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Studies on the Effects of Temperature During the Reduction Division and the Grain Filling Stage in Rice Plants

I. Effect of Temperature at the Reduction Division Stage in Indica-Japonica Crosses

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水稻의 減数分裂期 및 登熟期에 있어서 温度反應에 관한 研究

第1報 水稻 Indica×Japonica品種의 減数分裂期에 있어서의 低温의 影響

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ABSTRACT

The effect of temperature during the reduction division stage on the Indica-Japonica rice varieties were studied in artificial temperature-controlled cabinets (Bioclimatic Laboratory). Varieties used were indica-japonica crosses (Suweon 264, Suweon 258, Milyang 29), indica (IR36, Lengkwang) and japonica rice (Jinheung). The results obtained from this study are summarized as follows.

The most sensitive stage to low temperature, the tetrad stage, was observed in each variety with the following auricle distance: Jinheung, -12cm; IR36, -3cm; Suweon264, -9cm; Suweon258, -3cm; Milyang29, -6cm and Lengkwang, +1cm. The tetrad stage occured when the palea elongation was about 50 to 60% of the final palea length at flowering stage in all varieties. The percentage of degenerated spikelets at tetrad as influenced by low-temperature treatment was very low in Jinheung and Lengkwang, but very high in IR36. In indica-japonica crosses only the 7-days treatments had a very high percentage.

Between the 4-day and 7-day treatments as well as among all varieties, clear differences were observed in the low temperature induced sterility of "special spikelets" (upper position grains at tetrad). In the 7-day treatments except in Lengkwang, all varieties showed very high sterility. It appears that the treatments is over the critical limit for treatment. However in the 4-day treatments, the intervarietal differences in sterility were very clear. In Jinheung, sterility was 46.8%; IR36, 67.6%; Suweon264, 60.9%, Milyang29, 62.2%; Lengkwang, 27.8%.

A close relationship was observed between fertility and auricle distance. The lowest fertility of special spikelets was at the tetrad stage and the first contraction phase. Before and after the stage there was an increase in fertility. The palea length elongated nearly in a straight line from the spikelet formation stage to flowering. And there was a high correlation between palea length and auricle distance.

INTRODUCTION

Low temperature limits rice production and causes deterioration of grain quality. The effects

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vary according to the growth stage of the rice plants.

At anthesis, the order of low temperature (14°C) inhibition in salt absorption was phosphorus, ammonium, potassium, water, magnesium and calcium (Ishizuka and Tanaka, 1963).

Hayase and Satake(1970) found that cytological observation on the pollen developmental stage of rice plants couled at the meiotic division stage but they found that at tetrad the frequency of abnormal microspores. Sakai(1937) observed the microscopical abnormalities in the anther loculi 1 day after the initiation of treatment. In a later study(1949), he reported that the percentage of tapetal hypertropy increased as temperature decreased. The rate of tapetal hypertropy by cooling treatment was correlated with varietal resistance to sterile-type cool injury. Thus he postulated that abnormalities of meiotic division and hypertrophy to tissues were the major cause of sterility.

Nishiyama et al.,(1970) found that the frequency of tapetal hypertrophy was not so high compared with the percentage of sterility, and doubted Sakai's hypothesis. Nishiyama(1979) reported that at low temperature, an increase in sugar concentration caused an increase in turgor pressure, and this resulted the enlargement of tapetal cells.

The cause of the increase in sugar concentration in tapetal cells was considered to be the inhibition of translocation of nutrients from the tapetum to the microspores.

Satake and Hayase(1970) reported that the most sensitive stage to coldness just after meiosis was the tetrad and the early microspore stage. They denoted this stage as the young microspore stage. In a later study(1974), they indicated that the secondary sensitive stage occurred just before meiosis.

In Korea, lôw temperature is one of the major environmental factors limiting rice production. New high yielding rice varieties(Indica-Japonica crosses) were developed in 1965. These varieties were crossed between an early maturing, cold-tolerant Hokkaido variety, Yukara, and a widely adaptable Taiwanese variety, Taichung Native 1. F1 Hybrids were crossed with a high-yielding and blast-resistant variety, IR8 from IRRI.

