Studies on the Control of Flower Bud Formation by Temperature and Daylength in Rice Plants

IX. Aging Effect in Relation to Photoperiodic Induction

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Synopsis. The aged rice plants produced their flower bud primordia by fewer short-day treatments and under longer day-length as compared to the young plants. On the other hand, the floral initiation of the plants showing high intensity in the vigour of vegetative growth was delayed than that of the plants showing low intensity, although both the plants were sown on the same date.

From these facts, it is inferred that aging effect on floral induction is due to the decrease in the vigour of vegetative growth during the course of development.

It is known that floral induction is affected by the plant age. This phenomenon is called aging effect on floral induction. In rice plant, the investigations on the relation between age and the ability in floral induction have been undertaken by several workers as shown in KATAYAMA's review (1963). Most of these studies have been done with view to its practical application in cultivation or breeding. However, the physiological basis for the aging effect on floral induction is still obscure.

The experiments reported herein were carried out to reveal the number of photo-inductive cycles and the critical daylength for floral induction in relation to the age of plants. The meaning of "age" in connection with the floral induction was also considered.

Experiment 1. Relation between aging and photocycles required for floral induction Materials and Methods

"Zuiho", a highly photosensitive Japanese rice variety and "Norin 8", a moderately photosensitive one, were selected as the materials. A certain number of seeds of "Zuiho" were sown in pots (1/5000 a) on April 12, May 10, June 10 and 20 in series 1, and March 22, May 10, July 10 and August 5 in series 2 in 1963. In series 1, the plants grown under the long-day condition of 20 hours were divided into nine groups and exposed to three to ten cycles of short-day treatments (10 hours) from

July 11, and in series 2, one to ten cycles from September 2. After the short-day treatments, they were placed under the long-day condition of 15 hours. Then, the shoot apex of the main culm was microscopically observed on July 23 in series 1 and on September 16 and October 2 in series 2. Heading dates were also recorded. The seeds of "Norin 8" were sown on March 23, May 13, June 24 and July 24, 1964 and the experiments were conducted in the same manner as in "Zuiho".

To get the 15 and 20 hours photoperiods, the plants were illuminated by an intensity of about 200 lux provided by white fluorescent lamps in addition to the natural daylength. In order to grow the plants under favorable nutritional condition, ammonium sulphate at the rate of 0.5 g per pot was supplied at about three weeks interval during the growing period in addition to a basal dressing.

Throughout the experiments, the degree of aging was measured by the number of leaves on main culm.

Experimental Results

The floral stages on the 12th day after the beginning of treatment and their heading dates which were observed in the experiment of series 1 are given in Table 1. When the plants of various age groups received different short-day treatments, it was found in the category of each short-day treatment that the more increased the number of leaves, the more

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Table 1. Number of short-days needed for floral induction as influenced by aging

Number of leaves at the beginning of treatment (sowing time)	14.5 (April 12)		11.9 (May 10)		8.1 (June 10)		6.4 (June 20)	
No. of short-days	Floral stage ¹⁾²⁾	Heading date ¹⁾	Floral stage	Heading date	Floral stage	Heading date	Floral stage	Heading date
0	0	—	0	—	0	—	0	—
3	VII~VIII	Aug. 31*	III	—	0	—	0	—
5	XI	18.6	IX~X	Aug. 22	III	—	0	—
6	XI	14.9	IX~X	18	VI	Aug. 25*	III	—
7	XI~XII	14.4	XI~XII	15.9	VII~VIII	22*	IV	—
8	XII	11.6	XI~XII	14.1	VII	28*	V	—
9	XII	11.4	XII	13.2	X	16.3	VII	—
10	XI~XII	10.8	XII	11.2	IX~X	15.9	VI~VII	Aug. 22. 5*
Continued	XII	5.7	XII	6.2	IX~X	7.9	VI~VII	9.6

1) Average of 4 plants. 2) Observed at July 23, 12th day after the beginning of treatment. Floral stage II~III: differentiating stage of bract primordia; IV~VI: primary branch primordia; VII~VIII: secondary branch primordia; IX~XII: flower primordia (MATSUSHIMA, 1957).—: No heading at Sept. 5. *: partially headed.

progressed the floral stage and the earlier was the heading date. Moreover, it was recognized that number of short-day cycles needed for floral induction were reduced with the increase of the leaves. For example, some of the aged plants with 14 to 15 leaves produced panicles in response to only three short-days, while only a few of young plants with 6 to 7 leaves produced panicles even though they had received 10 short-day cycles.

