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著者	ITO Hideo, KATO Toru, KONNO Yoshitaka
journal or publication title	Tohoku journal of agricultural research
volume	14
number	2
page range	51-65
year	1963-11-08
URL	http://hdl.handle.net/10097/29427

FACTORS ASSOCIATED WITH THE FLOWER INDUCTION IN LETTUCE

By

Hideo ITO, Toru KATO and Yoshitaka KONNO

Department of Agronomy, Faculty of Agriculture, Tohoku University, Sendai, Japan

(*Received, May 7, 1963*)

Introduction

Seedstalks often develop before the lettuce plant is full grown, and this results in the loss to the grower.

In the previous report(4), the senior author showed that at high temperature, the leafy heads of lettuce became loosened and the stem elongated, being accompanied by blooming.

Thompson and Knott (7, 8) examined the influence of temperature upon lettuce and the result was in accordance with the author's experiment.

It seems that at higher temperature, the stem becomes elongated and this is followed by flower differentiation in the lettuce plant.

Bremer(1, 2) reported on the genetical factors which respond to the photoperiod. Cajlachjan(3), Rappaport(6) and Yamazaki(10) reported that the long-day was essential for flower induction in lettuce.

Tincker(9) showed that lettuce could be divided into two classes, first those whose preflowering period length depends on the length of the day, and secondly those in which the formation of the flowering stem does not depend on day-length.

In the author's experiment, the New York variety was indifferent to the photoperiod. Also in Thompson and Knott's experiment, the length of the day had no appreciable effect on the seedstalk development.

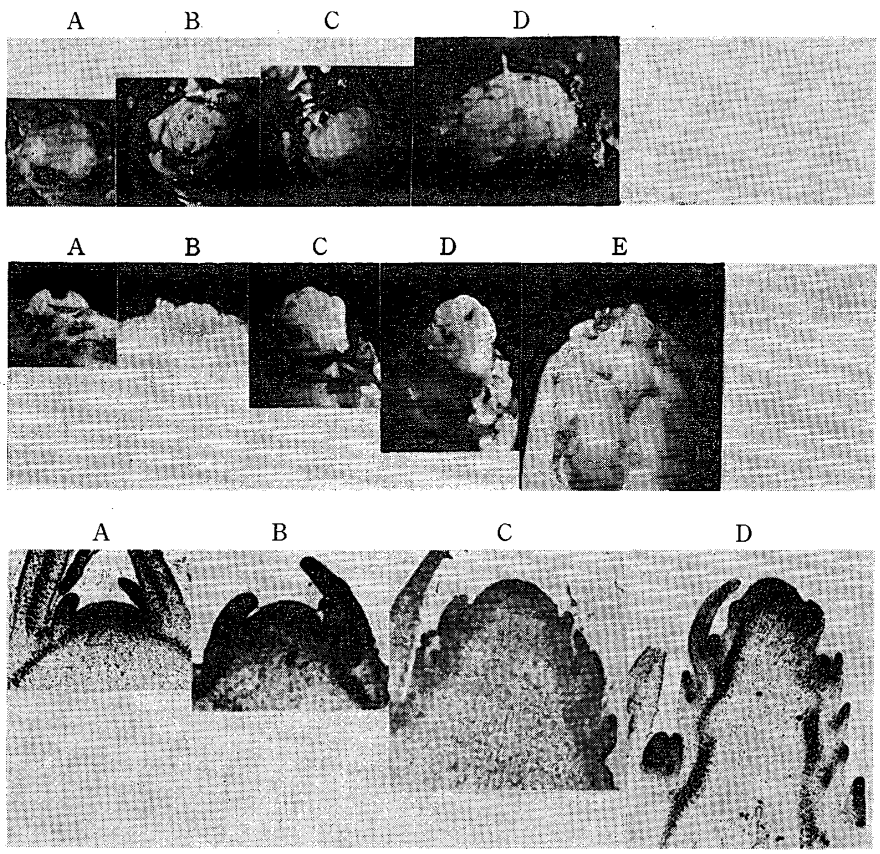
The present work was undertaken with the objective of making a further accurate study of the factors associated with the stem elongation and flower induction in the lettuce plant by means of phytotron.

Materials and methods

Varieties: Wayahead, Great Lakes, Imperial 847, Pennlake, Paris Market, New York and May King were used.

Temperature treatments were carried out in the phytotron and in the greenhouse with the electric heating system.

The growing points were examined under the binocular microscope. The stages of the development are discriminated as shown in Fig. 1.



A : Undifferentiation, B : Flower bud differentiation, C : Terminal bud differentiation, D : Lateral flower bud formation, E : Bract formation. Upper row : Top-view, Middle row : Side-view, Bottom row : Vertical section.

Fig. 1. The process of flower bud differentiation in the lettuce plant (Variety : Wayahead)

Results

1. The range of temperature needed for the bolting of the lettuce plant.

Experiment 1.

The seeds of the variety Wayahead were sown on May 2 in the 17°C greenhouse.

