The Emergence of Winged Viviparous Female in Aphid

VIII. Ecological Significance of the Emergence of Winged Form in the Life Cycle of Aphid

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INTRODUCTION

Since offspring of winged parthenogenetic females of aphids show a striking inclination to be wingless regardless of their environment, while the offspring of wingless parthenogenetic females may be winged or unwinged depending on a variety of environmental conditions, it may be easily imagined that there are some differences in constitutional factors in the offspring born from the winged and from the unwinged forms. I (VII, in press) have already pointed out that some hormones or hormone-like substances restraining the development of the wing buds seem to be secreted during the first instar of larvae from the winged family line and when such substances attain to a certain amount the duration of the first instar becomes elongated strikingly as compared with that of the unwinged family line. The present communication deals with the results of observations on the reactions of the both offspring to adverse life conditions caused by food quality, starvation and overcrowding to find whether there are any more differences between them.

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MATERIAL AND METHOD

The apple grain aphid, *Rhopalosiphum prunifoliae*, and the English grain aphid,

Macrosiphum granarium, were used as materials for the experiments. The offspring born from the two family lines were reared under an inappropriate circumstance and the rate of death was examined. And in another experiment the offspring were starved until all of them were dead, confining them individually in a small vial with a cork stopper. The humidity in the vial was carefully maintained to be always saturated by placing a lump of wet cotton in it. Constant temperatures of 10°, 15°, 20° and 25°C were maintained. Light was intercepted throughout the experiment. Death was observed every two hours except the night from 2 to 8 a.m. The complete death was judged by the loss of response to tactile stimulation of appendages such as antennae or legs.

RESULT

Experiment 1.—The offspring newly born from the two family lines of *Rhopalosiphum prunifoliae* were divided into two lots respectively. The individuals of the first lot of each family line were fed on the fresh leaves of *Hordeum vulgare* at a rate of 80 individuals per piece of 10 cm², and the other was reared by the same method, but the diet was not fresh but stale leavings once given to other individuals. Foods were not changed until 55 hours passed away. All the experiments were done at a constant temperature of 25°C. The total rate of death obtained during the period mentioned above is shown in Table 1.

According to χ^2 -test the difference for the rate of death between the two family

Table 1. The rate of death of offspring born from the two family lines of *Rhopalosiphum prunifoliae* fed on fresh or deteriorated leaves

Leaves	Family line	Total	Survival	Death	
				Number	%
Fresh	Winged	160(0)	147	13	8.1
	Unwinged	158(2)	139	19	12.0
Deteriorated	Winged	157(3)	134	23	14.6
	Unwinged	158(2)	94	64	40.5

The numbers in parentheses indicate individuals lost by unknown causes.

Table 2. Time to death in each instar of the starved offspring of two family lines of *Rhopalosiphum prunifoliae* at several constant temperatures

Instar	Family line	Time to death			
		10°C	15°C	20°C	25°C
1st	O (U)	88.7±10.9	45.5± 7.2	25.8± 4.0	18.4± 3.7
	O (W)	95.0± 9.9	55.5± 7.0	31.5± 4.5	23.7± 3.3
2nd	O (U)	120.5±16.8	56.0± 9.7	39.8± 5.9	30.3± 5.0
	O (W)	166.8±21.3	84.3±10.6	51.8± 6.6	40.7± 7.2
3rd	U O (U)	177.0±25.4	80.7±11.6	50.1± 4.3	36.3± 4.9
	U O (W)	182.5±27.1	90.5±13.3	58.2± 7.2	46.7± 6.0
	W O (U)	221.5±20.0	104.5±15.4	64.1± 6.2	54.1± 6.7
4th	U O (U)	223.1±18.6	103.7±16.5	64.5± 8.7	53.4± 5.7
	U O (W)	262.2±26.1	115.4±13.4	75.3± 7.4	58.1± 5.5
	W O (U)	278.2±25.9	140.5±18.2	94.2±15.0	73.2±10.4
Imago	U I (U)	204.4±18.8	109.7±20.6	69.2±10.4	55.7± 9.8
	U I (W)	256.5±24.7	137.0±18.1	89.5±12.4	64.3±10.2
	W I (U)	—	123.0±17.8	80.7±14.3	65.0±12.0

O (U).....Offspring born from the unwinged.

O (W).....Offspring born from the winged.

