STUDIES ON THE FLOWER FORMATION IN THE STRAWBERRY PLANTS

I. EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON THE FLOWER FORMATION

By

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Introduction

Temperature and photoperiod are the most important factors affecting the flower bud induction in the strawberry.

Sudds (13) reported that the flowering of the strawberry was hastened by exposure to 8-hour-day. Darrow, Waldo (2, 3), and Eguchi (4, 5, 8) determined that most varieties of strawberry are short-day plants. Darrow (2), Eguchi (6, 8) and Hartmann (10) reported that temperature may be as important as the photoperiod in inducing flower formation in the strawberry. Went (20) examined the influence of the combination of temperature with the photoperiod on flower bud formation in the strawberry plant in the phytotron and showed that temperature exerts a modifying influence on the response of the strawberry to the photoperiod. Eguchi *et al.* (9) and Yokomizo *et al.* (16, 17, 18) have reported that shading and transplanting also promoted to some extent the flower bud formation. And it is known that the lack of nitrogen fertilizer, affecting the nutrition of strawberry plants, induces the earlier flower bud formation.

Most of the investigations except that of Went (20) have treated the plants under the natural seasonal changes. Accordingly the effects of temperature and photoperiod, either working singly or together, are liable to be obscure.

The purpose of this paper is to investigate the sensitivity of the plants related with age and size and the effect of artificially controlled temperature and photoperiod, employing the phytotron, on the flower formation of the strawberry plants.

Materials and methods

The variety used was Robinson.

Runner plants are selected for uniformity from the mother plants during June to July and brought up in the nursery bed under midsummer hot, long day conditions.

Temperature and photoperiodic treatments are carried out in the phytotron.

After the last treatment, the plants are transferred to the continuously illuminated greenhouse (24°C) for the purpose of avoiding the effect of natural temperature and photoperiodic influences to stimulate the flower formation.

Results

1. Effect of temperatures on the flower bud formation.

Plants were exposed to 9°, 17° and 24°C under 8 hour or continuous illumination for various durations, commencing on Aug. 21.

After a definite period of the temperature treatment, the treated plants were again brought back to the continuously illuminated greenhouse (24°C) at three or four days intervals.

They were microscopically observed 25 days after the last treatments. The results are shown in Table 1.

Table 1. Effects of temperatures on the flower bud formation.

Temperature (°C)	Photoperiod (hr)	No. of plants	Number of days of temperature treatments					
			4	7	10	13	16	20
9	8	3	× × ×	× × ×	× × ○	○○○	○○○	○○○
	24	3	× × ×	× × ×	○○○	○○○	○○○	○○○
17	8	3	× × ×	× × ×	○○○	○○○	○○○	○○○
	24	3	× × ×	× × ×	× × ×	× × ×	× × ×	× × ×
24	8	3	× × ×	× × ×	○○○	○○○	○○○	○○○

○ : Flower bud formed × : None

The plants chilled at 9°C for less than 7 days failed to initiate the flower buds. After 10 and more days of 9°C temperature treatment, the plants formed flower buds under either 8-hour-day or continuous illumination.

The plants placed in 17°C greenhouse for 10 or more days under 8-hour-day formed flower buds. Under the continuous illumination, however, the plants failed to form the flower buds even with 20 days temperature treatment at 17°C.

At 24°C, the plants formed flower buds after 10 or more days treatments under 8-hour-day.

It seems that at the temperatures between 9°C and 24°C, plants form flower

buds after 10 days temperature treatments under 8-hour-day and at 9°C they form flower buds even under the continuous illumination.

2. Effect of photoperiod on the flower bud formation.

Plants were treated with a certain cycles of 8-, 12-, 16-, 20- and 24-hour-day treatment at 9°C and then brought back to the continuously illuminated greenhouse (24°C). The treatments were commenced on Aug. 24.

Table 2. Effects of photoperiods on the flower bud formation (Temperature: 9°C).