On June 8, half of the plants were transferred into the 23°C greenhouse. The plants transferred into the 23°C greenhouse bolted and bloomed on Oct. 1. The plants in the 17°C greenhouse showed no sign of stem elongation (Fig. 2).

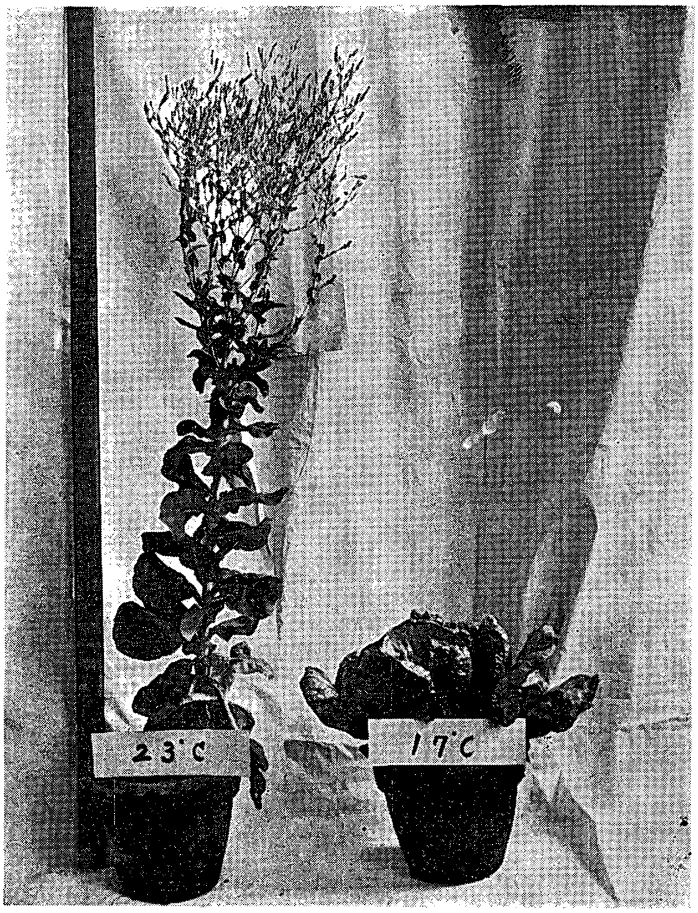


Fig. 2. Critical temperature for flower induction of lettuce plant.
Left : Plant exposed to 23°C for 110 days : Flowering
Right : Plant exposed to 17°C for 110 days : Non-bolting
The photograph was taken on Oct. 1.

It seems that a certain period of exposure to higher temperature above 20°C is needed for the lettuce plant to form flowers and to bolt.

Experiment 2.

The seeds of the variety Wayahead were sown on May 2 in 17°C greenhouse. On September 12, the plants were transferred into the 23°C and 30°C greenhouse.

It is shown in Fig. 3 that the plants placed in the 30°C greenhouse bolted and formed flower buds much earlier than the ones placed in the 23°C greenhouse. The higher the temperature, the earlier the flower differentiates and the longer the stem becomes elongated(Fig. 3).

2. Duration of high temperature needed for the flower induction.

The seeds of the Wayahead variety were sown on September 7 in the 17°C greenhouse.

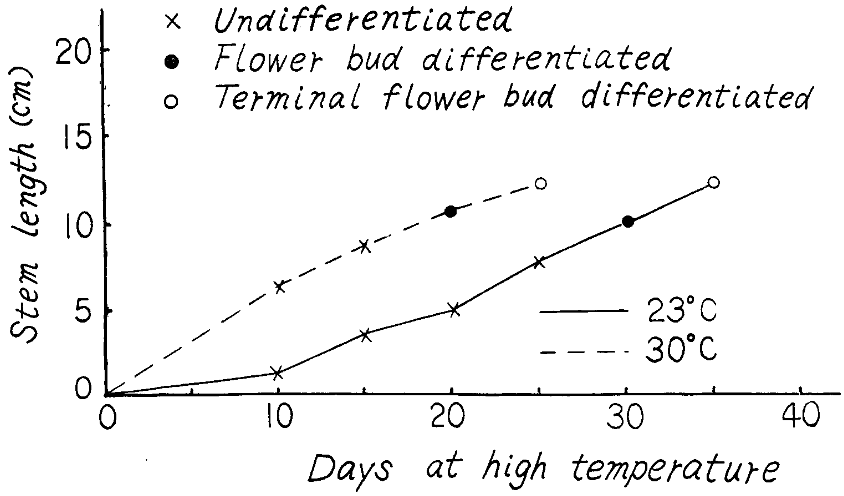


Fig. 3. Effect of high tempeiature on the flower induction of the lettuce plant.

On October 15, some of the plants were transferred into the 23°C greenhouse, and after a certain period of exposure to 23°C they were returned to the 17°C room(Fig. 4).