These new varieties were quite different in agronomic characteristics from the conventional varieties.

These varieties have several advantages as follows: resistance to lodging because of their short stature, high photosynthetic activity, and very high number of spikelets per panicle. However, several problems still remain unsolved, especially the effect of low temperature limiting factor in rice production.

In Korea, rice seedbeds are sown in early April, transplanted in mid-May to mid-June, and havested from late September to mid-October. During the growing season, the temperature varies with year and site. Temperature at the early seedling and late maturing stage is usually not high enough for rice growing, especially for the indica-japonica crosses, which are susceptible to low temperature. When temperature is abnormally low, rice plants suffer from cold damage. Germination, seedling growth, and grain filling have often been inhibited by low temperature, but the degree of damage differs among years and sites.

At present, indica-japonica varieties are cultivated on appoximately more 60% of the total rice area in Korea. These varieties have been adversely affected by low temperature.

Most of the studies on the effect of temperature treatment in rice have been done on indica and japonica varieties. However, studies on indica-japonica crosses are very few.

This study was performed to get detailed information due to low temperature effect on the reduction division. On the other hand, even though many studies have been done on the most sensitive stage to low temperature, however, identification of the most sensitive stage at tetrad is actually very difficult.

In the present study the objective was to develop the identification method of the most sensitive stage at tetrad. The study was conducted in the department of Plant the phytotron glasshouse room

Auricle distance is the distance between the flag leaf auricle and the penultimate leaf auricle. The auricle distance is 0(zero) if the penultimate leaf auricle and flag leaf auricle occupy the same position. The auricle distance is designated + (plus) when the auricle of the flag leaf is higher than the penultimate leaf auricle. Physiology and Phytotron at the International Rice Research Instituted, Los Banos, Laguna, Philippines and Phytotron, Crop Experiment Station, Office of Rural Development, Suweon, Korea.

MATERIALS AND METHODS

Varieties

The varieties used were Indica-Japonica crosses (Suweon 264, Suweon 258, Milyang 29); Indica (IR36, Lengkwang) and Japonica (Jinheung) rice.

Controlled environmental conditions

This experiment was conducted in the phytotron at IRRI with controlled moisture and temperature. The plants were grown in the phytotron glasshouse room before and after the low temperature treatment. The relative humidity of the phytotron glasshouse room was maintained above 70 percent while the temperature was kept at 29°C between 09:00 and 17:00 hr and 21°C during the night. Daylength was based on the natural conditions.

Cultural methods

Each pot contained 3.5 kg Maahas clay soil fertilized with 1 g N, 0.5 g P_2O_5, and 0.5 g K_2O and was put into a 4-liter plastic pot.

The seed space made 20 sowing holes uniform in size, depth and interval, in a circle by pressing the soil surface in pots. One pregerminated rice seed was placed in each hole.

The sown seeds were covered by fine upland soil.

Temperature treatment

Each variety was subjected to low temperature treatment at the young microspore stage (tetrad-1st contraction).

All varieties were subjected to low temperature treatment at 15°/15°C for 4 and 7 days.

In this experiment the 3 cm range of auricle distance of main stems was determined by measuring palea length just before treatment. Main stems having the corresponding auricle distance were tagged and treated.

After treatment, rice plants were again moved to the phytotron glasshouse room.

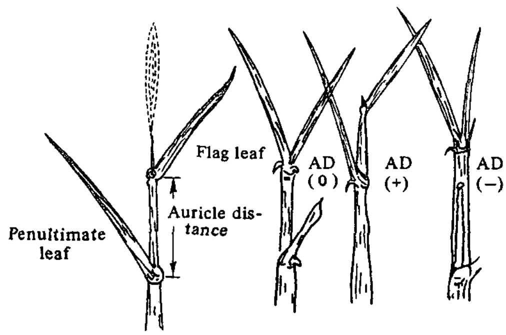

Fig. 1. Auricle distance and its estimation.