Photoperiod (hr)	No. of plants	Cycles of photoperiodic treatments					
		4	7	10	13	16	20
8	3	×××	×××	××○	○○○	○○○	○○○
12	3	×××	×××	○○○	○○○	○○○	○○○
16	3	×××	×××	○○○	○○○	○○○	○○○
20	3	×××	×××	○○○	○○○	○○○	○○○
24	3	×××	×××	○○○	○○○	○○○	○○○

○ : Flower bud formed × : None

As shown in Table 2, the plants, treated with 4~7 cycles of the respective photoperiodic treatment failed to form the flower buds and formed flower buds after 10 or more cycles of the photoperiodic treatments.

3. Effect of temperature and photoperiod on the flower bud formation.

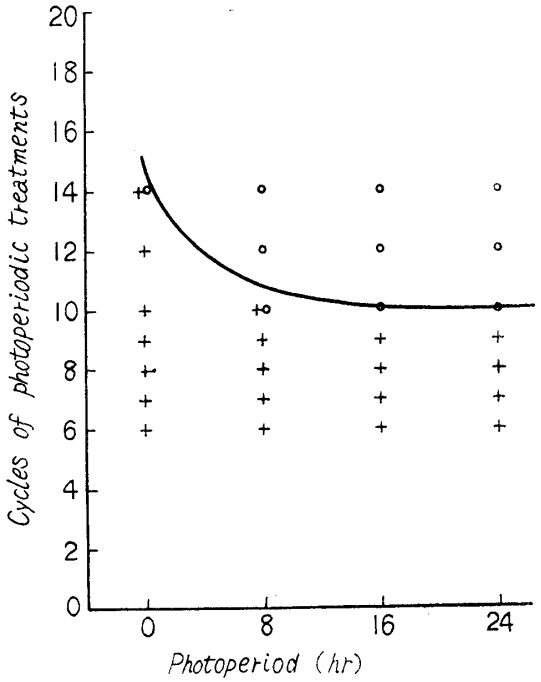
Plants were treated with the combinations of four different temperatures (9°, 17°, 24° and 30°C) and seven photoperiods (0-, 4-, 8-, 12-, 16-, 20- and 24-hour) for various durations commencing on Aug. 21. Plants were brought back to the continuously illuminated greenhouse (24°C) after the treatments of a definite length and examined for flower bud.

The results are shown in Figs. 1, 2, 3 and 4.

At 9°C, with less than nine cycles, no photoperiodic treatment induced flower bud formation. With 10 or more cycles of 8-, 16- and 24-hour photoperiodic treatment, plants formed flower buds. Plants placed under continuous darkness required 14 days treatment for the flower bud formation.

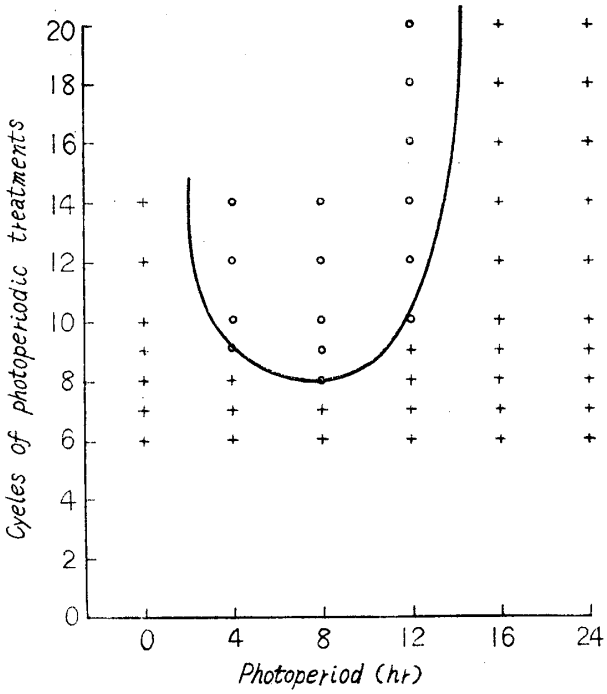
At 17°C, the plants placed under 16-hour or more longer photoperiods failed to form flower buds even with 20 cycles treatments. Plants formed flower buds, however, with 10 cycles of 12-hour-day, with eight cycles of 8-hour-day and with 9-cycles of 4-hour-day and under continuous darkness failed to form the flower buds even with 14 days treatment.

