Studies on Cool Injury in Bean Plants

VII. Sensitive stages to sterile type low temperature injury during floral bud development in relation to nitrogen status of soybean plants*

Koji HASHIMOTO and Tadashi YAMAMOTO

(Hokkaido National Agricultural Experiment Station, Hitsujigaoka, Sapporo, 061-01)

In this series of studies the authors have shown that the sterile type low temperature injury, the decrease in pod setting percentage and fertile seed percentage, is magnified by nitrogen (N) application when flowers are subjected to low temperature during prebloom stage. Furthermore, they suggested that there were close relations between the heavy shedding of flowers and the stage of floral bud development on the plants containing a high level of N under low temperature^{4,5,6}.

The duration of low temperature experiments reported so far was two weeks or longer since the long duration of treatment tended to cause distinguishable damage. However, lengthening the low temperature treatment makes it difficult to estimate the most sensitive stage precisely during floral bud development.

This experiment was designed to determine the most sensitive stage of floral bud through its development to sterile type low temperature injury with the plants grown under different N conditions by being subjected to a shorter period of low temperature treatment as 6 or 9 days.

MATERIALS AND METHODS

The soybean cultivar, 'Kitami-shiro' was planted on the bed at 3-day intervals from May 19 to 28 in 1971 and was transferred to nutrient solution when the unifoliate leaves fully expanded. The standard cultural solution used was shown in the previous paper⁴. The plants at the age of 21st,

24th, 27th and 30th day after planting were subjected to low temperature at 15°C for 6, 9 or 15 days in the natural light glasshouse of the phytotron¹⁶. Except for the period of the low temperature treatment, all plants were grown in the natural light glasshouse at 24°C for 14 hour day-period and 19°C for 10 hour night-period (24/19°C).

The N supply conditions were as follows: N-0: Without N, N-1: N was supplied for 5 days from 3 days before the beginning of low temperature treatment, N-2: N was supplied for 6 days from the beginning of low temperature treatment. The N supply conditions of control plants grown at 24/19°C were as follows: C-0: Without N, C-1, C-2, C-3 and C-4: N was supplied for 4 days from the age of 18th, 21st, 24th and 27th day after planting, respectively. N supply was made at 40 ppm as NH_4NO_3 . Each plot was replicated 3 times.

In order to avoid strong competitive interrelations among flowers and developing pods, flowers used for observation were allowed to set for 6 days in the 6- or 9- day low temperature treatments or 7 days for the 15-day low temperature treatment from the average onset of flowering. The number of flowers were restricted to at most 3 on each node of the main stem and the 1-node branches, and to 2 on each node of the 2-node branches. The pod setting percentage (pod setting rate) was calculated on the basis of the number of both the filled pods and the unfilled pods longer than 1 cm. The age of floral buds is expressed by the number of days before flowering under the control, 24/19°C, condition.

A supplementary experiment was conducted to relate the N percentage of the plant with the

* Received for publication on September 3, 1975
The outline of this paper was presented at the 154th Meeting (Oct. 1972) of the Crop Science Society of Japan.

Table 1 Pod setting percentage as influenced by the duration of low temperature treatment and the N supply conditions¹⁾

Duration of low temperature treatment	Pod setting percentage (%)			
	N-0	N-1	N-2	Mean
6 days	94.6 a ²⁾	66.9 bc	84.9 ab	82.1 A ²⁾
9	92.7 a	70.0 bc	75.1 abc	79.3 A
15	69.8 bc	51.9 c	52.1 c	57.9 B
Mean	85.7 A	62.9 B	70.7 B	

Note 1) Each value is the average of the 21st, 24th and 27th day treatments. Calculation was made with the first 3-day flowers from the average onset of flowering for the 6- and 9-day treatment, or the first 4-day flowers for the 15-day treatment. Pod setting percentage was calculated on the basis of the number of both filled pods and unfilled pods longer than 1 cm

2) Values followed by the same small letter or capital letter are not significantly different at the 5% level respectively based on Duncan's new multiple range test

magnitude of low temperature injury obtained in the above mentioned experiment. 'Kitami-shiro' was planted on March 25 in 1973 and was subjected to low temperature from the 25th day after planting and the N percentages of the leaves, the stem and the roots were determined at successive stages of growth. The plant tissue samples were oven dried at 70–80°C, and were weighted. Then they were ground with a laboratory mill and were used for chemical analysis. Total N was determined by the Kjeldahl method using salicylic acid for reducing nitrate.