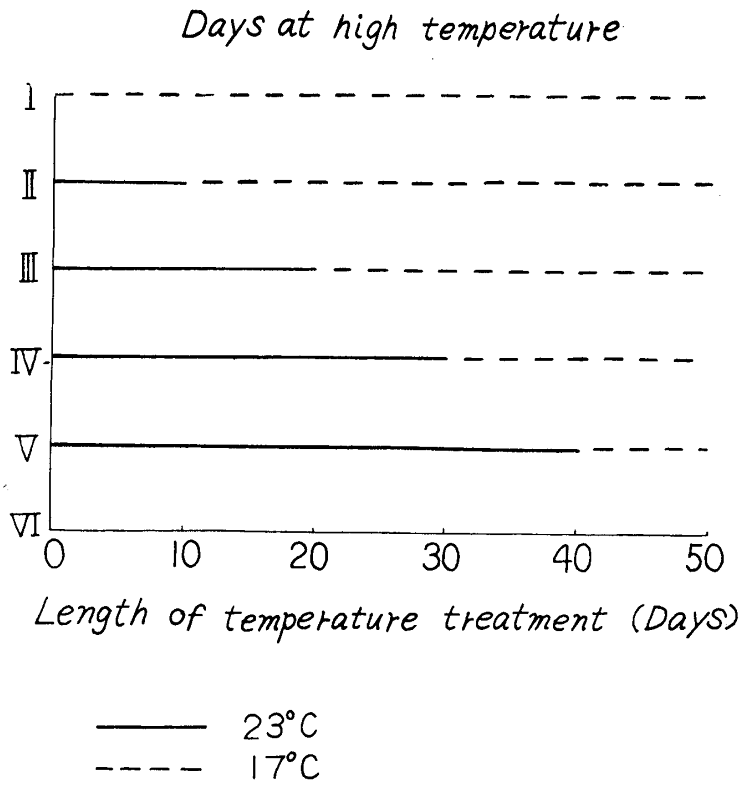
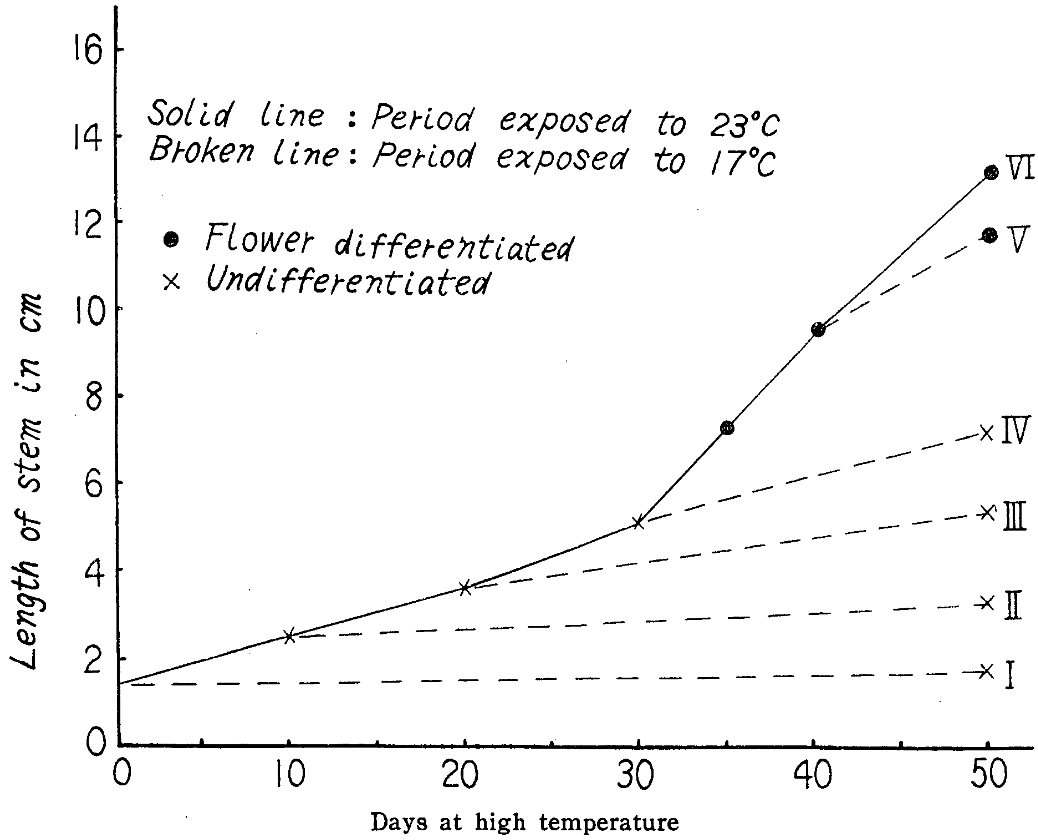


Fig. 4. Designs of the high temperature treatment.

The results are shown in Fig. 5.

Stem length is indicated as ordinate. Stems elongated as the time elapsed. Higher temperature favored the stem elongation. The longer the exposure to higher temperature, the longer the stem became elongated.



Variety : Wayahead
Seeds were sown on Sept. 7.

Fig. 5. Effect of high temperature on the stem elongation and flower induction.