At 24°C, the plants grown under long-day condition of more than 16-hour-day failed to form the flower buds even with 20 cycles. Under 12-hour-day, some plants were induced to form flower buds with 12~14 cycles treatments and all



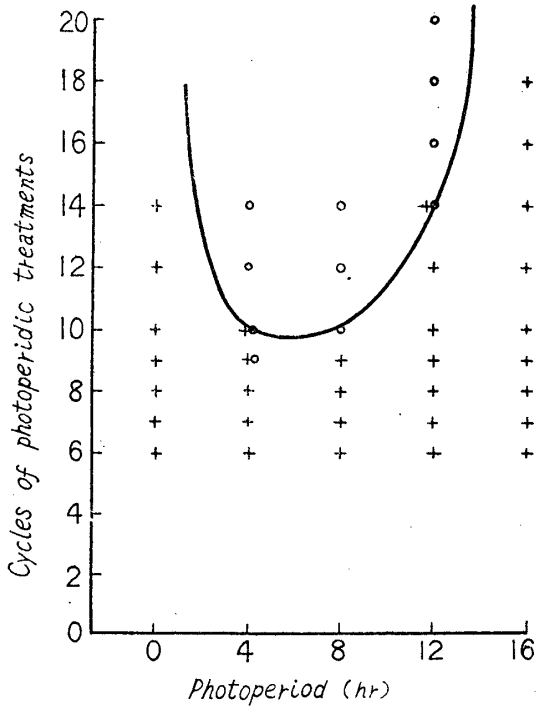
○ : Flower bud formed
+ : None

Fig. 1. Effects of photoperiods at 9°C on the flower bud formation.



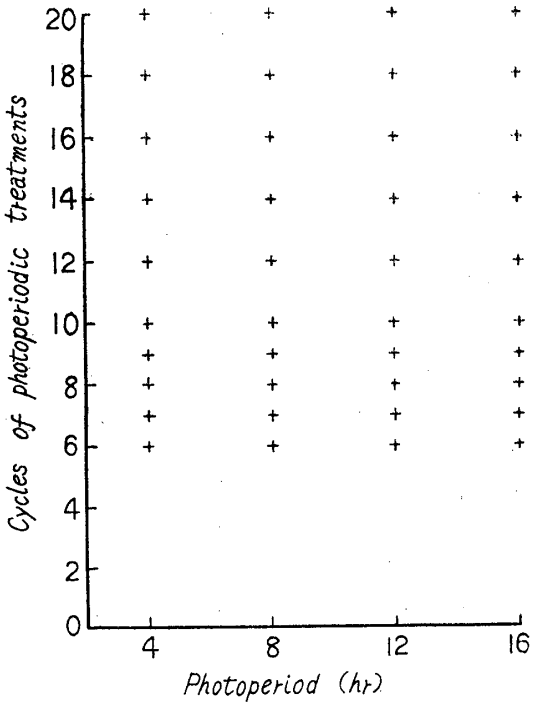
○ Flower bud formed
+ : None

Fig. 2. Effects of photoperiods at 17°C on the flower bud formation.



○ : Flower bud formed
+ : None

Fig. 3. Effects of photoperiods at 24°C on the flower bud formation.



○ : Flower bud formed
+ : None

Fig. 4. Effects of photoperiods at 30°C on the flower bud formation.

others formed flower buds after 16 cycles treatment. Under 8- and 4-hour-day, the plants formed flower buds with 10 cycles treatment. Plants grown under continuous darkness failed to form flower buds even with 14 days treatment.

At 30°C, the plants placed under any photoperiod failed to form flower buds even with 20 cycles treatments. Short-day was non-effective for flower formation at 30°C.

