THE EFFECT OF PHOTOPERIOD, TEMPERATURE AND POPULATION DENSITY ON THE PRODUCTION OF SEXUAL FORMS IN THE CABBAGE APHID, *BREVICORYNE BRASSICAE* L.

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There are two kinds of reproductive methods in the cabbage aphid (Fig. 1). One is parthenogenetic reproduction of viviparous females and the other is sexual reproduction. In the vicinity of Kurashiki, according to the writer's field observation, the latter has never been seen yet, while viviparous females may be seen in all the seasons. Even in cold winter time we can see adults producing offsprings during the warmer time of a day. In the more northern district of its distribution, as in Hokkaido, the male and the oviparous female appear in fall and sexual reproduction takes place (Fig. 2). It may be presumed that the appearance of sexual forms is controlled by certain environmental factors such as photoperiod, temperature and also population density. Yet, the cause of the appearance of the sexual forms is by no means clearly known. This is the reason why the writer has under taken the present study.

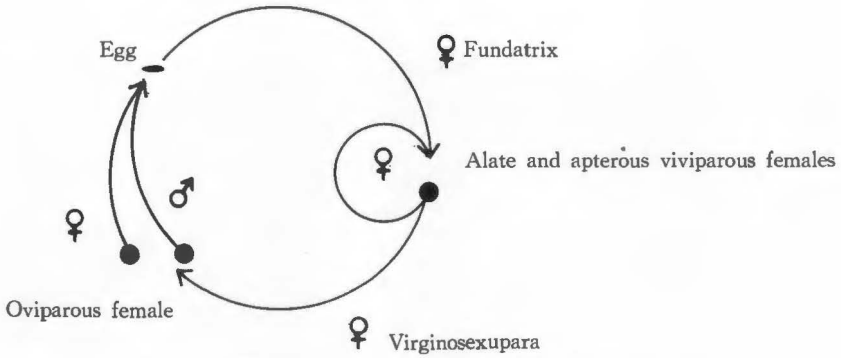

Fig. 1. Life cycle of the cabbage aphid, *Brevicoyne brassicae* L.

MATERIALS AND METHODS

The materials used in the present experiment were the decendants produced by wingless viviparous parents which have long been established in our laboratory by parthenogenetic reproduction. The stock was collected from the field of our institute in 1960 and has since been kept at the temperature of 17.5°C with 16 hours photopriod. The aphids used for the research have been reared under the various conditions of photopriod, temperature and population density. These individuals (the first generation) and their offsprings (the second generation) did not seem to have been affected by the above conditions in any way. All individuals

a

b

c

Fig. 2. Typical colony on the underside of a kale leaf.
(a) × ; Oviparous females, ○ ; Winged viviparous females
(b) Copulation (c) △ ; Egg