In the experiment of series 2, in which aged plants having 20 to 21 leaves were included, the floral stages were investigated on the 14th and 30th day after the beginning of short-day treatment. Although the results similar to series 1 were obtained in this experiment in respect to the initiation and development of flower buds, it was noticed that the floral initiation occurred in the plants with 20 or more leaves by only one short-day treatment.

Almost the same tendency as in "Zuiho" were obtained with the experiments in "Norin 8" using the plants with 18.4, 13.1 and 8.7 leaves.

Experiment 2. Relation between aging and critical daylength on floral induction

Materials and Methods

Seeds of "Zuiho" and "Norin 8" were sown

in pots (1/5000 a) on March 23, May 13, June 24 and July 24, 1964. All the plants were kept under long-day condition of 20 hours until August 24 when they had 18.6, 16.6, 13.9 and 9.4 leaves on main culm in accordance with the sowing dates. At this time, the plants were transferred to the conditions of 10, 13, 14, 15, 16 and 20 hours daylength. The floral stage of main culm was examined microscopically on September 3 and October 2 and the heading dates were recorded.

Experimental Results

The results of "Zuiho" are summarized in Table 2. It was observed on the 10th day after the beginning of the treatment that the plants with 18.6 leaves showed flower bud differentiation even under the long-days of 15 hours. On the other hand, plants with 9.4 leaves produced the flower bud primordia only under the short-days of 10 hours. On October 2, the 39th day after the beginning of treatment, the plants which were sown on March 23 and May 13 had 22.8 and 21.5 leaves, respectively. At this time, they clearly showed flower bud differentiation under 16 hours long-day condition. Moreover, some of them produced flower bud primordia even under 20 hours long-day treatment.

The results of "Norin 8" showed the same

Table 2. Floral induction under the various daylengths

Number of leaves at the beginning of treatment (sowing time)	18.6 (March 23)		16.6 (May 13)		13.9 (June 24)		9.4 (July 24)	
Days from the beginning of treatment	10	39	10	39	10	39	10	39
Daylength	Floral stage or heading date ¹⁾							
10 hrs.	X	Sept. 24	VIII	Sept. 22	VIII	Sept. 22	VII	Sept. 22
13	VIII	Sept. 27	VIII	Sept. 30	VIII	Sept. 26	0	XXI
14	VI	XVII	0	XIV	0	X	0	0
15	IV	XII	0	XII	0	V	0	0
16	0	VIII	0	IV	0	0	0	0
20	0	0*	0	0*	0	0	0	0

1) Average of 4 plants. *: Partially induced (floral stage III~V).

Floral stage XIII~XVI: reduction division of PMC; XVII~XXI: pollen formation (MATSUSHIMA, 1957).

Table 3. Relation between number of leaves on main culm and critical daylength for floral induction

Number of leaves	Zuiho							
	22.8	21.5	20.0	18.6	16.6	14.3	13.9	9.4
Critical daylength*	16	16	15	15	13	13	13	10
Number of leaves	Norin No. 8							
	23.0	20.8	18.4	18.0	16.5	16.1	13.1	8.7
Critical daylength*	16	16	16	15	14	14	13	13

* Critical daylength indicates the daylength which can induce floral initiation.

tendency as in "Zuiho."

The critical daylength for floral initiation estimated from the above mentioned results was shown in Table 3. The table clearly shows that the more increases the number of leaves, the longer is the critical daylength for floral initiation.