4. *Effect of temperature and 16-hour-supplement-illumination with electric lamps of various light intensities added to 8-hour-natural day-light on the flower bud formation.*

Supplemental illumination with electric lamps of 2, 16, 32 and 160 f.c. were given for 16 hours per day to the strawberry plants grown under 8-hour natural-day-light in the 17°C or 24°C greenhouse.

After the treatments for various lengths, having been commenced on Sept. 14, the plants were transferred to the greenhouse (24°C) continuously illuminated with electric lamps (160 f.c.) for all night and examined for flower buds.

Table 3. Effect of 16-hour-supplement-illumination with electric lamps of various light intensities added to 8-hour natural-day-light on the flower bud formation.

Temperature (°C)	Light intensity (f.c.)	Number of days of temperature and photoperiodic treatments					
		4	6	8	10	12	14
17	0	× × ×	× × ×	○○○	○○○	○○○	○○○
	2	× × ×	× × ×	○○○	○○○	○○○	○○○
	16	× × ×	× × ×	○○○	○○○	○○○	○○○
	32	× × ×	× × ×	○○○	○○○	○○○	○○○
	160	× × ×	× × ×	○○○	○○○	○○○	○○○
24	0	× × ×	× × ×	○○○	○○○	○○○	○○○
	2	× × ×	× × ×	× × ×	× × ×	× × ×	× × ×
	16	× × ×	× × ×	× × ×	× × ×	× × ×	× × ×
	32	× × ×	× × ×	× × ×	× × ×	× × ×	× × ×
	160	× × ×	× × ×	× × ×	× × ×	× × ×	× × ×

○ : Flower bud formed × : None

Under short day, plants formed flower buds after eight days at both of the temperatures, as shown in Table 3.

Even under long-day (8-hour solar radiation + 16-hour supplement electric light), the plants formed flower buds with eight days treatment at 17°C. Fig. 2 showed that at 17°C, the plants failed to form flower buds under long-day condition, plants having been brought up under hot, long-days of August. In this case, the plants are brought up under cool, short days of September. Plants have

been affected through the preceding environmental conditions before the artificial treatments. Seasonal influences of temperature and photoperiod are related in Chapter 6.

Plants placed at 24°C failed to form flower buds under the supplemented illumination. Even the electric lamp of 2 f.c. inhibits the flower formation at 24°C.

5. Effect of daily interposed high temperature treatment of various duratious on the flower formation.

Effect of the interposed artificial high temperature (24°C) treatment of 24, 20, 16, 12, 8 and 4 hour-duration on the flower formation was investigated with plants set under 8-hour-day or continuous illumination in 9°C greenhouse.

After daily high temperature treatment for various durations, commenced on Aug. 21, the treated plants were transferred to the continuously illuminated greenhouse (24°C).

They were examined for the flower buds 25 days after the last treatment.

Table 4 shows that under 8-hour-day after more than 10 days treatments with the interposition of various durations of high temperature, plants formed flower buds.

Under the continuous illumination, plants failed to form flower buds with daily high temperature treatment of 12-hour or longer duration, and with daily high temperature treatment of less than 8-hour, plants formed flower buds with 14~16 days treatment.

The less the duration of high temperature, the less days are needed for flower bud formation. It is indicated in Table 4 that the total sum of low temperature exposure to 9°C effective for the flower bud formation is about 240 hours and in the case of daily exposure to 9°C less than 12-hour, plants fail to form flower buds even after the total sum of hours exposed to 9°C goes over 360 hours. It is shown that effective daily low temperature is needed working for longer than 16 hours per day.

6. Relation of time factor with the sensitivity of the plants to the photoperiodic influences for flower formation.

Short-day treatments were conducted with six-leaved plants in July, August and September.

Six-leaved plants were selected for uniformity from the runner of mother plants on July 4, 27 and August 17 respectively. Short-day (8-hour) treatment was commenced on July 20, Aug. 10 and Sept. 1 for various durations at 17°C. After the treatments, plants were transferred to the continuously illuminated greenhouse (24°C). The results are shown in Table 5.