Auricle distance is the distance between the flag leaf auricle and the penultimate leaf auricle. leaf auricle. The auricle distance is 0 (zero) if the penultimate leaf auricle and flag leaf auricle occupy the same position. The auricle distance is designated + (plus) when the auricle of the flag leaf is higher than the penultimate leaf auricle.

Auricle distance is designated-(minus) when the auricle of the flag leaf is lower than the penultimate leaf auricle (Fig. 1).

Estimation of pollen developmental stage

The progress of pollen developmental stage was estimated from the "special spikelets" on main stems.

The term "special spikelets" refers to nine spikelets on 3rd, 4th and 5th positions in the upper three primary branches of a panicle (Fig. 2).

Pollen developmental stage was observed on slide preparations stained with acetocamine solution. Pollen developmental stages were divided into: before meiotic phase, meiosis phase, tetrad, 1st contraction phase, 1st recovering phase, 2nd contraction phase, 2nd recovering phase, pollen ripening phase and pollen ripe phase with the use of microscope.

Measurement of sterility

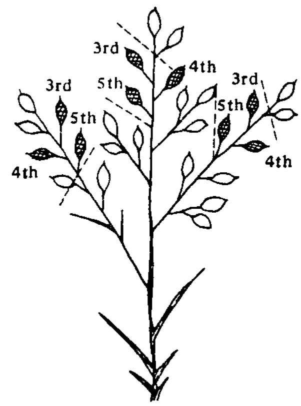

Fig. 2. Special spikelets

Sterility was determined twenty days after flowering by touching spikelets with fingers for both whole spikelets and the special spikelets of the same panicle.

RESULTS

1. Relation between the tetrad stage and auricle distance

In this experiment, the tetrad stage was observed at different auricle distances: in Jinheung, at -12 cm; IR36, -3 cm; Suweon 264, -9 cm; Suweon 258, -3 cm; Milyang 29, -6 cm; Lengkwang, + 1 cm (Table 1).

In Jinheung, a japonica variety, the tetrad stage occurred earlier than in IR36 and Lengkwang, indica variety. But in IR36 and Lengkwang, the tetrad stage formation was near the auricle distance zero. On the other hand, in indica-japonica crosses the formation of the tetrad stage was towards the indica variety. It was observed at the midpoint between indica and japonica varieties.

Palea length at tetrad in Jinheung was 3.0-3.5 mm; IR36, 4.5-5.0 mm; Suweon 264; 3.5-4.0 mm;

Table 1. Auricle distance and palea length in the special spikelets.

Auricle distance (cm)	Palea length (mm)						Remark
	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Leng-kwang	
-18	1.59	–	1.66	–	–	–	
-15	1.89	1.67	1.81	1.66	1.58	1 18	
-12	3.08*	2.24	2.39	1.71	2.19	1.57	
-9	3.93	3.68	3.99*	2.16	3.44	1.80	
-6	4.58	4.43	4.67	3.54	4.13*	2.00	
-3	4.79	4.76*	5.24	4.17*	5.70	2.67	
0	5.50	5 83	5.95	4.60	6.69	4.47*	Lengkwang Auricle
3	6.29	6.56	6.20	6.21	7.39	5.00	distance + 1; 4.49mm
6	6.56	7.02	6.18	6.60	7.41	5.15	
9	6.66	7.65	6.25	7.09	7.46	6.61	

*Tetrad.

Suweon 258, 4.0-4.5 mm; Milyang 29, 4.0-4.5 mm and 4.4-4.9 mm Lengkwang.

In this experiment, there was a constant elongation of palea till final palea length in most varieties, as shown by the nearly straight line in the figure between the auricle distance and palea length. (Fig. 3)

2. Relation between pollen developmental stage and palea length in the special apikelets

The palea length of the same pollen developmental stage was very different between varieties.

In Jinheung, the meiotic stage occurred at palea length between 2 to 3 mm but in other varieties it was between 4.5 mm (Table 2).

