Effects of Temperature on the Photoperiodic Responses of Tobacco*

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Most of cultivated tobacco plants are short-day or day-neutral[4,6,12]. And few are reported as the long-day plant[6]. Studies have shown a strong effect of temperature on the photoperiodic responses of many plants[3,7], including tobacco[11,14].

The authors reported recently several experiments[19,20] concerned with the occurrence of premature blossoming in flue-cured tobacco (Hicks I-2). And it was confirmed that temperature, especially in the field was causative of the occurrence of premature blossoming. Then the present studies were made to clarify the effects of temperature on the photoperiodic responses of a flue-cured tobacco, *Nicotiana tabacum* L var. Hicks I-2.

MATERIALS AND METHODS

Seedlings of a flue-curred tobacco, Hicks I-2 were used for all experiments. They were grown in a greenhouse, transplanted into 12-cm clay pot at 9~10 leaf stage. On the second or third day after transplanting they were subjected to experimental conditions. All photoperiodic treatments were carried out in temperature-controlled (±1.5°C) glass houses. In Experiment 1, 2 and 4, all plants received 8 hours (9:00~17:00) of natural dylight each day and then were covered with black curtains. To extend the photoperiod beyond 8 hours, incandescent lamps (ca. 250 lx at leaf sursace) were lit in the black curtains. The supplemental light was given for half of expected hours of supplemental light both before and after the 8-hour natural daylight. In Experiment 3 plants were exposed to natural daylight for 12 hours (7:00~19.00). Each experimental design is descrived later.

In all experiments 25~30 plants were used for each treatment. Every 10th day the number of visible leaves (external leaf number) was recorded and several seedlings in each treatment were dissected to determine the number of leaf-primordia and floral initiation. The time required for floral initiation was calculated from the number of leaves obtained at every 10th day and the total number of leaves obtained after dissecting the shoot apices.

EXPERIMENTAL RESULTS

Experiment 1. Photoperiodic responses at constant temperures.

Seedlings at 10 leaf stage grown under 14~15 hour daylengths at 20°~30°C were subjected to 8,-10-, 12-, 16-, 20- and 24-hour (continuous illumination) photoperiods at 10°, 15°, and 27°C in all combinations, except 10- and 20-hour photoperiods at 10° and 15°C, and 20-hour photoperiod at 27°C.

These treatments were continued until plants flowered. Seventy-five day after the beginning of the treatments, remaining plants which had already initiated flower buds were transferred to a greenhouse.

GROWTH; There was no difference in the rate of leaf emergence among photoperiodic treatments during the vegetative stage. However plants subjected to shorter photoperiods budded earlier. Fig. 1 shows the effects of temperature on the rate of leaf emergence. The higher the temperature, the earlier the plant's growth. The growth of plants exposed to 10°C were severely retarded.

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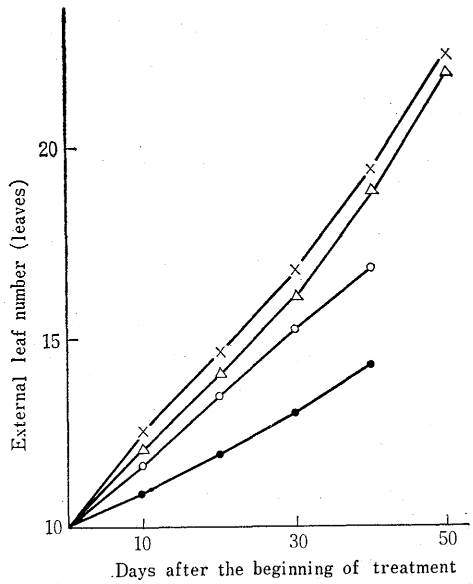

Fig. 1. Effects of temperature on the leaf emergence.

Note: —●— 10°C, —○— 15°C, —△— 20°C, —×— 27°C. All plants were exposed to 16-hour light and 8-hour dark cycle.

FLORAL INITIATION AND TOTAL LEAF NUMBER; All plants subjected to 8-hour photoperiod initiated flower buds almost at the same time with the exception of 27°C plot. Under 12-hour or longer photoperiods the time required for floral initiation was shortest at 15°C and followed by 10°, 20° and 27°C. At any temperature, the longer the photoperiod, the later became the time of floral initiation, however extentions of the photoperiod beyond 16 hours exerted little effect. Therefore this plant is a quantitative short-day plant[7]. (fig. 2. bottom)

Plants exposed to low tempratures of 10° or 15°C bore fewer leaves and a little difference in total leaf number among photoperiodic teatments was observed. At higher temperatures the photoperiodic responses displayed clearly. At all temperatures tested there was little difference in total leaf number among photoperiodic treatments when plants were subjected to more than 16-hour photoperiod (fig. 2. top).