Treatments more than 13 cycles, commenced on July 20, were effective for the flower buds formation. Treatments, 10 cycles, commenced on Aug. 10

Table 4. Effect of daily interposed temperature treatment of various durations on the flower bud formation.

Controlled room temperature (°C)	Photoperiod (hr)	Hours exposed to		Number of days of temperature treatment									Total sum of low temperature 9°C exposure needed for flower bud formation (hrs)
		high temperature per day	room temperature per day	6	8	10	12	14	16	20	25	30	
9	8	24	0	×××	×××	○○○	○○○	○○○	○○○	○○○			
		20	4	×××	×××	○○○	○○○	○○○	○○○	○○○			
		16	8	×××	×××	○○○	○○○	○○○	○○○	○○○			
		12	12	×××	×××	○○○	○○○	○○○	○○○	○○○			
		8	16	×××	×××	○○○	○○○	○○○	○○○	○○○			
		4	20	×××	×××	×○○	○○○	○○○	○○○	○○○			
		0	24	×××	×××	×○○	○○○	○○○	○○○	○○○			
	24	20	4	×××	×××	×××	×××	×××	×××	×××	×××	×××	(120)
		16	8	×××	×××	×××	×××	×××	×××	×××	×××	×××	(240)
		12	12	×××	×××	×××	×××	×××	×××	×××	×××	×××	(360)
		8	16	×××	×××	×××	×××	××○	×○○	○○○	○○○	○○○	256
		4	20	×××	×××	××○	×○○	○○○	○○○	○○○	○○○	○○○	240
		0	24	×××	×××	○○○	○○○	○○○	○○○	○○○	○○○	○○○	240

○ : Flower bud formed × : None

induced flower bud formation and 8~9 cycles treatments commenced on Sept. 1 were sufficient to induce the flower formation.

Table 5. Effects of photoperiod on the flower bud formation in six-leaved plants, treated in July, August and September. Plants developd to six-leaf-stage were selected for each experiment.

Time of treatments	Number of days of the treatment							
	6	7	8	9	10	13	16	20
July 20~	×××	×××	×××	—	×××	○○○	○○○	○○○
Aug. 10~	×××	×××	×××	—	○○○	○○○	○○○	○○○
Sep. 1~	×××	×××	×○○	○○○	○○○	○○○	○○○	○○○

○ : Flower bud formed × : None

It seems that the effect of the preceding environmental conditions and the growth status of the seedling before the treatment influence the sensitivity of the plants to the photoperiodic influences, though the plants were selected for uniformity in the apparent size.

7. *Relation of age and size with the sensitivity of the plants to the temperature and photoperiodic influences for flower formation.*

It is shown in Table 6 that flower buds initiate in the first runner plant on Oct. 3~10 and in the second and third runner plants on Oct. 10~17. It seems

Table 6. Sensitivity of the plants as related with age. Floral development of the runner plants under the natural environmental conditions. (Variety : Victoria)

Plant age (Represented by the portion on the runner)	Date	No. of plants	Mode of the growing point						
			Undifferentiated	Dome shaped	Flower differentiated	Sepals formed	Petals formed	Stamens formed	Pistils formed
First runnner Plant	Sep. 26	5	5						
	Oct. 3	5	3	2					
	Oct. 10	5	2	2	3	1	1		
	Oct. 17	5				2	2	1	
Second runner plant	Sep. 26	5	5						
	Oct. 3	5	5						
	Oct. 10	5		1	4				
	Oct. 17	5			1	4			
Third runner Plant	Sep. 26	5	5						
	Oct. 3	5	5						
	Oct. 10	5	2	2	1				
	Oct. 17	5		2	3				

that flower formation is affected by plant age and size.

Plants (Table 7) were treated with two photoperiods (8-hour and 24-hour day) and two temperatures (9°C and 17°C) for various durations commencing on Sept. 13. After the treatment, plants were transferred to the continuously illuminated greenhouse (24°C).