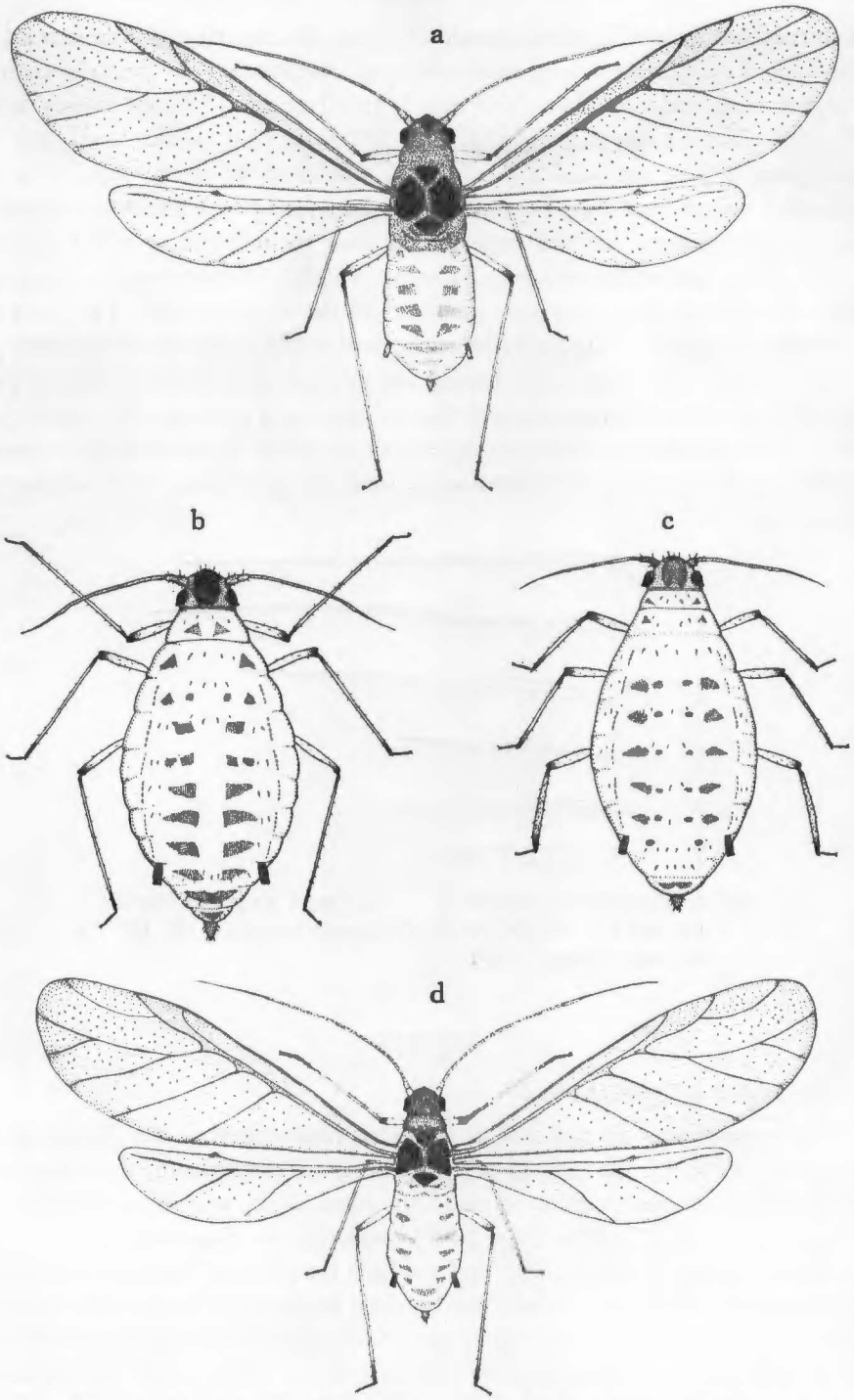

Fig. 3. Four main forms of the cabbage aphid, *Brevicoryne brassicae* L.
(a) winged viviparous female; (b) wingless viviparous female;
(c) oviparous female; (d) male.

have turned out to be viviparous females. Then the experiment was carried out successively for five generations under the same conditions. In this trial each generation was started with about 100 early born offsprings. About twenty individuals were placed in one container (4.5×2.0^{cm}) with food. The food-plant was a fresh piece of kale leaf (2.5×2.5^{cm}), and was renewed every day. The test aphids were reared until they became adults, for which the forms were examined under the microscope. In this experiment, four main forms of aphid appeared (Fig. 3.). They are (a) the winged viviparous female ; (b) the wingless viviparous female ; (c) the wingless oviparous female ; (d) the winged male. The latter two are the sexual forms. These may be recognized easily by the body structures, as are shown in Fig. 4. Oviparous female has sensoria like structure on the swollen hind tibiae, but viviparous female has no such structures on the slender hind tibiae. A winged male has numerous sensoria on third, fourth and fifth antennal segments , and alate viviparous female has these things only on the third antennal segment.