Experiment 3. Relation between floral induction and rate of leaf emergence in plants with or without tillers.

Materials and Methods

Seeds of "Zuiho" were sown in pots on March 25, May 10, June 10 and July 10, 1965. And the seedlings individually grown in the pots were kept under the long-day condition of 20 hours. In one half of these plants, all the sprouts of tillers were removed on every third day and the main culm grew alone during the entire course of development (hereafter referred as "plant without tillers"). In the other half, the plants grew with all tillers (hereafter referred as "plants with

tillers").

Both the plants with and without tillers were divided into two groups. In the first group, plants were kept under the long-day condition of 20 hours throughout the experiments, and the number of leaves on the main culm was investigated on every 5th day from July 25 to August 25. The rates of leaf emergence in the plants with various number of leaves were calculated from their respective data. In the second group, the plants were transferred from the long-day condition to the natural daylength on June 30. And then, the shoot apex in main culm was microscopically observed on every 5th day to determine the time of floral initiation. The heading dates were also recorded.

Experimental Results

The number of leaves on main culm linearly increased during the period from July 25 to August 25 in the experiment of series 1. The rate of leaf emergence for five days decreased

with the increase of leaves in both the plants with and without tillers as shown in Table 4. On the other hand, the rate of leaf emergence in a plant without tillers was higher than a plant with tillers though they were sown on the same date. When the plants without tillers were compared to the plants with tillers in the same number of leaves, the rate of leaf emergence was higher in the former than the latter. For example, the rate of a plant without tillers which was sown on May 10 (0.96) was higher than that of a plant with tillers sown on March 25 (0.44), although the both plants had about 20 leaves. In general, the rate of leaf emergence in a plant without tillers was superior to that in a plant with tillers. Therefore, it was found from the results that the rate of leaf emergence did not always run in parallel with the growing period (number of days from sowing) or the number of leaves on main culm.

The variation in the dates of floral initiation and heading of the plants with and without tillers was shown in Table 5. It was recognized that the floral initiation of plants without tillers was delayed as compared to the plants with tillers and that the number of leaves on main culm at the time of floral initiation of the former was higher than that of the latter even though both the plants were sown on the same date. Therefore, it can be stated that the growing period from sowing to floral initiation as well as the number of leaves on main culm at the time of floral initiation are different between the plants with and without tillers. The heading dates in both the plants showed the same tendency as for the time of floral initiation except for the plants sown on June 10. Consequently, it does not always hold true that floral induction under natural daylength de-

pends on the growing period or the number of leaves on main culm. On the other hand, it was found as mentioned above that the rate of leaf emergence in a plant without tillers was always superior to that in a plant with tillers independently of the growing period and the number of leaves on main culm. Therefore, it can be concluded that the floral initiation of a plant showing high rate of leaf emergence is delayed as compared to a plant showing the low rate.

Discussion

In recent years, it was reported in rice plant that the sensitivity to short-days increased during aging (SASAMURA, 1960; KATAYAMA, 1964. SUGE, 1968). In this investigation, a similar phenomenon was observed, and especially, only one cycle of short-day was enough for flower bud differentiation in aged plants with 20 leaves. At first sight, this phenomenon seems to be due to an increase of the photosensitivity with age. In the experiment under various daylengths, however, it was observed that the more advanced the plant age, the longer was the critical daylength, and in a plant having more than 20 leaves, the floral induction could occur even under the long-day condition of 20 hours. Consequently, it is unreasonable to consider that the aging effect on floral induction is a phenomenon of

Table 4. The rate of leaf emergence per 5 days in the plants of various age

Sowing date	With tillers		Without tillers	
	Number of leaves	Rate	Number of leaves	Rate
March 25	20.0	0.44	26.1	0.88
May 10	16.3	0.52	20.7	0.96
June 10	13.1	0.68	15.5	1.24
July 10	9.1	1.20	9.6	1.49