Table 7. The growth status of plants at the beginning of the temperature and photoperiodic treatments.

Plant age (Represented by the portion on the runner)	Top weight (g)	Plant height (cm)	Number of expanded leaves	Stem diameter (cm)
First runner plant	20.5	26.7	9.2	1.13
Second runner plant	7.6	22.8	6.1	0.81
Third runner plant	2.1	14.6	4.1	0.49

Table 8 shows that all the plants formed flower buds with eight cycles of 8-hour-day photoperiodic treatment at the both of temperatures. Under the con-

Table 8. Sensitivity of plants as related with age. Flower bud formation under the artificially controlled temperature and photoperiod.

Plant age (Represented by the portion on the runner)	Temerature (°C)	Photoperiod (hr)	Number of days of temperature and photoperiodic treatments				
			6	8	10	12	14
First runner plant	9	8	×	○	○	○	○
		24	×	○	○	○	○
	17	8	×	○	○	○	○
		24	×	○	○	○	○
	24	8	×	○	○	○	○
Second runner plant	9	8	×	○	○	○	○
		24	×	○	○	○	○
	17	8	×	○	○	○	○
		24	×	○	○	○	○
	24	8	×	○	○	○	○
Third runner plant	9	8	×	○	○	○	○
		24	×	×	○	○	○
	17	8	×	○	○	○	○
		24	×	×	×	○	○
	24	8	×	○	○	○	○

○ : Flower bud formed × : None

tinuous illumination, at 9°C, the younger plants formed flower buds two days later than the older plants and at 17°C they were four days later than the older.

It may be concluded that no differences are found in the responses of the plants with different ages or sizes under the favorable photoperiodic and/or temperature conditions for flower buds formation, but under the unfavorable conditions the response of younger plants slowed down a little.

Discussion

It is shown that low temperature of about 9°C is the critical for the flower bud formation in the strawberry plant. At 9°C, the flower bud formation occurs under either short-day or continuous illumination. At 17° and 24°C, photoperiods longer than 16 hours failed to induce the flower bud formation and short-day in the range of 4~12 hours induces the flower bud formation. At 30°C, even the short day treatment such as four or eight hours failed to induce the flower bud formation.