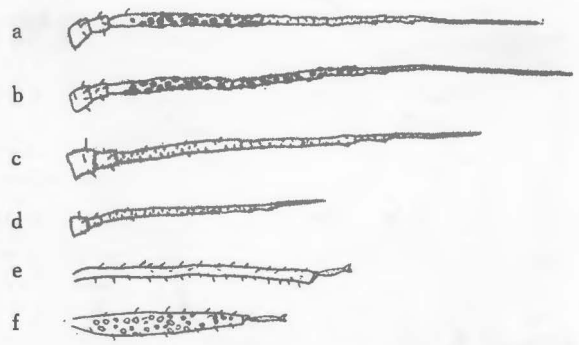

Fig. 4. Antenna and hind tibiae. (a) winged viviparous female ; (b) male ; (c), (e) wingless viviparous female ; (d), (f) oviparous female. (×50)

RESULTS

1. *The effect of photoperiod*

The rearing was carried out at different rooms having the following day lengths of 0, 4, 8, 12, 13, 14, 16 and 24 hours. The temperature was regulated at 17.5 °C and relative humidity varied approximately between 50 and 80 percent. A fluorescent lamp (Toshiba FL—20W), operated by time switches, gave the daily photoperiod of 4—16 hours ; and the light intensity on the rearing container was about 800—1000 lux. About one hundred newly born larvae from the stock culture were reared respectively under the above eight different photoperiods, and their progeny was examined for their body structure. The results obtained were as follows : As is apparent from Table 1, oviparous females were produced from the third to fifth generations under the conditions less than 13 hours photoperiods. Oviparous females were never produced in any generations under the long day

conditions such as longer than 14 hours. Therefore, it is evident that the appearance of oviparous female is determined by the day length under which both the mother and grandmother are reared. An analysis of variance showed that there is significant difference at 1% level in the production of oviparous females between the two photoperiods 14 hours and the less. There was no significant difference between the photoperiods of less than 13 hours.

2. *The effect of temperature*

The effect of temperature has also been studied by exposing wingless grand mother and mother during their life time to the three different constant temperatures under the typical long day (16 hours) and the short day (8 hours) conditions. All the results are summarized and shown in Table 2. In the Table, the percentages of production of oviprous females in the third, fourth and fifth generations are summed up. According to the χ^2-test, the difference in the percentage are significant at 1% level between each temperatures. It can be seen from these results, that the production of oviparous females increases gradually under short day condition as the temperature becomes lower.

1) At 25°C. Only viviparous females were produced, whether the day length was long or short. From the results in the Table 2, it is apparent that high temperature of 25°C stops the tendency of short day to favour the production of oviparons females.
2) At 20°C. Although oviparous famales were produced only under the short day condition, the percentage was very low. This temperature seems too high for the production of these forms.
3) At 15°C. With respect to the production of oviparous females the influence of this temperature was similar to 20°C, but the effect was about four times as strong as that temperature.

3. *The effect of crowding*

Experiments were carried out to see whether the overcowding influences the production of oviparous females or not. The method of rearing was essentially the same as that which the author (Kawada, 1964) used in the previous experiment. A definite number of newly born larvae were placed in a cage under three different densities as shown in Table 3 (viz., 1, 10, 40.).

With respect to the time of appearance of oviparous female the results of this experiment were the same as the previous two trials which have already been stated. No oviparous females were produced in the first and the second generations. It is apparent from the records in Table 3 that the production of this form differs in three cases under short day condition.

For example, under the temperature of 25°C, the percentage of production was zero in the cases of low and intermediate population densities, while it was 5.2 percent in the case of high density. χ^2-test indicates that the difference between high population density and others were significant at 1% level. At the

TABLE
Offsprings records of apterous viviparous

Generation	0			4			8		
	N	V	O	N	V	O	N	V	O
1	99	99	0	89	89	0	80	80	0
2	96	96	0	97	97	0	86	86	0
3	118	114	4	102	101	1	101	90	11
4	101	92	9	92	91	1	100	91	9
5	83	81	2	112	100	12	96	80	16
T	497	482	15	492	478	14	468	432	36

N : Number of individuls used.
V : Number of viviparus females.
O : Number of oviparous females.
T : Grand total.
* : Only one male was appeared.