Experiment 2. Effects of alternating temperatures

Seedlings at 9 leaf stage grown under ca. 12 hour daylengths 20°～25°C were subjected to 8-, 12-, 16- and 20-hour photoperiods at 10°C, 10°C/20° C(10°C in the light period and 20°C in the dark period), 20°C and 20°C/10°C, except 16-hour photoperiod at 10°C/20°C and 10°C. Besides these treatments, 10- and 14-hour photoperiods at 20°C were added. The treatments were continued for 70 days until budding and

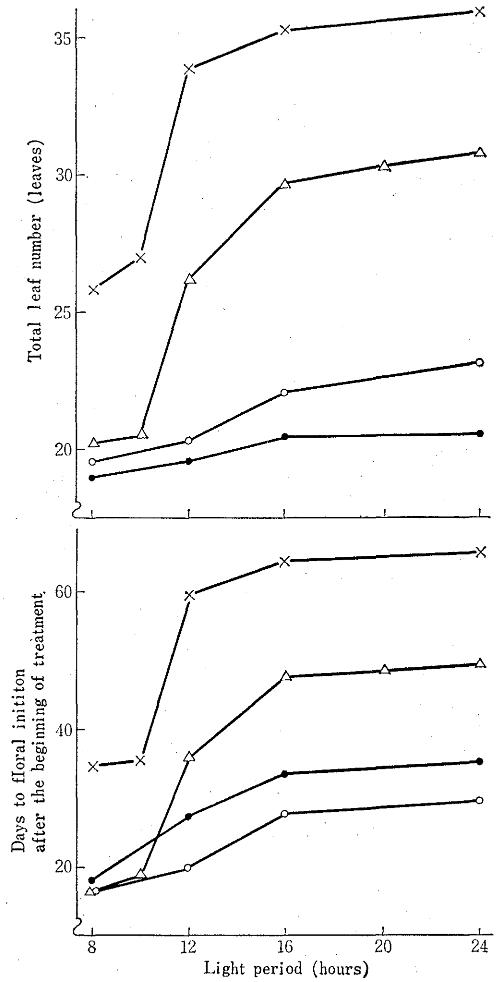

Fig. 2. Effects of photoperiods on total leaf number (top) and time required for floral initiation (bottom) at constant temperatures.

Note: —●— 10°C, —○— 15°C, —△— 20°C, —×— 27°C. All plants received 8 hours of natural day-light, supplemented with incandescent light during the remaining period.

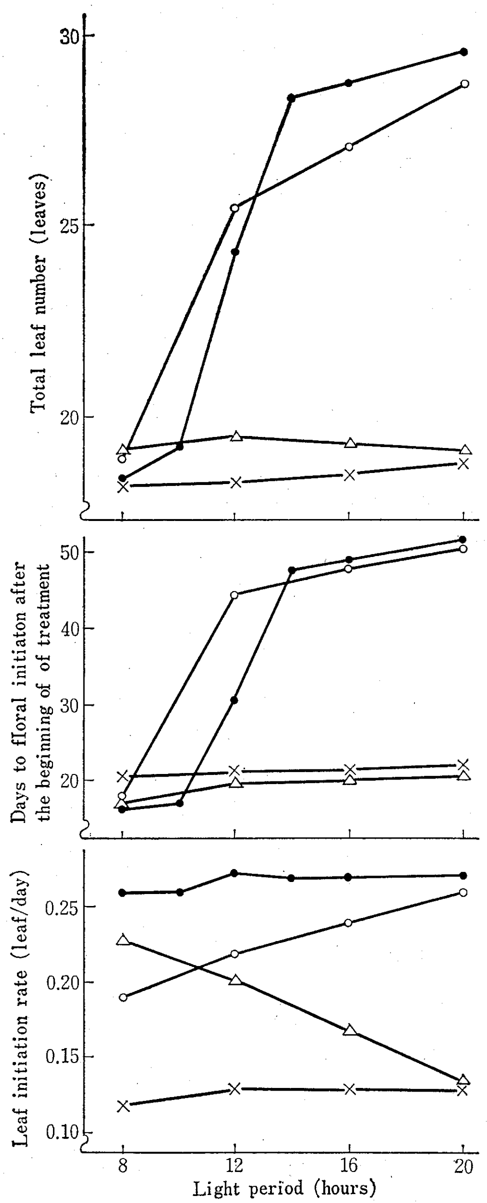

Fig. 3. Effects of day- and night-temperature on total leaf number (top), time required for floral initiation (middle) and rates of leaf-primordium initiation (bottom).