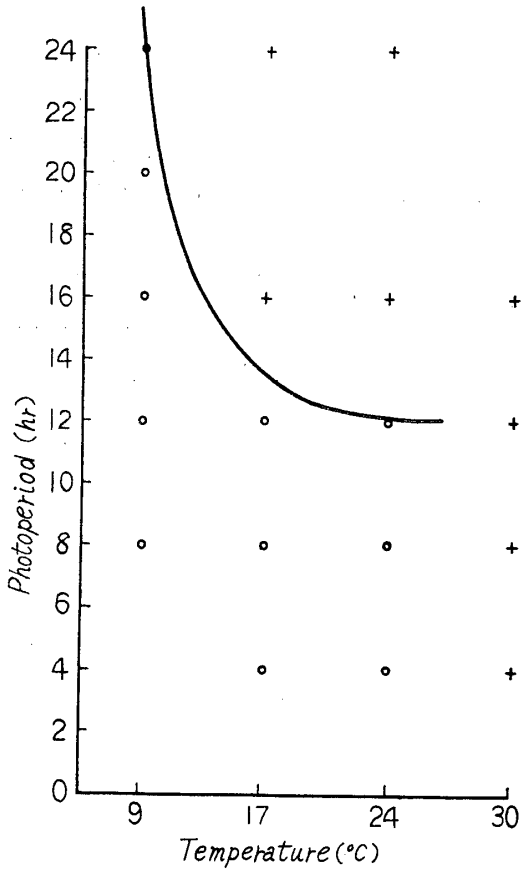


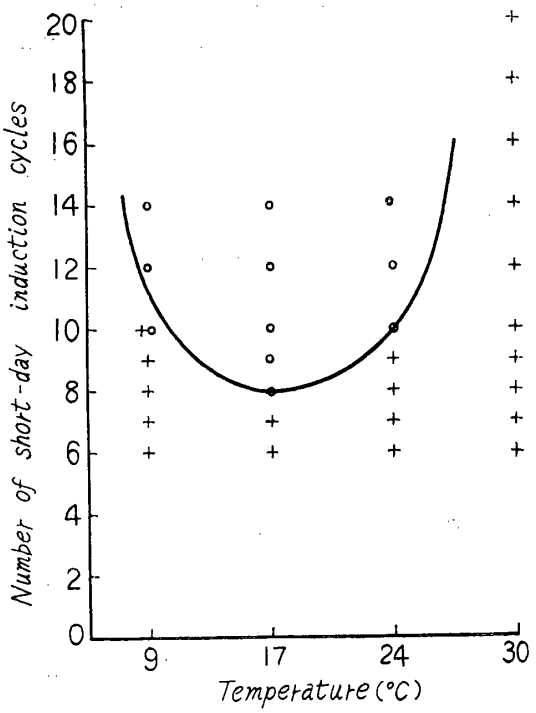
Fig. 5. Interrelations between critical photoperiod and temperature to induce the flower bud formation.

Considering the results of the other investigators (1, 2, 3, 4, 5, 6, 8, 10, 14, 15, 19, 20), it may be safely concluded that the flower bud formation of the strawberry plant is induced at the temperatures below 12~14°C indifferent with the length of day. At the temperatures in the range of 17° to 24°C, short-day below 12-hour-day is necessary for flower formation and as the temperature rises from 9° towards 24°C, the shorter photoperiod is needed (Fig. 5). At the temperature above 30°C, no flower buds are induced even under short-day.

In the range of 17° to 24°C, the strawberry plant behaves as a short-day plant.

It is very interesting that critical repetition cycles of photoperiodic treatments needed for the flower bud initiation vary relating with temperature and photoperiod (Fig. 1, 2, 3, 6).

At 9°C, flower buds initiate with 10 cycles of 16-hour-day or continuous



○ : Flower bud formed
\+ : None

Fig. 6. 8-hour-day photoperiodic cycles needed for flower bud formation at 9°C, 17°C, 24°C and 30°C.

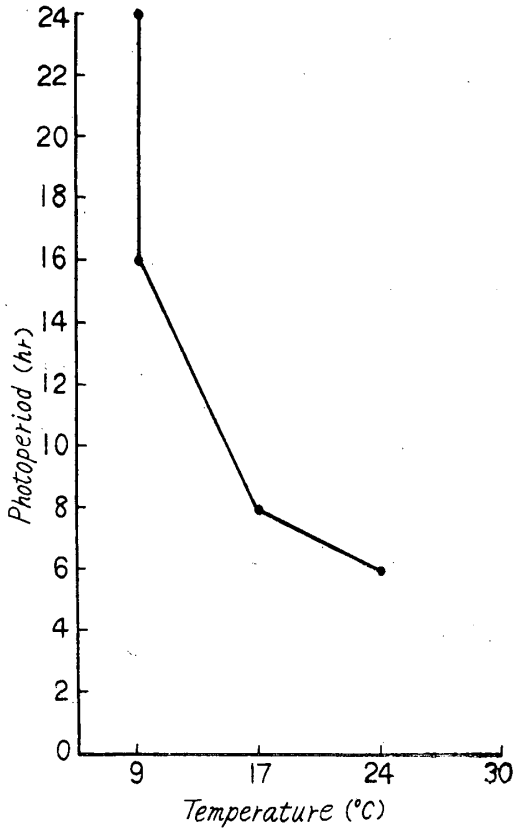


Fig. 7. Interrelations between optimum photoperiod and temperature to induce the flower bud formation.

illumination and with 10～12 cycles of 8-hour-day, at 17°C, with eight cycles of 8-hour-day, with 10 cycles of 12-hour-day and with nine cycles of 4-hour-day, and at 24°C, with 10 cycles of 4- and 8-hour-day, and 14～16 cycles of 12-hour-day.