TABLE 2
Offsprings records of apterous viviparous mother and grandmother reared through their life time under long (16 hours) or short (8 hours) photoperiods at three different temperatures

Photoperiod	8 hours			16 hours		
Temperature	15°C	20°C	25°C	15°C	20°C	25°C
Number of individuals observed	311	301	366	270	230	285
Number of viviparous females	265	289	366	270	230	285
Number of oviparous females	46	12	0	0	0	0
Percent of oviparous females	14.79	3.99	0	0	0	0

TABLE 3
Offsprings records of apterous viviparous mother and grandmother reared their life time under different conditions of population density, photoperiods and temperatures

Photoperiod	8 hours											
Temperature	15°C				20°C				25°C			
Density	N	V	O	P	N	V	O	P	N	V	O	P
d=1	95	95	0	0	89	89	0	0	81	81	0	0
d=10	80	74	6	7.5	117	115	2	1.71	98	98	0	0
d=40	111	96	15	13.51	111	101	10	9.01	96	91	5	5.21

N : Number of individuals used.
V : Number of viviparous females.
O : Number of oviparous females.
P : Percent of oviparous females.

temperature of 20° and 15°C, there also significant differences at 1% level between high population density and others.

Thus, under high population density, the percentage was always larger than

1
females reared at temperature of 17.5°C

Photoperiods															
12			13			14			16			24			
N	V	O	N	V	O	N	V	O	N	V	O	N	O	V	
78	78	0	100	100	0	91	91	0	88	88	0	87	87	0	
101	101	0	93	93	0	103	103	0	116	116	0	101	101	0	
111*	109	1	90	87	3	120	120	0	90	90	0	85	85	0	
118	98	20	83	76	7	91	91	0	104	104	0	105	105	0	
87	85	2	89	75	14	93	93	0	95	95	0	111	111	0	
494	471	23	455	431	24	498	498	0	493	493	0	489	489	0	

those which were obtainsed under lower ones, But high population density does not affect the appearance of oviparous females under the long day condition; thus no oviparous females appeared under this condition at any temperature.

It is interesting to note that in the case of individual rearing, oviparous females were not produced in any combination of photoperiod and temperature according to the result of this experiment.

4. *Male production*

In this experiment, only one male individual was produced at 17.5°C in 12 hours day length. It was apprent that under the conditions of these experiments the production of male was more limited that of oviparous females.

DISCUSSION

The relation between the production of sexual forms and the environmental factors such as photoperiod and temperature has already been reported by many scientists including Bonnemaison (1951), Lees (1959) and others. The results obtained in the present work are substantially the same as those already reported.

16 hours												
15°C				20°C				25°C				
N	V	O	P	N	V	O	P	N	V	O	P	
94	94	0	0	90	90	0	0	84	84	0	0	
90	90	0	0	85	85	0	0	80	80	0	0	
103	103	0	0	103	103	0	0	113	113	0	0	

The present study shows that crowding is one of the major factors responsible for the sexual forms.

The relationship between photoperiod and the production of oviparous females is shown in Table 1. These results of systematic tests showed that a daily photoperiod of 13 hours was critical in this species for producing oviparous females. When newly hatched larvae from the stock culture were exposed to 0 — 13

hours photoperiods at the temperature of 17.5°C, all of them became viviparous females. The effect of short day does not appear before the third generation is reached. Not only mother stage but also the grand mother stage seems to influence the production of oviparous females according to the result of this exderiment. The effect of continuous darkness (except a short exposure to light at the time of changing the food) was also almost the same as the effect of the short day condition.