RESULTS

1. Effects of the duration of low temperature and the N supply condition on the pod setting percentage

Table 1 shows the summarized data to demonstrate the effects of the duration of low temperature treatments and the N supply conditions on the pod setting percentage. The pod setting percentage was significantly affected by the duration of low temperature treatment and the N supply conditions.

Although the pod setting percentage tended to decrease with an increase of the duration of low temperature, no statistically significant difference was observed between the 6- and the 9-day treatment. The 15-day treatment reduced pod setting percentage regardless of the N supply conditions and the mean was significantly lower than that of

the other two treatments.

The mean pod setting percentage of N-0 was higher than those of N-1 and N-2 in three durations of low temperature, and did not decrease in the 6 and the 9-day treatment when compared to the results on the control plants shown in Table 2. The mean pod setting percentage of N-1 was the lowest among three N supply conditions and the percentage of the 6-day treatment of N-1 was as low as that of the 15-day treatment of N-0. On the other hand, the mean pod setting percentage of N-2 was similar to those of N-1 in the 9- and 15-day treatments but lay between that of N-1 and N-0 in the 6-day treatment.

Fig. 1 shows the mean pod setting percentage in relation to the age of the plant at the beginning of each low temperature treatment. In the 6-day treatment the pod setting percentage of N-1 changed considerably with the age of the plant at which the low temperature was imposed. While the percentage of N-2 and N-0 showed no marked change. In the 9-day treatment the pod setting percentage changed considerably with the age of the plant not only in N-1 but also in N-2. The 24th day treatment caused the largest decrease of pod setting in N-1 and N-2. The pod setting percentage of the plots in 15-day treatment was generally very low. It was higher in N-0 than in N-2, but the trend of change with the age was similar in those N conditions, the younger the plants were the higher

Fig. 1 Pod setting percentage as influenced by the time and duration of low temperature treatment, and of N supply

Note 1) Calculated with the flowers opened in first 3 days from the average onset of flowering

2) ○—○ N-0, ●—● N-1, ▲—▲ N-2

the percentage. However, in N-1, the older the plants were the higher in the pod setting percentage.

Fig. 2 shows the pod setting percentage as varied with the date of flowering in cases of the 6- and the 9- day treatments from the 24th and 27th day.

In the 27th day treatment the flowers which opened earlier generally had a higher pod setting percentage, and the flowers which opened from the 3rd to 6th day in the 6-day treatment of N-1 and in the 9-day treatment of N-1 and N-2 showed an extremely low pod setting percentage. On the contrary, in the cases of the corresponding plots in the 24th day treatment, the pod setting percentage of the flowers that opened during the first 3 days was very low. It indicated that the flowers with a low pod setting percentage were subjected to low temperature at similar limited ages before flowering in both the 24th and the 27th day treatments.

2. Effects of duration of low temperature and the N supply condition on the fertile seed percentage

The mean of fertile seed percentage was significantly affected by the duration of low temperature and the N supply condition at the 1% level (Table 3), and also by the age of the plants at the 5% level respectively (Table 4). The significance of

Fig. 2 The pod setting percentage of the flowers opened on successive date as influenced by the time and duration of low temperature treatment and of N supply

Note: ○—○ N-0, ●—● N-1, ▲—▲ N-2

the interaction between the duration of low temperature treatment and the N supply condition also exceeded the 5% level.

The fertile seed percentage was decreased with extension of the duration of low temperature treatment or with N supply. No damage was observed

in the 6- and the 9- day treatments of N-0 in comparison to the results of the controls (Table 2). However, the mean of the 15-day treatment of N-0 decreased to the similar low values which were obtained in the 6- or 9- day treatment of N-1 and N-2 (Table 3).

The mean fertile seed percentage was affected with the age of plant at which the plants were subjected to low temperature and N supply condition. When N was supplied the fertile seed percentage decreased more especially in the case that the plants were subjected to low temperature from the 21st and the 24th day (Table 4).

3. N percentage of the plant as affected by the N supply conditions

The N percentage of the plant increased linearly during the period of N supply both before and during the low temperature treatment (Fig. 3). The increase of N percentage was the largest in the stem and was the smallest in the roots. After the discontinuation of N supply the N percentage of the leaves was kept almost constant for 2 or 3 days, while that of the stem immediately began to decrease, but was kept a comparatively high level

for 3 days under the N-1 condition and for 5 days under the N-2 condition. The peak of N percentage was slightly higher in N-1 than in N-2, although general pattern of the change of N percentage was similar in both conditions.