At 23°C, the flowers are induced after 35 days exposure and no flowers are induced in the other plots. It is indicated that 35 days exposure to 23°C is needed for flower induction.

3. The effect of daily length of high temperature (25°C).

The seeds of the variety Wayahead were sown on Sept. 5. Beginning on October 12, the daily temperatures were controlled as shown in Table 1.

Table 1. Effect of daily interposed higher temperature treatment of various duration on the flower induction under natural day-length.

Hours exposed to		Date of flower induction	No. of days to flower induction	Length of stem(cm) (Dec. 20)
25°C	17°C			
24	0	Nov. 10	30	50.4
16	8	Dec. 10	60	10.5
8	16	—	— *a	7.5
0	24	—	— *b	7.0

* a, b Undifferentiated

The plants daily exposed to 25°C for 16 hours differentiated flowers within 60 days and those daily exposed to 25°C for 24 hours differentiated flower buds in 30 days. None differentiated flower buds, being exposed to 25°C for less than 8 hours daily.

It seems that daily longer exposure to 25°C favored the stem elongation and hastened the flower induction, and exposure to 25°C for less than 8 hours daily failed in flower induction even after two months experiment.

4. Influence of the combinations of low and high temperature period on the stem elongation.

Design of the treatment is shown in Fig. 6.

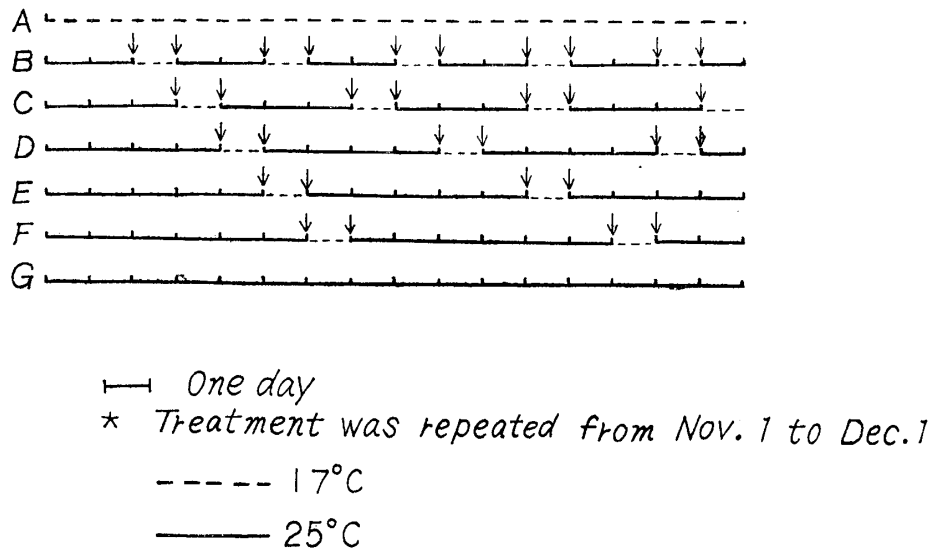


Fig. 6. Diagram showing the designs of the combinations of low and high temperature period.

It is indicated in Table 2 that one day low temperature to two, three and four days high temperature (25°C) combinations scarcely resulted in the stem elongation. One day low temperature to five days high temperature combination resulted in the slight stem elongation. High temperature treatment longer than six days to one day low temperature treatment resulted in marked stem elongation. Low temperature so often prevailed restricted the stem elongation against the influence of the high temperature treatment.

Table 2. Influence of the combinations of low and high temperature period on the stem elongation.

Plot	No. of total days exposed to 25°C	Stem length (cm) (Dec. 1)
A	0	5.4±0.4
B	20	5.4±0.2
C	23	5.6±0.3
D	24	5.6±0.3
E	25	6.2±0.2
F	26	11.8±0.6
G	30	13.1±0.4

5. Age of the plant associated with the sensitivity to high temperature.

Seeds of the variety Wayahead were sown on February 1 in the 17°C greenhouse.

Beginning on March 17, the plants were successively transferred into the 23°C greenhouse and examined for flower induction and stem elongation.