U O (U).....Offspring without wing buds, born from the unwinged.

U O (W).....Offspring without wing buds, born from the winged.

W O (U).....Offspring with wing buds, born from the unwinged.

U I (U).....Unwinged imago born from the unwinged,

U I (W).....Unwinged imago born from the winged.

W I (U).....Winged imago born from the unwinged.

lines is not significant in the new leaf lot, but in the stale leaf lot it is significant at 1% level. The difference between both lots is not of significance in the winged family line, but significant at 1% level in the unwinged one. This indicates that the change in the quality of diet exerts its effect upon the rate of death more markedly in the unwinged than in the winged family line.

Experiment 2.—The offspring derived from both forms of *Rhopalosiphum prunifoliae* were starved individually during

each instar at constant temperatures of 10°, 15°, 20° and 25°C until all of them died. The results are shown in Table 2.

The lower the temperature is, the more slowly takes place the hunger death. The relation may be expressed by the equation

$$Y=aX+b,$$

where Y is the velocity of death (reciprocal of the time to death), X is temperature, and a (temperature coefficient) and b are the constants. The values of a and b are calculated in Table 3 with the esimatep

Table 3. Values of a , b and X_0 for the data presented in Table 2

Instar	Family line	a	b	X_0 ($^{\circ}\text{C}$)	Significance of difference
1st	O (U)	0.29	-1.95	6.7	O (U) : O (W) = 5%
	O (W)	0.22	-1.24	5.6	
2nd	O (U)	0.16	-0.76	4.5	O (U) : O (W) = 5%
	O (W)	0.13	-0.66	5.1	
3rd	UO (U)	0.15	-0.93	6.2	UO (U) : UO (W) = 5%
	UO (W)	0.11	-0.51	4.6	UO (U) : WO (U) = 5%
	WO (U)	0.10	-0.48	4.8	UO (W) : WO (U) = non-sig.
4th	UO (U)	0.10	-0.50	5.0	UO (U) : UO (W) = non-sig.
	UO (W)	0.09	-0.54	6.0	UO (U) : WO (U) = 1%
	WO (U)	0.07	-0.30	4.3	UO (W) : WO (U) = 5%
Imago	U I (U)	0.09	-0.40	4.4	U I (U) : U I (W) = 5%
	U I (W)	0.08	-0.42	5.2	U I (U) : W I (U) = 5%
	W I (U)	0.07	-0.26	3.7	U I (W) : W I (U) = non-sig.

Symbols as in Table 2.

values of X_0 . X_0 is the temperature just above which the death from hunger begins to occur, but just below which the animals enter into a state of cold dormancy.

Table 2 shows that the time to death caused by starvation becomes longer with the age of the nymphs. In all instars except for the fourth, the time to death is shorter in the unwinged form of the wingless family line than in the unwinged form of the winged family line. But from the result of this experiment, it may safely be said that, after the offspring in the wingless line is determined to be the alate form in future, their resistance to hunger becomes greater abruptly to the same degree as that of the winged line. The temperature coefficient, a , indicates the largest value in every stage of the wingless-type individuals of the wingless line and contrarily the smallest value in the alate-type individuals of the latter. The value of X_0 is $5.1 \pm 0.8^{\circ}\text{C}$ on an average.

Experiment 3.—Both the offspring born from the unwinged females of *Rhopalosiphum prunifoliae* which had repeated several times the unwinged generation (U^5) and those born from the unwinged form produced directly from the winged females (W^2) were reared under the same condition as in Experiment 1. Deteriorated leaves which had same stale appearance were furnished to both lots. Table 4 shows the result.

Table 4. The rate of death during the adverse condition of the first two instars of the larvae in the fifth or later generation of the unwinged family line (U^5) and in the second generation of the winged (W^2) in *Rhopalosiphum prunifoliae*

Lot	Total	Survival	Death	
			Number	%
U^5	157 (3)	69	88	56.1
W^2	169 (0)	84	76	43.1

The numbers in parentheses indicate individuals lost by unknown causes.

According to χ^2 -test, there is no significant difference in the rate of death between the two lots.

Experiment 4.—Quite the same materials as in Experiment 3 were starved by the same method as in Experiment 2 under constant temperatures of 15° , 20° and 25°C with the result shown in Table 5.