Note:

Sign	Temperatnre (°C)	
	Day	Night
—×—	10	10
—△—	10	20
—○—	20	10
—●—	20	20

then plants were transferred to a greenhouse.

Fig. 3 shows the results, in which the leaf initiation rate was obtained by dividing the number of leaf-primodia initiated during the treatments by the number of days required for floral initiation.

GROWTH; At constant temperatures no difference in leaf initiation rates among plants subjected to different photoperiods was observed. Under alternating temperatures, the rate of leaf initiation was lowered by increasing duration of the low-temperature treatment irrespective of whether it was given during the light or the dark period. As a whole, however, the temperature during the light period exerted a little stronger effect on the leaf initiation rate than that during the dark period.

FLORAL INITIATION AND TOTAL LEAF NUMBER; When plants were subjected to 8-hour photoperiod the temperature during the light period had little effect on the time required for floral initiation. Under 12-hour or longer photoperiods, however, the temperature during the light period had pronounced effects on the floral initiation, i.e., low temperature during the light period promoted the floral initiation to the same extent as short day. When the temperature during the light period was 20°C, low temperature during the dark period was slightly promotive under 16-hour or longer photoperiods, but inhibitory under 12-hour or shorter photoperiods.

Under all experimental conditions tested, except at 10°C, the earlier the floral initiation, the fewer was the total leaf number. Curves for days to floral initiation and total leaf number in fig. 3 are very similar. The floral initiation of plants exposed to 10°C was some later than that of plants exposed to 10°C/20°C, but on the contrary the total leaf number of the former plants was fewer than that of the latter.

Experiment 3. Effects of different temperatures intercalated at various tims during the light period.

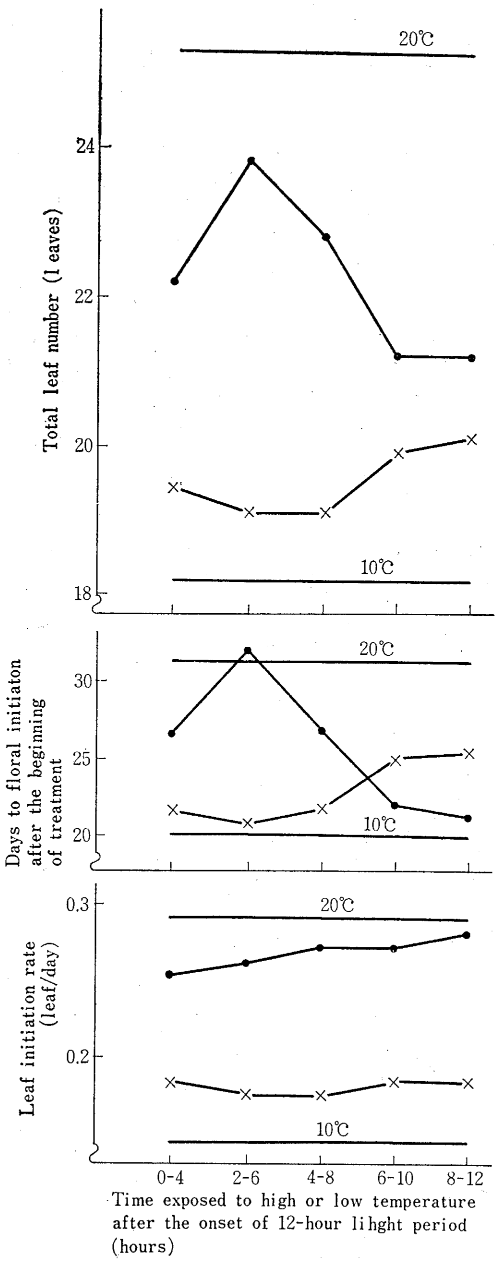

Fig. 4. Effects of high (20°C) and low (10°C) temperature intercalated at various times in 12-hour light period on total leaf number (top), time required for floral initiation (middle) and rates of leaf-primordium initiation (bottom).

Note: High (—×—) and low (—●—) temperature were given for 4 hours during 10°C and 20°C light period respectively.