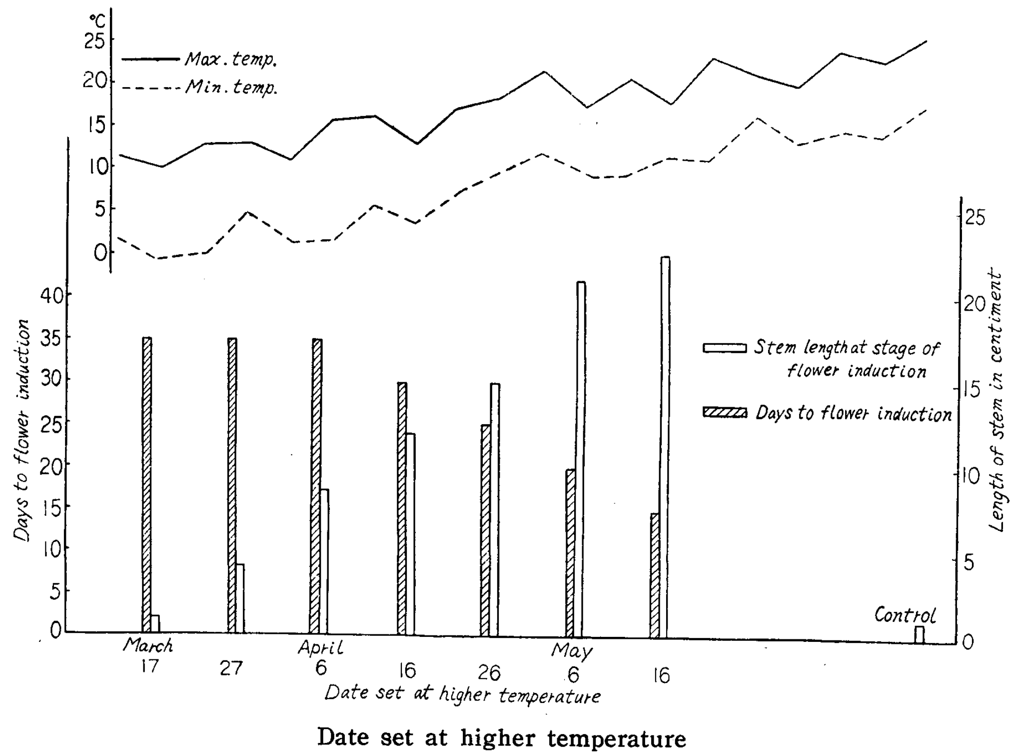
Growth status of the plants on the successive date of the high temperature exposure set in is shown in Table 3.

Table 3. Growth status of the lettuce plant
Variety: Wayahead
Seeds were sown on Feb. 1

Date	March		April			May	
	17	28	6	16	26	6	16
Expanded leaves	5.5	7.0	7.5	8.3	10.0	12.0*2	12.8
Stem diameter (mm)*1	2.0	2.3	4.0	5.8	8.3	9.2	10.4
Stem length (cm)	1.0	1.0	1.0	1.0	1.0	1.0	1.0

*1 Just below the cotyledon
*2 Head is formed on May 6

Plants with 7.5 expanded leaves and the stem 4 mm in diameter needed 35 days exposure to high temperature for flower induction and the plants with the well developed leafy head and the stem 10 mm in diameter needed only 15 days exposure to high temperature (Fig. 7).



Date set at higher temperature
Fig. 7. Number of days to flower induction needed for the lettuce plant of different ages.

Stems less elongated in the case of the younger plant at high temperature. In the cases of the older plants, stems elongated markedly at high temperature and long stems developed before the flower induction. The plants treated on May 16 (105 days from seed sowing) had the stems 22.5 cm long at the stage of the flower induction.

6. Size of the plant associated with the sensitivity to high temperature.

The varieties: Imperial 847, New York, Great Lakes and Paris Market were used.

The plants were grouped according to their size. Plant size is indicated with the stem diameter.

The results are shown in Fig. 8 and 9.

It is indicated that the larger the plants, the less the high temperature exposure needed for flower induction becomes. The larger plants respond to high temperature exposure much more sensitively than the smaller plants.

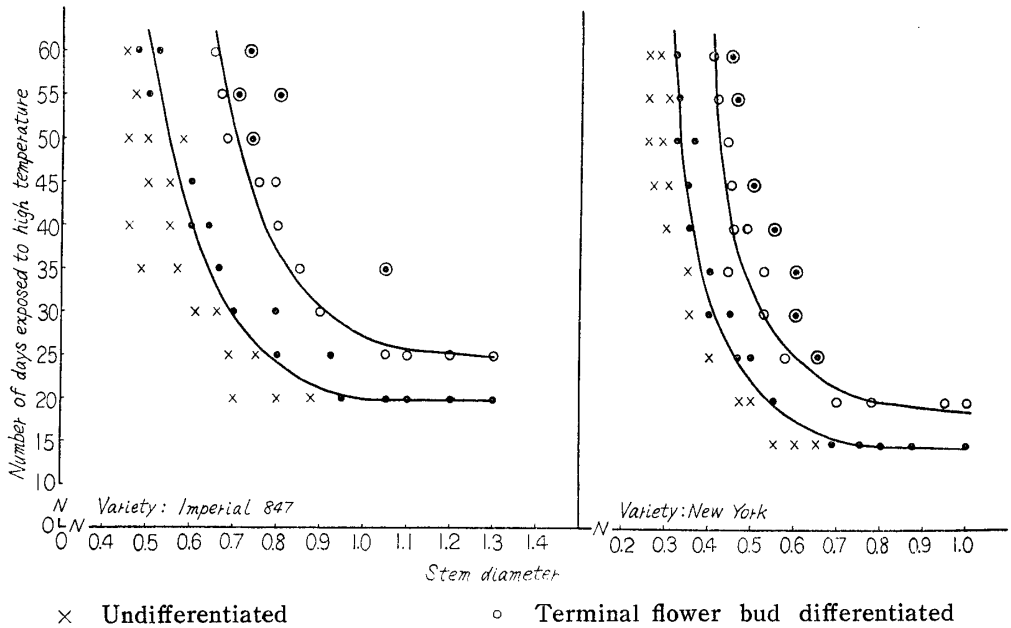
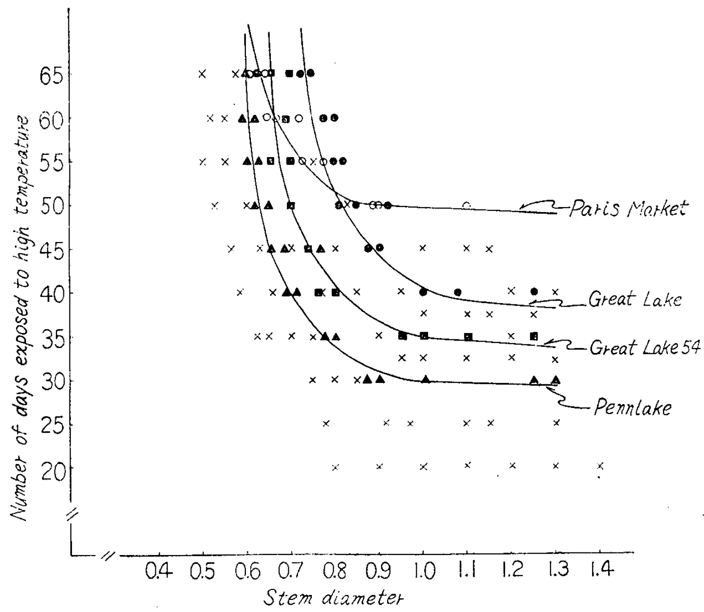