According to distribution analysis, there is no significant difference between the two family lines in every instar.

Experiment 5.—The offspring of *Macrosiphum granarium* were treated by the same method as in Experiment 1 with the result indicated in Table 6.

There are no significant differences not only between the family lines in each lot but also between the same lines corresponding to one another.

Experiment 6.—Similar observation to

Table 5. Time to hunger-death of the larvae in the fifth or later generation of the wingless family line (U⁵) and in the second generation of the winged line (W²) in *Rhopalosiphum prunifoliae*

Instar	Family line	Time in hours		
		15°C	20°C	25°C
1st	U ⁵	41.9± 6.8	27.5± 5.8	20.2± 3.9
	W ²	46.0± 7.7	26.8± 4.0	22.2± 4.6
2nd	U ⁵	54.2± 9.9	37.2± 6.9	26.5± 5.4
	W ²	52.0± 8.4	35.7± 7.1	25.3± 5.3
3rd	U ⁵	77.0±11.2	48.3±10.3	38.5± 7.0
	W ²	82.3±13.3	53.2± 8.8	35.8± 7.8
4th	U ⁵	113.3±17.2	60.3±11.1	55.2±10.7
	W ²	99.9±14.9	67.3±12.6	50.3± 9.5

Table 6. The rate of death of the offspring born from the two family lines fed on fresh or deteriorated leaves in *Macrosiphum granarium*

Leaves	Family line	Total	Survival	Death	
				Number	%
Fresh	Winged	159(1)	134	25	15.7
	Unwinged	160(0)	143	17	10.6
Deteriorated	Winged	160(0)	140	20	12.5
	Unwinged	157(3)	129	28	17.8

The numbers in parentheses indicate individuals lost by unknown causes.

Table 7. Time to hunger-death in every instar of two family lines of *Macrosiphum granarium* at various temperatures

Instar	Family line	Time in hours		
		15°C	20°C	25°C
1st	O (U)	44.0± 6.4	29.8± 4.2	22.5± 6.0
	O (W)	42.2± 7.3	32.0± 5.9	23.6± 7.4
2nd	O (U)	52.8± 9.6	36.3± 7.9	28.2± 4.1
	O (W)	56.1± 8.7	35.0± 7.3	27.5± 6.4
3rd	U O (U)	71.1±10.8	51.5± 9.8	38.0± 7.4
	U O (W)	85.5±12.7	58.5±11.2	44.3±10.1
	W O (U)	82.0±13.4	60.2±10.3	42.2± 8.6
4th	U O (U)	106.2±20.4	70.3±17.6	54.5±12.9
	U O (W)	109.5±18.1	73.2±15.0	53.8±13.0
	W O (U)	119.8±21.4	85.3±13.1	64.4±14.7
Imago	U I (U)	121.1±23.3	79.4±16.4	61.8±10.8
	U I (W)	118.4±24.9	83.1±15.7	63.9±14.2
	W I (U)	105.7±19.4	78.6±13.0	58.2±17.1

Symbols as in Table 2.

Table 8. Values of a , b and X_0 for the data presented in Table 7

Instar	Family line	a	b	X_0 (°C)	Significance of difference
1st	O (U)	0.20	-0.72	3.6	O (U) : O (W) = non-sig.
	O (W)	0.19	-0.50	2.6	
2nd	O (U)	0.17	-0.57	3.4	O (U) : O (W) = non-sig.
	O (W)	0.19	-0.91	4.7	
3rd	UO (U)	0.11	-0.27	2.6	UO (U) : UO (W) = non. ($\approx 5\%$)
	UO (W)	0.11	-0.46	4.2	UO (U) : OW (U) = non. ($\approx 5\%$)
	WO (U)	0.12	-0.55	4.6	UO (W) : WO (U) = non-sig.
4th	UO (U)	0.09	-0.38	4.2	UO (U) : UO (W) = non-sig.
	UO (W)	0.10	-0.52	5.2	UO (U) : WO (U) = 5%
	WO (U)	0.07	-0.23	3.3	UO (W) : WO (U) = 5%
Imago	UI (U)	0.08	-0.35	4.4	UI (U) : UI (W) = non-sig.
	UI (W)	0.08	-0.30	3.7	UI (U) : WI (U) = non-sig.
	WI (U)	0.08	-0.23	2.9	UI (W) : WI (U) = non-sig.

