die nur 8 Stunden täglich im Licht gewesen waren, so war die Nachkommenschaft meist flügellos. Die Nachkommenschaft verhielt sich also entsprechend den Lichtbedingungen, denen ihre Elterngeneration ausgesetzt wurde, nicht entsprechend jenen, welchen die Pflanzen unterworfen waren.

Es folgt aus diesen Resultaten, daß die Periodizität des Lichtes direkt auf die Aphiden wirkt, und nicht indirekt durch eine Veränderung in der Photosynthese der Wirtspflanze. (Nur ein Experiment schien auf einen Einfluß der Pflanze hinzuweisen; seine Resultate können gegenwärtig noch nicht mit denen aller anderen in Einklang gebracht werden.)

Aphiden, die zuerst ständig im Licht waren und dann einer 8- bzw. 12-Stunden-Hellperiode unterworfen wurden, brachten ungefähr den gleichen Prozentsatz geflügelter Nachkommen hervor, gleichgültig, ob sie während der entsprechenden 16- bzw. 12-Stunden-Dunkelzeit gefüttert wurden oder hungerten. D. h. Hunger in der Dunkelheit beeinflußte die Vermehrung oder Verminderung der Flügelproduktion nicht beträchtlich. Dazu kommt, daß das Hungernlassen der Elterngeneration während der Dunkelheit die Geburt der ersten geflügelten Nachkommenschaft nach dem Lichtwechsel und dem Beginn des Hungerns nicht beschleunigte, aber auch nicht verzögerte. Hingegen, Aphiden, die 8 bzw. 12 Stunden täglich im Hellen gefüttert wurden, und dann die entsprechenden 16 bzw. 12 Stunden im Licht hungerten, brachten mehr geflügelte Nachkommenschaft hervor als solche, die dauernd bei ständigem Licht gefüttert wurden, jedoch nicht so viel wie solche, die bei 8- bzw. 12-Stunden-Licht dauernd gefüttert wurden. Weiterhin zeigte sich, daß die ersten derjenigen geflügelten Nachkommen, deren Eltern im Licht gehungert hatten, zeitlich eher nach Beginn der Hungerperiode geboren wurden als die geflügelten Nachkommen von Eltern, die nach dem Lichtwechsel nicht gehungert hatten. Die erste geflügelte Nachkommenschaft von Eltern, die im Licht gehungert hatten, erschien (in verschiedenen Experimenten) 16—34 Stunden nach Hungerbeginn, gegenüber von 44 Stunden bei Eltern, die im 12-Stunden-Licht nicht gehungert hatten. Hunger im Licht oder irgendein mit Hunger verbundener Faktor verursachte also nicht nur die Erzeugung vieler geflügelter Nachkommen, sondern beschleunigte sie auch.

Aus den obigen Ergebnissen kann man schließen, daß die aktuelle Determination der Flügel während der letzten 16—34 Stunden vor der

Geburt stattfindet. Wann innerhalb dieser Periode sie sich vollzieht, zeigt keins der Experimente.

Wurde eine Elterngeneration, die anfänglich in 8-Stunden-Licht war, dauerndem Licht ausgesetzt und 16 Stunden lang an jedem Tag (im Licht) nicht gefüttert, so wurden mehr geflügelte Nachkommen erzeugt als von Eltern, die in ständigem Licht dauernd gefüttert wurden. Ja, die erwartete Produktion einer vorwiegend flügellosen Nachkommenschaft nach einer bestimmten Periode wurde etwas aufgeschoben. Hunger im Licht ruft daher nicht nur eine Veränderung hervor und beschleunigt nicht nur jegliche Veränderung, die ein Wechsel des Lichts veranlaßt, sondern muß als definitiv begünstigender Faktor für Flügelproduktion betrachtet werden.

Bibliography.

Ackerman, L. (1926): The physiological basis of wing-production in the grain aphid. Journ. of Exp. Zool. **44**, 1—61. — **Davidson, J.** (1924): Factors which influence the appearance of the sexes in plant lice. Science **59**, 364. — Ders. (1927 a): The biological and ecological aspect of migration in aphides. Part I. Science Progress **21**, 641—658. — Ders. (1927 b): On the biological and ecological aspect of migration in aphides. Part II. Ibid. **22**, 57—69. — **Ewing, H. E.** (1926): Wing production in plant lice. Americ. Naturalist **60**, 576—579. — **Garner, W. W.** and **Allard, H. A.** (1920): Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Journ. of Agricult. Research **18**, 553—606, 16 pls. — Ders. (1921): Flowering and fruiting of plants as controlled by the length of day. U. S. Dept. Agr. Yearbook 1920. 377—400. — **Marcovitch, S.** (1923): Plant lice and light exposure. Science **58**, 537—538. — **Mordvilko, A.** (1927): L'anolocyclie chez les Pemphigiens des Pistachiers. Cpt. rend. hebdom. des séances de l'acad. des sciences. Paris **185**, 295—297. — **Schneider-Orelli, O.** and **Leuzinger, H.** (1926): Untersuchungen über die virginoparen und sexuparen Geflügelten der Blutlaus des Apfelbaumes. Vierteljahrsschr. d. naturforsch. Ges. Zürich **71**, Beiblatt Nr. 9, 1—84, 3 pls. — **Shull, A. F.** (1918): Genetic relations of the winged and wingless forms to each other and to the sexes in the aphid *Macrosiphum solanifolii*. Americ. Naturalist **52**, 507—520. — Ders. (1926): Life cycle in aphids affected by duration of light. Anat. Record. **34**, 168—169.