It is remarkable that at 9°C, flower buds initiate with less repetition of photoperiodic cycles under 16-hour-day or continuous illumination than under 8-hour-day.

At 17°C, on the other hand, it is shown that under 8-hour-day flower buds initiate with the least repetition of photoperiodic cycles as compared with the plants set under 4-hour-day or 12-hour-day.

At 24°C, under 4～8-hour-day flower buds inititiate with the least repetition of the photoperiodic cycles (Fig. 7).

Went (20) observed in his experiments in the phytotron that short-day is most effective at 17°C, critical photoperiodic repetition being nine cycles, at 20°C and 24°C being 11 cycles, at 23°C being 15 cycles and at 10°C more than 16 cycles are needed for flower bud formation.

Although high temperature (24°C) interposed during low temperature (9°C)

treatment under continuous illumination diminishes the stimulating effect of low temperature for flower initiation, flower buds are induced when daily low temperature duration goes over 16 hours (Table 4).

The effect of low temperature and short-day treatment varies with the changes of the seasons (Table 5). The minimum cycles of short-day and low temperature necessary for the flower bud differentiation decreases as season progresses from July to September. It may be due to the seasonal changes of temperature and photoperiod accompanied by the elapse of the time from summer to autumn. Strawberry plants are under the influence of the environmental factors preceding the treatments.

The sensitivity of the plants to temperature and/or photoperiod varies with the size and age of the plant (Table 8). The older or larger plants are more sensitive than the younger or smaller plants. Under the favorable conditions of temperature and photoperiod, plants of the different size and age form flower buds all with the minimum cycles of the treatments, the difference of the sensitivity of the plants being utterly masked. Under the unfavorable effect of the temperature or photoperiod, the older or larger plants form flower buds with the less repetition of the treatments than the younger or smaller plants. Rickey *et al.* (12) findings are just in accordance with these results.

Hill (11) and Eguchi (7) reported that the strawberry plants form flower buds all simultaneously at a certain time. In the fall, towards the end of September, strawberry plants, indifferent with their age or size, form flower buds under the effect of the favorable low temperature and short-day, both favorable for flower induction in strawberry plants.

Summary

1. The flower buds initiate in strawberry plants under short-day and even under continuous illumination at the low temperature of 9°C. At 17° and 24°C, the flower buds are formed only under short-day between 4- and 12-hour-day-length, 8-hour-day being most effective for the flower bud differentiation. At 30°C, plants failed to form the flower buds even under 4- or 8-hour-day.

It may be concluded that at the temperatures below 24°~26°C, short-day and low temperature under various day-lengths are effective for the flower initiation in strawberry plants. At the temperatures below 24°~26°C, the minimum necessary replication of photoperiodic treatment (4~12-hour-day) is 8~12 cycles.

2. Strawberry plants are very sensitive to the supplementary electric light. Illumination of 2 f.c. lamps, supplemented to 8-hour-day, inhibited the flower initiation at 24°C.

3. High temperature (24°C) interposed during low temperature (9°C) treatment under continuous illumination diminishes the stimulating effect of low temperature for flower intiation. Flower buds are formed with the daily high

temperature interruption less than eight hours and no flower buds are formed with the high temperature interruption longer than 12 hours. Under 8-hour-day, plants formed buds with the interruption of any durations of high temperature.

4. The minimum necessary replication of low temperature and/or photoperiodic treatments for flower induction decreases as time elapses from July to September. Plants tend to respond more sensitively as the season progresses from summer to autumn. It is due to the fact that plants are influenced by the environmental factors, the seasonal changes of temperature and photoperiod preceding the treatments.

5. The sensitivity of the plants to temperature and/or photoperiod varies with the size and age of the plant. The older or larger plants are more sensitive than the younger or smaller plants.

Under the unfavorable condition of temperature or photoperiod, the older or larger plants respond much more sensitively to the stimulating effect than the younger or smaller plants. Under the favorable stimulating conditions of photoperiod and temperature, however, plants with different size and age, with different sensitivity, form flower buds all at the same time.

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