The N percentage of N-0 plants was low and steady.

Table 2. Pod setting percentage and fertile seed percentage as influenced by a short period of N supply before flowering under the control, 24/19°C, condition¹⁾

Designation	Period of N supply ²⁾	Pod setting percentage	Fertile seed percentage
C-1	18—22	89.5%	86.6%
C-2	21—25	92.7	79.3
C-3	24—28	88.6	91.2
C-4	27—31	94.4	98.5
C-0	Non	92.7	87.8

Note 1) Calculation was made with the first 3-day flowers from the average onset of flowering

2) Figures are expressed as days from planting

3) Refer to note 1) in Table 1

Table 3 Fertile seed percentage as influenced by the duration of low temperature treatment and the N supply conditions¹⁾

Duration of low temperature treatment	Fertile seed percentage			
	N-0	N-1	N-2	Mean
6 days	89.8 a ²⁾	79.5 bc	82.7 b	84.0 A ²⁾
9	90.7 a	77.9 bc	77.6 bc	82.1 A
15	77.0 bcd	70.9 d	75.6 cd	74.5 B
Mean	85.8 A	76.1 B	78.7 B	

Note 1) Each value is the average of the 21st, 24th and 27th day treatment

2) Refer to note 2) in Table 1

Table 4 Fertile seed percentage as influenced by the time of low temperature treatments and the N supply conditions¹⁾

Time of low temperature treatment	Fertile seed percentage			
	N-0	N-1	N-2	Mean
27th day ²⁾	87.2 a ³⁾	80.3 bcd	81.5 bc	83.0 A ³⁾
24th	85.2 ab	71.4 e	79.1 cd	78.5 B
21st	85.2 ab	76.6 cde	75.4 de	79.1 B

Note 1) Each value is the average of 6-, 8 9- and 15-day treatments

2) Days after planting when the plants were subjected to low temperature

3) Refer to note in Table 1

Fig. 3 Changes of the N percentage of various organs of the plants grown in different N supply conditions

- Note 1) The thick lines show the period of N supplied
 2) Plants were subjected to low temperature at 25th day after planting
 3) ○—○ N-0, ●—● N-1, ▲—▲ N-2

DISCUSSION

Under the 24/19°C condition in the glass-house of the phytotron most of plants began to flower from the 34th day after planting regardless of the date of sowing. The delay of the average onset of flowering caused by low temperature was 3 days for the 6-day treatment, and 4–5 days for the 9-day treatment and 7–8 days for the 15-day treatment. The data presented so far suggest that the speed of floral bud development under the 15°C condition was half of that under the 24/19°C condition.

On the basis of above information, the data obtained in this experiment were discussed about the age of floral buds of the plants subjected to the 15°C condition judging from the date of flowering under the 24/19°C condition.

Relations between the age of floral buds at the beginning of low temperature treatment and the pod setting percentage under the 6- and the 9-day treatments are shown in Fig. 4.

Fig. 4 Changes of the pod setting percentage with the age of floral buds at the beginning of low temperature treatment

- Note 1) The age was estimated by the speed of the floral bud development under low temperature, and from the flowering date of each flower
 2) ●—● N-1, ○—○ N-2

The pod setting percentage is generally influenced by the internal and external conditions of the flowers plant, such as the sequence and pattern of flowering^{10,13}, competitive interrelations among the flowers and developing pods¹¹, day length¹⁵, temperature^{7,11,16}, etc. Although sizable fluctuation existed, it is apparent that there is a specific age of floral buds when the pod setting percentage

becomes very low under the N-1 condition of the 6-day treatment (Fig. 4a) and the N-1 and N-2 conditions of the 9-day treatment (Fig. 4b) and the 15-day treatment.

The curves of pod setting percentage fell to a minimum at 12, 10.5 and 11.5 days before flowering for the N-1 condition of the 6-day treatment and for the N-1 and N-2 conditions of the 9-day treatment, respectively. Low pod setting percentage was observed during the period from 9 to 13 days before flowering in the N-1 condition of the 6-day treatment, and from 9.5 to 12.5 days before flowering in the N-1 and N-2 conditions of the 9-day treatment.