At the msot sensitive stage to low temperature, which was tetrad, palea length in Jinheung was

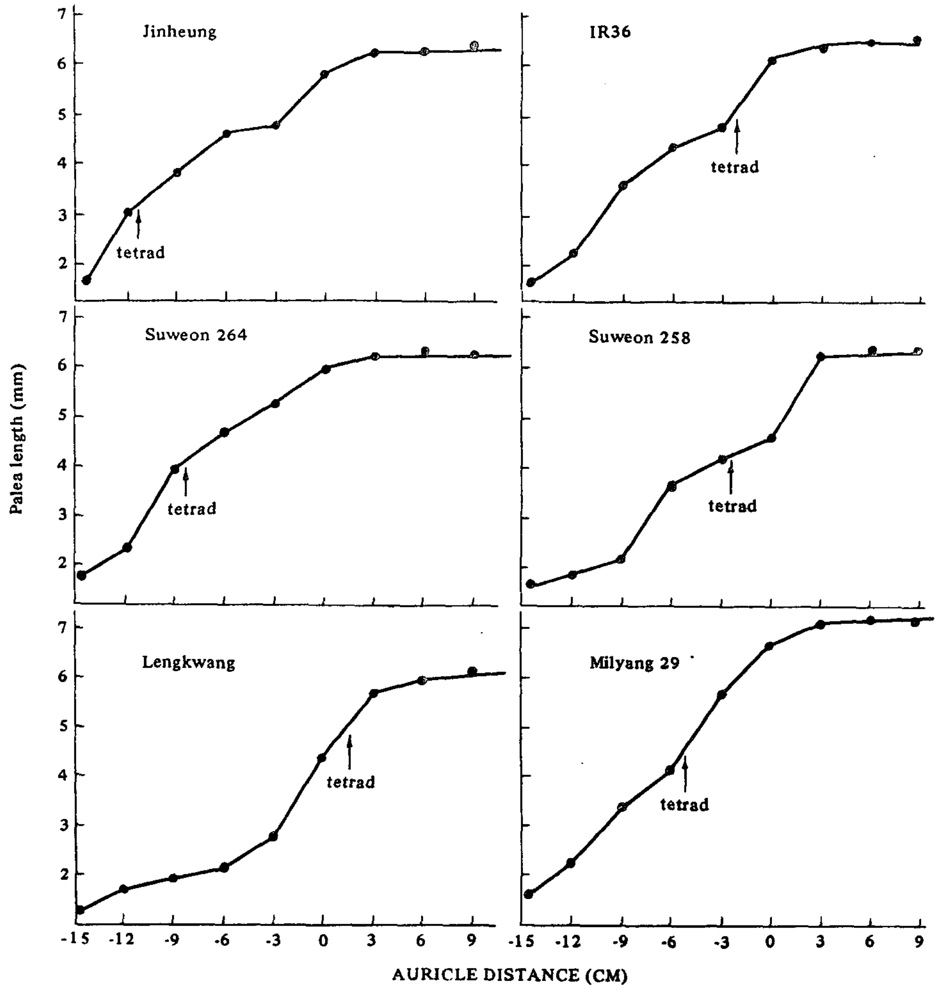

Fig. 3. Relation between auricle distance and palea length in the special spikelets.

Table 2. Relation between pollen developmental stage and palea length in the special spikelets.

Pollen developmental stage	Palea length (mm)					
	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Leng-kwang
Before meiotic division	1.9-2.4	3.4-4.0	2.5-3.0	3.0-3.5	3.5-4.0	3.5-4.0
Meiotic division	2.4-3.0	4.0-4.5	3.0-3.5	3.5-4.0	4.0-4.5	4.0-4.4
Tetrad	3.0-3.5	4.5-5.0	3.5-4.0	4.0-4.5	4.5-5.0	4.4-4.0
1st contraction phase-1st recovering phase	3.5-4.4	5.0-5.5	4.0-4.4	4.5-5.0	5.0-5.5	4.9-5.4
2nd contraction phase-2nd recovering phase	4.4-5.4	5.5-6.5	4.4-6.4	5.0-6.4	5.5-7.0	5.4-6.4
Pollen ripening phase-Pollen ripe phase	5.4-6.9	6.5-7.5	6.4-7.4	6.4-7.5	7.0-7.9	6.4-7.9

Table 3. Relation between the elongation of palea on the pollen developmental stage and palea length at the flowering stage.