Table 5. Floral induction in the plants at various age under natural daylength

Sowing date	March 25		May 10		June 10	
	Control	Treated	Control	Treated	Control	Treated
Date of floral initiation*	July 30	Aug. 10	Aug. 10	Aug. 15	Aug. 15	Aug. 20
Number of leaves at the time of initiation*	18.6	22.7	16.0	19.3	13.3	16.0
Heading date*	Aug. 31	Sept. 13	Sept. 13	Sept. 16	Sept. 22	Sept. 17

* : Average of 4 plants. Control : Plants with tillers. Treated : Plants without tillers.

increase in sensitivity to short-days with age. Floral induction in rice plant is generally promoted by short-day treatment and inhibited by long-day treatment (NOGUCHI *et al.* 1967 a,b), namely, floral induction seems to be regulated by antagonism between the promotion of short-days and the inhibition of long-days. Therefore, the aging effect may be explained as a phenomenon of decrease in the sensitivity to the inhibiting effect of long-days during the course of aging. Also from this point of view, the experimental results by SASAMURA (1960) and KATAYAMA (1964) are quite understandable.

The growing period (number of days from sowing) or the number of leaves of main culm has generally been used as an index of plant age (SASAMURA, 1960 ; KATAYAMA, 1964 ; SUGE, 1968). In this experiment, the degree of aging was also shown by the number of leaves. But, the meaning of "age" must be discussed in connection with floral induction. In the third experiment which was undertaken by using the plants with and without tillers, it was found that a plant showing a high rate of leaf emergence always showed a delay in floral induction as compared to a plant showing a low rate. The rate of leaf emergence may be considered as an index for showing the vigour of vegetative growth in plant. Therefore, it is inferred from the experiment that the floral initiation is essentially conditioned by the vigour of vegetative growth. On the other hand, the decrease in the vigour of vegetative growth generally results from the extension of growing period and the increase of leaves on main culm. Consequently, it is considered that the "age" related to floral induction which generally accompanies with the growing period or the number of leaves is essentially based on the decrease in the vigour of vegetative

growth during the course of development.

As the inhibition of flower bud differentiation seems to be caused by the promotion of vegetative growth under a long-day condition (NOGUCHI *et al.*, 1967 b), it may be overcome by the decrease in the vigour of vegetative growth of plant. Therefore, it is concluded that the aging effect on floral induction is due to the decrease in the vigour of vegetative growth, which seems to be the nature of aging, rather than the increase in photosensitivity during the course of plant development.

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水 稻 の 幼 穂 形 成 機 構 に 関 す る 研 究

第 9 報 花 成 に 影 響 す る Aging effect

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水稻においても, Age が進むほど出穂しやすくなる
ことが知られている。このような Aging effect の本質
について検討する目的で, 瑞豊ならびに農林 8 号を供試
して実験を行なった。

葉令(主稈葉数)が進んだ植物体では, 1, 2 回の短日
処理によつて幼穂分化と出穂がみられた。一方, 葉令が
進めば, いわゆる限界日長時間も長くなり, 20 時間日長
下でさえも時として瑞豊の幼穂分化がみられた。したが
つて花芽形成に影響する Aging effect を単純に Aging
によつて短日感応性が増大する現象と理解することは妥
当でない。長日条件による花芽形成の抑制効果が Aging

によつて低下するとも考えうるのである。

長日による花芽形成の抑制は長日による栄養生長の助
長に関係しているので, 葉令または生育日数は大である
にもかかわらず, 栄養生長(出葉速度)の旺盛な材料も
含めて実験を行なつてみた。その結果, 幼穂分化・出穂
は, 葉令や生育日数よりも, むしろ栄養生長能の強さに
密接に関連して変動することが明らかとなつた。したが
つて, 花芽形成に対する Aging effect の本質は, 葉令
や生育日数の増加にともなつて一般的にはおこる栄養生
長能の強さの低下にあると推察された。