In the 15-day treatment the decrease of pod setting percentage was large and extensive. The decreases took place not only in the N-1 and N-2 conditions but also in the N-0 condition, and the change of the pod setting percentage with the age of floral buds was less clear when compared with those in the 6- and 9- day treatments. In the N-2 condition the pod setting percentage during the period from 10.5 to 14.5 days was at a very low level and it was at the minimum at 12.5 days before flowering. In the N-1 condition it decreased extensively during the period from 7.5 to 12.5 days before flowering, and there was no distinct minimum.

In the N-1 plants the trends of the change of pod setting percentage as influenced by the flowering date were similar in both the 6- and the 9- day treatments (Fig. 1). This result suggest that the period of the plants keeping a high N percentage under low temperature was not much different between those treatments. On the other hand, the pod setting percentage in the N-2 condition did not decrease markedly in the 6-day treatment, but decreased in the 9-day treatment. This phenomena could be explained by assuming that the N percentage of the N-1 plants at the 6th day under low temperature was at the level of a lower limit to induce a decrease of the pod setting percentage (Fig. 3).

On the basis of this assumption, it can be said that the N percentage of the N-1 plants was kept

higher than the critical level from the beginning to the end of the 6-day treatment, and the N percentage of the N-2 plants reached the critical level at the 5th day in the leaves and at the 3rd day in the stem and roots under low temperature, respectively, and then it was kept above the critical level until the end of the 9-day treatment. Therefore, the N percentage might be kept higher than the critical level existed for 1–3 days in the 6-day treatment and for 4–7 days in the 9-day treatment.

Fig. 5 is a diagram to demonstrate the sensitive stage to low temperature during floral bud development on the basis of the assumption explained above. The horizontal lines in parallelograms show the range of the age of floral buds developed under

Fig. 5 Diagrammatic representation of floral age sensitive to low temperature as estimated by the pod setting percentage of the flowers opened on each day of the plants in high N status

- Note 1) The horizontal lines in parallelograms show the ranges of the age of floral buds developed under low temperature where marked reduction was observed
- 2) The dotted areas show the age of floral bud developed on the plants in a high N status under low temperature
- 3) The thick line in each parallelogram shows the case when minimum value was obtained

low temperature, when a large decrease of pod setting percentage was observed. The thick line in each parallelogram shows the age when the pod setting percentage was at its minimum. The dotted area shows the age of floral buds of the plants expected to have a higher N percentage than the critical level under low temperature.

Let us look at the cases of the 6- and 9-day treatments in which the N-0 plants showed little decrease of pod setting percentage. Considerable decrease of the pod setting percentage was observed when the floral bud was subjected to low temperature during 6-day period, which is equivalent to 3-day period of floral bud development under the normal condition, starting from between 11 and 9 days before flowering under high N status of the plants. Furthermore, the trends of change in pod setting percentage of the N-1 and N-2 conditions of the 15-day treatment coincided with those of the 6- and 9- day treatments.

From above discussion it can be concluded that under high N status of the plant, the sensitive age of floral buds to low temperature is between 13 and 15 days before flowering and the highly sensitive age is between 11 and 7 days before flowering.

The ovule number per pod was considerably higher at the 1st to 6th day flowers of the C-1 plants and the 1st to 5th day flowers of the C-2 plants than at the 1st to 6th day flowers of the C-4 and C-0 plants (Fig. 6). In contrast, the ovule number per pod of the C-3 plants changed with the flowering date, the number of the 1st to 3rd day flowers was as low as that of the C-4 and C-0, whereas, the number of the 4th to 6th day flowers was as high as that of the C-1 and C-2.

Fig. 7 shows the changes of means of ovule number when the plants were subjected to low temperature for 6 and 9 days. The trend observed in the N-1 condition of the 27th day treatment is similar to that for the C-3 in Fig. 6. N was supplied to those two plots from the 24th day after planting. The trend observed in the N-1 condition of the 24th day treatment was similar to that for the C-2: N was supplied to these plots from the 21st day after planting.