Fig. 8. Days to flower induction and to terminal flower buds differentiation in various sized lettuce plants.

In the case of New York variety, the length of exposure needed for flower induction lessens rapidly as the plant grows and in the case of Paris Market the length of exposure lessens little with plant growth.

7. Varietal differences in the sensitivity to high temperature for flower induction.

The varieties New York, Imperial 847, Pennlake, Great Lake 54, Great Lake



× Undifferentiated
Flower differentiated
▲ Pennlake
■ Great Lake 54
● Great Lake
○ Paris Market

Fig. 9. Varietal differences in number of days to flower bud differentiation of various sized lettuce plants.

and Paris Market were used.

The length of high temperature exposure needed for the flower induction of the full developed, headed plant was determined.

The results are indicated in Table 4.

New York variety with stems about 0.7 cm diameter was induced to initiate flowers through 15 days exposure to 23°C and Imperial 847 plant with stems exceeding 0.95 cm in diameter needed 20 days exposure to 23°C. Great Lake and Great Lake 54 variety needed 35—40 days exposure and Paris Market variety with stems 0.9 cm in diameter needed 50 days exposure to 23°C for flower induction.

Table 4. Varietal differences in the critical duration of high temperature for the flower induction in lettuce plants.

Variety	Plant Size represented with the stem diameter (cm)	Number of days to flower induction
New York	≧0.70	15
Imperial 847	≧0.95	20
Pennlake	≧0.90	30
Great Lake 54	≧0.95	35
Great Lake	≧1.00	40
Paris Market	≧0.90	50

* Stem diameter was measured just below the cotyledon.

8. Progress of flower induction.

In Fig. 1, the progress of flower induction in the lettuce plant is shown.

Terminal flower buds differentiate about 5 days after the first sign of flower induction as indicated in Fig. 8. The length of the interval is a little less in the larger plant than in the smaller one.

9. Effect of light intensity and nitrogen fertilizer.

On May 1, seeds of the variety Wayahead were sown in pots. Ammonium sulphate (3 g), superphosphate (3 g) and potassium chloride (3 g) were supplied to each pot.

Beginning on May 27, half of the plants were shaded with a sheet of cheese cloth and half of the shaded and unshaded plants were fertilized with ammonium sulphate (2 g per pot) at 5 days intervals.

On June 30 and July 7 the growth and auxin content in the apex were measured.

The results are indicated in Table 5. The growth and the progress of the flower induction of the shaded plants is considerably restricted as compared with those of the unshaded plants.

Nitrogen supply accelerates the growth and the progress of flower induction of the shaded and unshaded plants. Auxin content reflected the vigor of the growth.

10. Effect of short-day.

Seeds of the varieties Wayahead and Great Lake were sown on May 15.

The plants were set under short-day, a) for 20 days beginning on June 20, and b) for 35 days beginning on July 5.

The growth status of the plants on July 5 is indicated in Table 6.

It is indicated in Table 7 that the short-day exposure restrict the leaf development and leafy head formation at the natural temperatures from June to early August.

In Fig. 10, it is shown that the flower induction and the stem elongation are restricted under 8-hour-day length as compared with the plants placed under natural day length from June to early August.

Table 6. The growth status of plants at the beginning of the short-day treatment (July 5).