Symbols as in Table 2.

that in Experiment 2 was made in *Macrosiphum granarium* at temperatures of 15°, 20° and 25°C. Tables 7 and 8 indicate the result.

The time to starvation-death in *Macrosiphum granarium* becomes also longer with a fall of temperature and with the age of animals (significant at 1% level). But as to the other points, the results are not in agreement with those in Experiment 2 except in the fourth instar, where the offspring of the winged-type in the unwinged line are different significantly (at 5% level) from those of the wingless-type in the both family lines in the rate of death from hunger. The value of X_0 is $3.8 \pm 0.8^\circ\text{C}$ on an average in this species of aphid.

DISCUSSION

Experiment 1 shows that, when food is fresh, the effect of high population density upon the rate of death the winged family line is almost the same with that upon the unwinged family line; but when it is stale, the effect upon the winged line appears not only to be far weaker than that upon the unwinged line but also almost equal to that upon the both family lines which are fed on fresh food. Accordingly, it is safely be concluded that, in *Rhopalosiphum prunifoliae*, the rate of death in the winged line is hardly influenced by food so far as it is not so highly dete-

riorated, although the former in the unwinged is liable to be affected by the deterioration of food. I observed that most corpses of the larvae adhered to the inner wall of vial on which a large quantity of drops or thin layer of water evaporated from food leaves remained. I think that the sensitivity to the freshness of food may be greater in the offspring of the unwinged line than in those of the winged one. So, when the offspring of the unwinged line are fed on the stale leaves they will wander about the wet wall of vial searching for fresh food and will die from drowning. The offspring of the winged line, on the other while, will soon take plant juice from the stale leaves, because they are relatively indifferent to the freshness of food.

According to my long experience in rearing, it seems that the general constitution of the body is stronger in the offspring of the winged line than in those of the unwinged line (except the winged-type). Experiment 2 clearly proves that the resistance to starvation in the apterous form is far greater in the former than in the latter. The temperature coefficient, a , of the temperature-time-to-death equation, $Y = aX + b$, is always smaller in the family line of the winged than in the unwinged line. This seems to mean that the effect of temperature upon the rate of consumption of the body substrate is

smaller in the former than in the latter. It should be noted, however, that the resistance to starvation of the larvae of the latter becomes great to almost the same degree as that of the former after the form is determined to be alate in future. The value of X_0 , which is the temperature when Y is zero in the equation $Y=aX+b$, or the temperature at which it does not affect the rate of death by starvation but induces the animals to enter into a state of cold-dormancy is 5.1°C on an average. This value is 1.1°C lower than the developmental threshold, 6.2°C (NODA, in press). The latter is the temperature just above which the rate of development becomes perceptible. So in the case of our aphids, they mostly sting their proboscis into the tissues of the host plant and seem to suck the juice at such a low temperature so far as they stay on the food leaves. In the case of starvation, however, there is only catabolism but no development. So it is natural that the value of X_0 is lower than that of the developmental zero. Experiments 3 and 4 clearly indicate that the sensitivity to food quality and the resistance to hunger seen in the first generation of the winged family line may disappear in the second generation.

It can be easily imagined that all the phenomena mentioned above may be the peculiar modes of adaptation in passing through the adverse condition for life. So when the host plant wits or when much overcrowded, the apterous females, at least in *Rhopalosiphum prunifoliae*, produce a great number of migrants, the offspring of which can stand against unfavourable conditions. This seems to have an importance in the life cycle of aphids together with the strengthening of constitution of the body of the winged forms themselves since the third nymphal stage, during which the wing buds become visible. It is highly regrettable that, in *Macrosiphum granarium*, these points cannot be proved. In this, the number of individuals died from drowning in the condensed water of

vial was smaller even in the unwinged family line of the stale leaf lot, unlikely to *Rhopalosiphum prunifoliae* (see Experiments 5 and 6). After all, the offspring born from the winged line are likely to be different from those of the unwinged one in the points of sensitivity for the freshness of food and of the resistance to hunger in *Rhopalosiphum prunifoliae*, the alate form of which hardly produces the same form. But those phenomena just mentioned above could scarcely be observed in *Macrosiphum granarium*. So in the latter species in which the offspring of the winged line can easily transform into the same form, the emergence of the winged form seems to mean only to produce the form capable of migration.