Fig. 6 Changes of the ovule number per pod in relation to the time of N supply under 24/19°C condition

Fig. 7 Changes of the ovule number per pod in relation to the time of N supply under the 6 and 9 day treatments

Without exception the ovule number per pod increased when N supply was started at 13–15 days before flowering. Kato⁸⁾ and Nagata⁹⁾ indicated that the stage of ovule differentiation is at 10 days before flowering. Fukui et al.^{1,2)} also confirmed that the duration from the ovule differentiation to flowering is 10 days irrespective of varieties, day-length and high temperature condition in a greenhouse. Accordingly, it can be concluded that the N supply starting from more than 3 days before the ovule differentiation increases the ovule number per pod.

In the N-1 condition of the 24th and 27th day treatments, the flowering date with an increased number of ovules per pod coincides with the date with a considerable decrease in the pod setting percentage.

Referring to the cytological information of the floral bud development^{1,2,8,9)}, the changes of ovule

number per pod in relation to N application, and the changes in the pod setting percentage, the highly sensitive stage of floral buds to low temperature is from 1 or 2 days before the differentiation of anther primordia via meiosis to the tetrad. This sensitive stage during floral bud development of soybeans nearly coincides with that of rice plants, although in soybeans it may be slightly earlier than that in rice plants¹²⁾.

N application for a few days seems to be sufficient to induce heavy shedding of flowers, if the floral buds are subjected to low temperature during the most sensitive stage. The flowers whose ages are a few days younger or older than the sensitive stage can escape from the damage due to low temperature (Fig. 2). High N status is not always detrimental, but is detrimental during definite stages of floral bud development.

A considerable decrease of the pod setting percentage was observed in the plants maintaining high N status during a 6-day low temperature treatment despite the floral buds developed under a favorable condition for the last 7 to 9 days before flowering (Fig. 5). This result indicates that an irreversible damage occurs during the floral bud development under low temperature. Goto and Yamamoto³⁾ revealed that the major cause of heavy shedding of flowers was the failure of fertilization due to the indehiscence of anthers, poor pollen discharge from the anthers and poor pollen germination. Togari and Kashiwakura¹⁴⁾ observed that a high rate of N application under a shaded condition increased the sterile spikelets in the rice plant, mostly due to the failure of the anther to dehisce. It can be said that an irreversible damage on a certain step of stamen development which leads to a failure of fertilization due to abnormalities in the organ occurs easier when the N percentage of the plant is above the critical level under low temperature.

As shown in the previous experiments^{4,5)}, a decrease of pod setting percentage was accompanied with a decrease of the fertile seed percentage. It is indicated that the sensitive stage of the decrease of fertile seed percentage by low tempera-

ture is the same with the sensitive stage to the decrease of the pod setting percentage.

SUMMARY

This experiment was designed to determine the most sensitive stage to sterile type low temperature injury, the decrease in pod setting percentage (pod setting rate) and fertile seed percentage, with the plants grown under different N condition by being subjected to shorter periods of low temperature as 6 or 9 days.

When the N percentage of the plants is high under low temperature, the sensitive ages of floral buds to the sterile type low temperature injury are during the period between 13 and 5 days before flowering and the highly sensitive ages are during the period between 11 and 7 days before flowering corresponding to the stages of floral bud development from 1 or 2 days before the differentiation of the anther primordium via meiosis to the tetrad.

A considerable decrease of the pod setting percentage was observed in the plants maintaining high N status during a 6-day treatment of low temperature despite the floral buds developed under a favorable condition for the last 7 to 9 days before flowering. This result indicates that an irreversible damage occurs during the floral bud development under low temperature. It can be said that the damage on a certain step of stamen development which leads to a failure of fertilization due to abnormalities in the organ occurs easier when the N percentage of the plant is high under low temperature.

The flowers whose ages are a few days younger or older than the sensitive stage can escape from the damage due to low temperature.

High N status in the plants is not always detrimental, but is detrimental during definite stages of floral bud development.

LITERATURE CITED

- 1.* FUKUI, J. and T. GOTOH 1962. Varietal differences of the effects of day-length and temperature on the development of floral organs in the soy-bean. I. Developmental stages of