Variety	Mode of the growing point	Stem length (cm)	Top weight (gr)	Head weight (gr)
Wayahead	Flower bud undifferentiated	4.8	105.8	88.2
Great Lake	Undifferentiated	4.0	162.0	125.0

Table 5. Effects of nitrogen and light intensity on the flower bud differentiation of lettuce

Date investigated	Treatment		Total weight	Number of leaves			stem		The largest leaf		Auxin of apex *1	Stage of flower bud *2		
				expanded	unexpanded	total sum	length	diameter	length	width		I	II	III
June 30	unshaded	++N	62.5 gr	16.5	38.8	55.3	1.80 cm	1.42 cm	15.7	10.8	15.3	●●●	●●	
		N	47.0	16.9	34.0	50.9	1.60	1.35	15.0	9.8	14.0	●●○○	●	
	shaded	++N	42.5	16.0	24.5	40.5	2.00	1.28	16.2	11.3	13.3	●●●●●		
		N	39.7	15.5	25.0	40.5	2.00	1.25	14.2	11.0	12.0	●●●●●		
July 7	unshaded	++N	117.2	16.0	42.6	58.6	3.20	1.58	15.2	13.3	20.6	●	●●●●●	●●●●
		N	95.5	17.0	38.0	55.0	2.80	1.43	15.8	10.6	18.7	●●●	●●●●●	●●
	shaded	++N	78.0	19.0	30.0	49.0	3.85	1.37	18.2	11.7	15.2	●●●●●	●●●●	●
		N	74.0	17.8	28.5	46.3	4.00	1.34	20.3	11.6	14.6	●●●●●●	●●●	●

*1 Auxin is represented in total curvature degrees per 15 plants
*2 I Undifferentiated
II Differentiated
III Terminal cluster differentiated

Table 7. Effect of short-day treatment on the growth of lettuce plants
(Seeds were sown on May 15
Day-length was controlled from June 20 to July 10)

Variety	Photoperiod	Top weight (gr)	Number of leaves			Leaf size (cm)		Stem height (cm)
			Outer	Head	Total	Length	Width	
Wayahead	Long-day(natural)	102	14	51	65	13.0	12.4	2.4
	Short-day (8 hr)	56	21	19	40	16.2	11.4	1.9
Great Lake	Long-day(natural)	90	13	32	45	16.0	14.0	1.5
	Short-day (8 hr)	66	17	19	36	18.6	14.4	1.0

11. Defoliation and flower induction.

Seeds of the variety Wayahead were sown on April 15.

Beginning on May 20, the plants were defoliated in various ways as

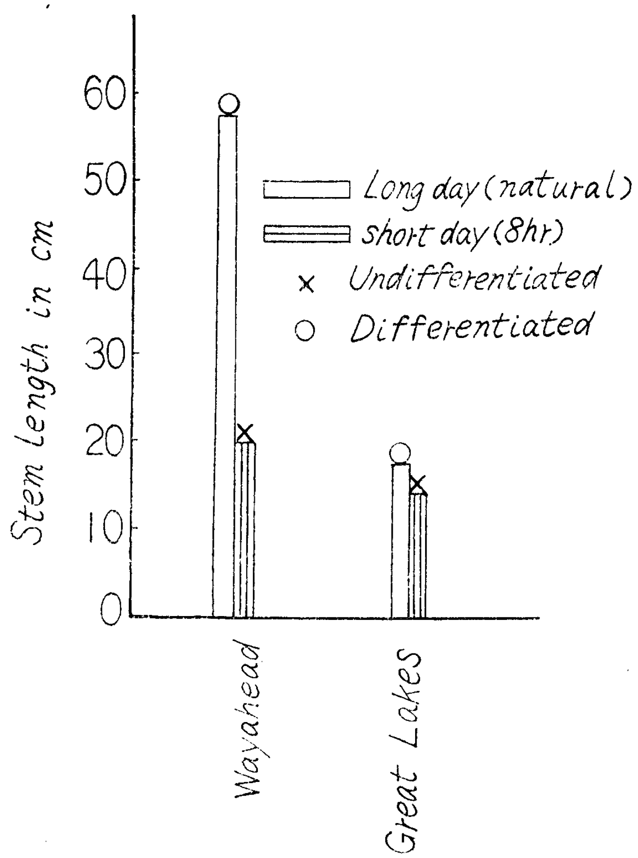


Fig. 10. Effect of short day treatment on the bolting in lettuce plants.
Short day treatment was made from July 5 to Aug. 10.

	June			July			Aug.	
	1～10	11～20	21～30	1～10	11～20	21～31	1～10	11～21
Av. Max. temp.	21.9	24.2	22.7	22.9	25.3	30.3	31.2	30.6
Av. Min. temp.	14.6	14.6	14.4	16.4	19.9	22.2	22.1	20.7

indicated below;

i) Untreated

ii) Half defoliated plot......leaves defoliated alternately from the outermost.

iii) 8 leaves plot......defoliated except for the outer 8 expanded leaves.

iv) 3 leaves plot......defoliated except for the outer 3 expanded leaves.

v) Immature leaves plot......defoliated successively except for the folding-immature leaves.

vi) Apical bud plot......defoliated except for the apical parts of the plants including a tiny few folding-immature leaves.