Seedings at 9 leaf stage grown under ca. 13 hour daylengths at 20°~25°C were subjected to 12-hour photoperiods at 10°C and 20°C, and 4 hours of 20°C and 10°C were applied at various times during the 12-hour light period (7:00~19:00) respectively. The 12-hour photoperiod was chosen because tobacco seedlins recieved nearly equal photoperiods in the field. Forty-five days after the beginning of the treatments, all plants which had already initiated flower buds were transferred to a greenhouse (fig. 4).

Growth; Rates of leaf initiation were retarded by the exposure to low temperature and accelerated by that of high temperature. However no significant differences in the rate were observed among the plants exposed at different times.

Floral Initiation and Total Leaf Numbere; Th floral initiation was promoted by the exposure to low temperature and inhibited by that of high temperature. The last several hours were most sensitive to temperatures and the 3- 7th hour was the least sensitive.

Effects of the exposure to low or high temperature upon the total leaf number showed the same trends as those on the floral initiation. The total leaf number was decreased by the exposure to low temperature and increased by that of high temprature.

Experiment 4. Effects of low temperature intercalated at various tims during the dark period.

Seedlings at 9 leaf stage grown under ca 13 hour daylengths at 20°~25°C were subjected to 8- and 12-hour photoperiods at 20°C, and 3.5 hours of low temperature (6°C) was given at various times during the dark period. Sixty days after the beginning of the treatments, al[1] plants which has already initiated flower buds were transferred to a greenhouse (fig. 5).

Growth; Low temperature applied during the dark period retarded the leaf initation, however there were no significant differences in the rate of leaf initiation among plants exposed to low temperature at different times in both photoperiodic treatments.

Floral Initiation and Total Leaf Number;

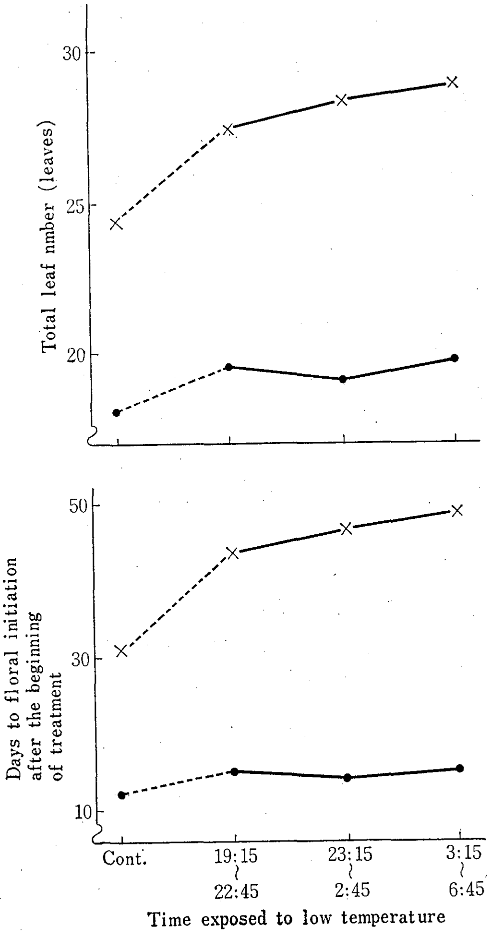

Fig. 5. Effects of low temperature (6°C) intercalated at various times in the dark period on total leaf number (top) and time required for floral initiation (bottom).

Note: Low temperature of 6°C was given for 3.5 hours during 20°C dark period. —●— 16-hour dark, —×— 12-hours dark.

Under 12-hour photoperiod low temperature given during the dark period retarded the floral initiation and increased the total leaf number. There was a tendency that low temperature given in the latter part of 12-hour dark period was more effective than that given in the earlier part.

Under 8-hour photoperiod low temperature given at any time during the dark period retarded the floral initiation and increased the total leaf number. However no difference in the effects of low temperatures given at different times was observed.

DISCUSSION

There are many reports on the effect of temperature upon photoperiodic responses[3,7]. Some short day plants[1,8,9,14,16] were reported to be induced by low temperature substituting for short day. Roberts and Struckmeyer[14] reported that Maryland Mammoth, a short-day tobacco, resulted in flowering at low temperature of 12.8°C even under long days. Muraoka et al.[11] obtained similar results with a flue-cured tobacco, Bright Yellow. Such was also the case in other flue-curred tobacco, Hicks I-2, used in the present experiments.