- floral organs of the soy-bean. Jap. J. Breed. **12**: 17—27.
- 2.* ———, ——— and S. MATSUMOTO 1962. ——— II. Comparison of development of floral organs. Jap. J. Breed. **12**: 75—80.
 - 3.* GOTO, K. and T. YAMAMOTO 1972. Studies on cool injury in bean plants. III. Abnormalities in the reproductive processes relating to pod dropping as affected by cool temperature before anthesis in soybean plants. Res. Bull. Hokkaido Natl. Agr. Exp. Stn. **100**: 14—19.
 - 4.* HASHIMOTO, K. and T. YAMAMOTO 1970. Studies on cool injury in bean plants I. Effect of nitrogen under low temperature on the pod setting and fertility of soybeans. Proc. Crop Sci. Soc. Japan **39**: 156—163.
 - 5.* ———, ——— 1970. ——— II. Effects of time and period of nitrogen application on the soybeans treated with low temperature before flowering. Proc. Crop Sci. Soc. Japan **39**: 164—170.
 6. ———, ——— 1974. ——— VI. Direct and indirect effects of low temperature and levels of nitrogen and phosphorus in the nutrients on the yield components of soybeans. Proc. Crop Sci. Soc. Japan **43**: 52—58.
 7. HOWELL, R. W. 1960. Physiology of the soybean. Advances in Agronomy **12**: 263—310.
 - 8.* KATO, I. 1964. Histological and embryological studies on fallen flowers, pods and abortive seeds in soybean, *Glycine max* (L). Bull. Tokai-Kinki Natl. Agr. Exp. Sta. **11**: 1—52.
 - 9.** NAGATA, T. 1962. Soybeans. Yokendo Co., Tokyo pp. 311.
 - 10.* OIZUMI, H. 1962. Studies on the mechanism of branching and its agronomic consideration in soybean plants. Bull. Tohoku Natl. Agr. Exp. Sta. **25**: 1—96.
 11. SAITO, M., T. YAMAMOTO, K. GOTO and K. HASHIMOTO 1970. The influence of cool temperature before and after anthesis, on pod setting and nutrients in soybean plants. Proc. Crop Sci. Soc. Japan **39**: 511—519.
 12. SATAKE, T. and H. HAYASE 1970. Male sterility caused by cooling treatment at the young microspore stage in rice plants. V. Estimations of pollen developmental stage and the most sensitive stage to coolness. Proc. Crop Sci. Soc. Japan **39**: 468—473.
 - 13.** TAJIRI, T. and T. TATENO 1952. An ecological study of soybean. I. Fruiting behavior. Bull. Chugoku-Shikoku Nat. Agr. Exp. Sta. **1**: 26—34.
 - 14.* TOGARI, Y. and KASHIWAKURA 1958. Studies on the sterility in rice plant induced by super-abundant nitrogen supply and insufficient light intensity. Proc. Crop Sci. Soc. Japan **27**: 3—5.
 15. VAN SCHAIK, P. H. and A. H. PROBST 1958. Effects of some environmental factors on flower production and reproductive efficiency in soybeans. Agron. J. **50**: 192—197.
 16. YAMAMOTO, T. 1970. The Hokkaido National Agricultural Experiment Station Phytotron. JARQ **5**(1): 52—58.
- Note *Written in Japanese with English summary.
 ** Written in Japanese.

〔和 文 摘 要〕

豆 類 の 冷 害 に 関 す る 研 究

第7報 花器発育期間における障害型冷害敏感期と
大豆個体の窒素の状態との関係

橋 本 鋼 二・山 本 正

(農林省北海道農業試験場)

本実験は、花器発育期間における障害型冷害（結莢率および稔実歩合の低下）に対する敏感期と大豆個体の窒素の状態との関係を明らかにするために、6ないし9日間の従来より短い低温処理期間によつて検討した。

低温条件下における植物体中の窒素含有率が高いと、*開花の13ないし5日前にあたる花の障害型冷害に対する感受性を高め、とくに開花の11ないし7日前——葯の分化する1ないし2日前から減数分裂期を経て四分体期に至る——の花はいちじるしく障害を受けやすくなる。植物体が低温下で多窒素状態であれば、6日間処理でも上述の低温感受性の高い生育段階の花に障害が生じやすく、結莢率に相当の低下が認められた。これは、開花前7ないし9日間は通常の生育環境に戻して発育させたにもかかわらず、一旦受けた障害が回復しないことを示している。落花のいちじるしい増加の原因は、雄性器官の機能的な異常によるものと考えられる。

低温処理によつて障害を受けやすい生育段階より2、3日若いか、または発育が進んだ花器は短期間の低温処理では被害を免かれる。これらのことは、低温下で植物体が多窒素状態にあることが、ある限られた発育時期の花器についてのみ有害になることを示している。