The effec of the temperature also was studied. It was found that temperature is also causative factor for producing the oviparous females only under short day condition. From the results of Table 2, at 25°C the percentage of the oviparous females was zero, at, 20°C it was 3.99 percent, at 15°C it was maximum amounting to 14.79 percent. Thus, oviparous females decreased gradually as temperature becomes higher. On the other hand, under long day condition oviparous female was never produced under three temperatures of 25°, 20° and 15°C. It was evident, temperature has nothing to do with the appearance of oviparous female under long day condition.

Table 3 shows that high population density (a density of 40 per capsule) tends to produce more oviparous females than the low one. Thus overcrowding can be regarded as one of the important factors responsible for the oviparous females production in this species. It is not apparent whether the populaiton density acted directly upon the aphids or indirectly through undernourishment brought about by overcrowding. To solve this problem, more detailed studies must be made by underfeeding them or by giving them wilted plants.

Thus, we can draw a general conclusion that, in the cabbage aphid the infuence of short day is distinctly strong in every case, because, lacking this condition, oviparous females have neven been produced under any combination of crowding and temperature. Overcrowding can be regarded as equally an important factor as short day in producing this form, because the oviparous female never appears in individual rearing no matter how satisfactory the photoperiod and temperature may be. On the other hand, temperature does not strongly upon the production of this form.

In Kurashiki this aphid is active from early spring ; suddenly and abruptly its population increases in May, with the highest population peak in middle June ; it suddenly decreases after summer ; but it gradually increases again in fall ; in winter it decreases again and very low population density can be found in fields. In this district both photoperiod and temperature are favorable enough to produce oriparous females in the winter, but the population density is not satisfactory for production of the oviparous female.

It is sure that this factor may be one of the reasons why sexual forms are not found in the fields in Kurashiki. Thus, it seems that parthenogenetic reproduction is normal in these warmer places.

SUMMARY

The effect of photoperiod, temperature and population density on the production of sexual forms in the cabbage aphid has been studied.

1) In this study four forms were produced; winged and wingless viviparous females, oviparous female and male.
2 Oviparous females were produced at the temperature below 20°C, only when the parents and grand parents were reared under photoperiod less than 13 hours.
3) High populantion density promotes the production of oviparous females under short photoperiod
4) Only one male was produced at the temperature of 17.5°C and 12 hours photoperiod.

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LITERATURE CITED

Bonnemaison, L. 1951. Contribution à l'étude des facteurs provopuant l'apparition des formes ailées et sexuées chez les Aphidinae. Ann. Inst. Rech. Agron. Ser. C. Ann. Epiphyt. 2 : 1—380.

Davidson, J. 1929. On the occurence of the parthenogenetic and sexual forms in Aphis rumicis L. with special reference to the influence of environmental factors. Ann. Appl. Biolu. 16 : 104—134.

Essig, E. O. 1949. The most important species of aphids attacking cruciferous crops in California. Hilgardia. 18 : 407—412.

Hori, M. 1929. The important species of aphid attacking agricultural and horticultural crops in Hokkaido. (In Japanese) Hokkaido Agr. Exp. Sta. Res. 23 : 1—163

Kawada, K. 1964. The development of winged forms in the cabbage aphid, *Brevicoryne brassiace* Linnaens L. The influence of population density, photoperiod and temperature. Ber. Ohara Inst. 12 : 189—195.

Kenten, J. 1955. The effect of photoperiod and temperature on reproduction in *Acyrthosiphon pisum* (Harris) and on the forms produced. Bull. Ent. Res. 46 : 599—624.

Lees, A. D. 1959. The role of photoperiod temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton 1. The influence of the these factors on apterous virginoparae and their progeny. Jour. Ins. physiol. 3: 92—117.

Markkula, M. 1953. Biologisch-Ökologische Untersuchungen über die Kohlblattlaus, *Brevicoryne brassicae* (L.) (Hem., Aphididae). Ann. Zool. Soc. Fennicae 15 : 1—113.