In most short-day plants[3], low temperature given in the inductive dark period inhibits the floral initiation and that given in the light period has little effect. In tobacco plants[10], however low temperature given in the light period plays a decisive role in the floral initiation, i.e. it results in rapid flowering irrespective of the length of photoperiod. Low temperature given in the dark period was inhibitory when the photoperiod was 8~12 hours, but slightly promotive when the photoperiod was longer than 16 hours. Then low temperature is considered to have dual effects:

1) It accelerates the floral initiation irrespective of the length of photoperiod (flower promoting effect).

2) It retards the dark-period process which is required for floral initiation of short-day plants (flower inhibiting effect).

Under long day conditions without inductive dark period, only the flower promoting effect may appear. Even under short days low temperature given in the light period may have only flower promoting effect, but that given in the dark period may have dual effects. In the latter case, the flower inhibiting effect may exceed the promoting one resulting in flower inhibition.

Working with *Kalanchoë blossfeldina*, Schwabe[17] reported as follows: Under short days the floral induction was retarded by low temperature, especially by low night temperature, however inhibiting effects of long day on flowering were reduced when long-day treatments were conducted at low temperature and low temperature during the dark period after long light-period was also effective in inhibiting the long-day effect on flowering. According to Schwabe's idea, the flower promoting effect of olw temperature in tobacco may also be brought by inhibiting the long-day effect. Oka et al.[13] are of the same opinion.

There are several reports[2,5] observing that low temperature after the dark period accelerates the floral initiation of short-day plants. In tobacco it was observed that low temperature applied soon after the dark period was comparatively effective to the floral induction (fig. 4), which would be due to the same mechanism observed in *Xanthium*[2]. However the last several hours of 12-hour light period were most sensitive to temperature in tobacco.

Preceding the beginning of Experiment 4, some ranges of low temperatures were examined. Then low temperatures of 2° and 6°C were more effective than that of 10°C and the effectiveness of the former two was nearly equal in floral responses. Therefore in Experiment 4 the low temperature of 6°C was chosen.

Under 8-hour photoperiod low temperature intercalated during the dark period had less influence upon the floral initiation than that under 12-hour photoperiod. Under 8-hour photoperiod the darkperiod process may go on comparatively smooth with little interruption by low temperature intercalated during the inductive dark period in tobacco.

It is reported that in some short-day plants[5,18] flowering is inhibited most when the inductive dark period is interrupted near the middle with low temperature. However in *Xanthium*[15] low temperature applied at the first several hours of inductive dark period promotes flowering and inhibits when applied near the end. Such a tendency was observed in tobacco under 12-hour photoperiod.

Neverthelese effects of low temperature during the dark period upon the floral induction of tobacco are two-sided, one is promotive and the other inhibitory. The mechanism of these low temperature effects upon the photoperiodic responses still remains to be solved, and so do the mechanism of the flower-promoting effect of low temperature during the light period.

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Summary

Effects of temperature on the photoperiodic responses of a flue-cured tobacco, *Nicotiana tabacum* L. var. Hicks I-2 were investigated.

This plant is a quantitative short-day plant. Low temperature accelerated the floral initiation under any photoperiod, so that the photoperiodic response appeared clearly at relatively high temperatures (20°～27°C), but was obscure at low temperatures (10°～15°C).

Low temperature given during the light period accelerated the floral initiation and reduced the total leaf number. The most effective time of low temperature given in the 12-hour light period was the last several hours of the light period, and the least effective time the 3～7th hour.

Low temperature below 10°C given during the dark period was inhibitory when the photoperiod was 12 hours or less, however slightly promotive when the photoperiod was more than 16 hours. In 12-hour dark period low temperature given in the later part of the dark period was a little more effective than that given in the earlier

part, but not in 16-hour dark period.

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〔和 文 摘 要〕

タバコの日長反応におよぼす温度の影響

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黄色種 H-2 を供試し，日長反応におよぼす温度の影響を調べた．

1） 低温（10～15°C）下では，花芽分化が促され着葉数少なく，日長の影響は明らかでなかつた．比較的温度の高い（20～27°C）条件下で日長反応は明瞭となつた．また終夜照明下でも開花し，本品種は quantitative short-day plant と言える．

2） とくに明期の低温は花芽分化を促し，着葉数を減少させた．12時間日長の場合，最も低温に敏感なのは暗期直前の数時間で，最も鈍感な時期は明期開始後3～7時間目頃であつた．

3） 暗期の低温（10°C 以下）は12時間以下の日長条件下では花芽分化を抑制し，16時間以上の日長条件下では花芽分化を促した．12時間日長の場合，暗期の後期に与えた低温ほど花成抑制効果が強く，着葉数が多くなる傾向がみられたが，8時間日長下ではその時期的差異は明らかでなかつた．