On June 5 and June 15, the plants were observed under the binocular microscope.

The results are indicated in Fig. 11.

During the course of the experiment the maximum temperature was above 20°C.

It is shown in Fig. 11 that defoliation retards the progress of flower induction. Defoliation even to the apical plant, however, does not inhibit the flower induction. It is very interesting that the lettuce plant is able to be induced to differentiate flowers even in the leafless condition.

Plot \ Stage	I	II	III	IV	V	VI	VII	VIII	IX	X
Untreated	•	• •	• •		○ ○	○	○ ○ ○	○ ○	○ ○	
Every other leaf defoliated	•	• • •	•		○ ○	○ ○ ○	○ ○ ○	○	○	
Defoliated except for 8 mature-leaves	• •	• •	•	○	○ ○	○ ○ ○	○ ○	○ ○		
Defoliated except for 3 mature-leaves	• • •	•	•	○ ○	○ ○ ○	○ ○	○ ○	○		
Defoliated except for immature-leaves	• • •	• ○ ○ • ○ ○	○ ○	○	○ ○ ○					
Defoliated to the apex	• • ○ • •	• ○ ○ ○ ○ ○	○ ○	○	○					

I Undifferentiated
II Differentiated
III Terminal cluster differentiated
IV Lateral cluster differentiated
V Bracts of the terminal cluster formed
VI Flower primordia formed
VII Petals formed
VIII Stamens formed
IX Carpel formed
X Pappus formed

• Determined on June 5.
○ Determined on June 15.

*1 Defoliation was made on May 20, on the seedlings sown on April 15 in the greenhouse.
*2 During the course of experiment the max. temperature was above 20°C.

Fig. 11. Effect of defoliation on the flower bud differentiation of lettuce plant.

Discussion

It seems that the stem starts to elongate through growth progressing at high temperature (above 20°C) and flower induction needs a certain critical length of growth at high temperature (Fig. 2, 3 and Fig. 5).

High temperature above 20°C is effective for flower induction in the lettuce. The higher the temperature, the less are the days needed for the flower induction (Fig. 2, 3). At 17°C, stem elongation and flower induction were not seen even after 5 months from the day when the seeds were sown. In practice, seeding may take place during the cool weather of early fall if the plants have been subjected to high temperatnre for a considerable period earlier in growth.

It is shown in Table 1 that daily more than 16 hours exposure to high temperature is needed for flower induction and less than 8 hours daily high temperature exposure failed in flower induction.

The large and old plants respond to high temperature more sensitively than the small and young plants (Fig. 8, 9). A less period of exposure to high temperature is needed for the large and old plants.

Duration of high temperature needed for flower induction in the plant of full size is as follows:

15 days for Wayahead and New York,

20—30 days for Imperial 847 and Pennlake,

35—50 days for Great Lake, Great Lake 54 and Paris Market.

The relationships between high temperature exposure and flower induction have been ascertained also in the field experiment.

The full sunlight, long-day and abundant nitrogen supply promote the plant growth, being followed by the early flower induction. The large and old plants differentiate flower buds earlier and need less exposure to high temperature.

Shading, short-day, less nitrogen supply and defoliation restrict the plant growth and retard the flower induction.

Defoliation even to the apex, however, does not inhibit the flower induction. It may be safely concluded that the flower is induced by the effect of high temperature above 20°C even in the leafless state, being due to the physiological conditions in the apex.

Reports of the physiological conditions associated with the flower induction will be published at another opportunity in this Journal.

Summary

1. This paper describes the stem growth and flower induction of the lettuce plant as related with temperature, light intensity, day-length, nitrogen supply and defoliation.

2. Stems elongate through growth progressing at high temperatures (above

20°C) and flowers differentiate after a further longer exposure to high temperature.

Full-size plant needs the following days of exposure to 23°C:

Varieties	Days of exposure to high temperature
Wayahead, New York	15
Imperial 847, Pennlake	20—30
Great Lake, Great Lake 54, Paris Market	35—50

3. At 30°C, plants need less days of exposure for flower induction than at 23°C.
4. At 17°C, stem elongation and flower induction were not seen even after 5 months from the day when the seeds were sown.
5. Daily more than 16 hours exposure to high temperature is needed for flower induction. Less than 8 hours exposure to high temperature daily failed in flower induction.
6. Large plant or old plant needs a less period of exposure to high temperature for flower induction than the small or young plant.
7. Full-sunlight, long-day and abundant nitrogen supply hasten the plant growth, being followed by the earlier flower induction. Shading, short-day, less nitrogen supply and defoliation retarded the plant growth and flower induction.

Even the leafless plant, being defoliated to the apex, however, differentiates flowers at high temperature.

8. It may be concluded that the stem elongation and flower induction in the lettuce plant are due to the physiological conditions in the apex brought about through the influence of high temperature above 20°C.

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