SUMMARY

1. In order to know if there are any differences in physiological characters between the winged and the unwinged family lines other than the hormonal relations during the first nymphal instar of the winged line as supposed by me in the 7th report of this series, some comparative observations were made on the reactions to unfavourable life conditions such as overcrowding, feeding on deteriorated food leaves and starvation in the both family lines of two species of aphids, *Rhopalosiphum prunifoliae* in which the winged forms are readily produced from the unwinged mothers but not from the winged, and *Macrosiphum granarium* in which the winged forms are easily produced not only from the unwinged but also from the winged.

2. In *Rhopalosiphum prunifoliae*, the offspring born from the winged mothers are relatively indifferent to the freshness of food and have a great resistance to starvation in their own generation. But these characters disappear in the second generation. In the unwinged family line, the progenies become to possess also a marked degree of resistance to the unfavourable life conditions, after they grow to the third instar, whence the wing buds

become visible.

In *Macrosiphum granarium*, these phenomena can hardly be recognized.

3. The appearance of the winged form seems to bear certain significances in the life cycle of *Rhopalosiphum prunifoliae*. In this, not merely the winged forms themselves are highly resistant to external factors since the later stage of their larval development but give rise to the next generation which possesses also a marked degree of resistance to unfavourable environmental conditions. In *Macrosiphum granarium*, the meaning seems to be con-

fined only to the production of the form capable of migration.

LITERATURE CITED

- NODA, I. (1951) Mem. Ehime Univ. Sec. II (Sci.), 1: 137~145.
 NODA, I. (1954) Mem. Ehime Univ. Sec. II, Ser. B (Biol.), 2: 61~70.
 NODA, I. (1956) Mem. Ehime Univ. Sec. II, Ser. B, 2: 309~316.
 NODA, I. (VI, in press).
 NODA, I. (VII, in press).
 UCHIDA, S. (1957) Jap. J. Appl. Ent. Zool. 1: 46~52.

摘 要

アブラムシの有し型胎生雌の出現について

VIII. アブラムシの生活環における有し型出現の生態的意義

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キビクビレアブラムシでは無し(翅)型から有し(翅)型が容易に出現するが、有し型からはほとんど有し型が出現しない。したがって有し型から生じた幼虫はその生理的性質が無し型からの幼虫に比べて著しく異なっているのではないかと考えられる。これについて筆著(VI,印刷中)は前者の第1令幼虫期間の長さに着しい個体差のあることを考慮に入れて、この期間中にしが(翅芽)の発達を抑制するホルモンまたはホルモン様物質が分泌されており、その分泌量がある限度を越すとその超過量に応じて体の成長をも抑制するようになるのではないかと考えた。なおこのほかにも両幼虫間になんらかの差のあることが予想されるので、絶食、古葉の摂取などの異常生活条件に対するこれらの両系幼虫の反応を観察し、その結果から有し型出現の生態的意義を明らかにしようとした。これを要約すると次のとおりである。

1) キビクビレアブラムシの有し型から生まれた幼虫は無し型からの幼虫に比べて食草の新鮮度に対する感受性がやや鈍く、絶食に対する耐久性も強いようである。しかしこれらの性質が見られるのはその幼虫1代かぎりであって、次の代には消失する。これに対して無し型か

らの幼虫は古くなった食草をきろう性質がいくらか強く、飢餓に対する耐久性も弱いようである。すなわち前者は後者より生活条件の低下に対し強い耐性を示す。一方無し系幼虫でも第3令以後、しがが見え始めてくると有し系幼虫とほとんど変わらない程度に飢餓に対する耐性が強くなる。

しかし有し型からも有し型の出やすいムギヒゲナガアブラムシにおいてはこのような現象がはっきりと見られなかった。

2) したがって、キビクビレアブラムシの生活環において、有し型胎生雌が出現するということは、単に移動型を生じ生活に不都合な区域から好都合な区域へ分散して次世代を生むということのほか、有し型それ自体の体質が発育の途中第3令以後から強くなるとともにその強さを次の世代へ伝えるということをもあわせ意味するのではないと思う。すなわち有し型の出現によりそれ自身をも含めて2代連続して健全世代を生ずることとなる。これに対しムギヒゲナガアブラムシにおける有し型出現の意義は単に移動可能の型の出現と四散に限定されるように思われる。