Pollen developmental stage	Elongation of palea length (%)					
	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Leng-kwang
Before meiotic division	31.2	47.4	38.7	45.1	46.3	50.7
Meiotic division	39.1	54.5	45.8	52.1	52.5	56.8
Tetrad	47.1	60.9	52.8	59.0	58.6	62.8
1st contraction phase-1st recovering phase	57.2	67.3	59.9	65.9	64.8	69.9
2nd contraction phase-2nd recovering phase	71.0	77.6	76.1	79.2	77.2	79.7
Pollen ripening phase-Pollen ripe phase	89.1	90.4	84.2	96.5	92.0	96.0
Palea length at the flowering stage (mm)	100.0 (6.9)	100.0 (5.7)	100.0 (7.1)	100.0 (7.2)	100.0 (8.0)	100.0 (7.4)
Sx	±0.055	±0.097	±0.103	±0.048	±0.065	±0.094

3.0-3.5 mm; IR36, 4.5-5.0 mm; Suweon 264, 3.5-4.0; Suweon 258, 4.0-4.5 mm; Milyang 29, 4.5-4.0 mm and Lengkwang, 4.4-4.9 mm. The range in palea length from 1st contraction phase to 1st recovering was 3.5-4.0 mm in Jinheung, 5.0-5.5 mm in IR36, 4.6-4.4 mm in Suweon 264, 4.5-5.0 mm in Suweon 258, 5.0-5.5 mm in Milyang 29, and 4.9-5.4 mm in Lengkwang.

Table 3 shows the relation between elongation of palea on the pollen developmental stage at the flowering stage. Because the palea length corresponding to a pollen developmental stage varied between varieties, actually identifying the tetrad stage is usually very difficult. But in this experiment, the tetrad stage occurred when the palea elongation was about 50 to 60% of the final palea length at flowering stage in all varieties.

3. Relation between auricle distance and dry weight of special spikelet.

With regards to dry weight and auricle distance, there was large variation among varieties in the indica and japonica groups (Table 4).

Table 5 shows the relation between auricle

Table 4. Auricle distance and dry weight of special spikelets.

Auricle distance (cm)	Dry weight of special spikelet (g/27 spikelet)					
	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 39	Leng-kwang
-18	0.0012	–	0.0020	–	–	–
-15	0.0015	0.0025	0.0025	0.0018	0.0010	0.0018
-12	0.0032*	0.0034	0.0041	0.0024	0.0015	0.0025
-9	0.0055	0.0043	0.0061*	0.0029	0.0036	0.0033
-6	0.0073	0.0059	0.0102	0.0041	0.0048*	0.0039
-3	0.0086	0.0065*	0.0125	0.0052*	0.0080	0.0043
0	0.0107	0.0089	0.0153	0.0096	0.0109	0.0049*
3	0.0175	0.0139	0.0252	0.0161	0.0143	0.0079
6	0.0263	0.0183	0.0301	0.0187	0.0204	0.0120
9	0.0312	0.0235	0.0315	0.0271	0.0310	0.0175

*Tetrad

Table 5. Relationship between auricle distance and percent dry weight of special spikelets.

Auricle distance	Percent dry weight of special spikelets (relative value)					
	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Leng-kwang
-18	3.8	–	6.3	–	–	–
-15	4.8	10.6	7.9	6.6	3.2	10.2
-12	10.3*	14.5	13.0	8.9	4.8	14.3
-9	17.6	18.3	19.4*	10.7	11.6	18.9
-6	23.4	25.1	32.3	15.1	15.5*	22.3
-3	27.6	27.7*	39.7	19.2*	25.8	24.6
0	24.3	37.9	48.6	35.4	35.2	28.0*
3	56.1	59.1	80.0	59.4	46.1	45.1
6	84.3	77.9	95.6	69.0	65.8	68.6
9	100.0 (0.0312)	100.0 (0.0235)	100.0 (0.0315)	100.0 (0.0271)	100.0 (0.0310)	100.0 (0.0175)

*Tetrad

( ) : Dry weight of 27 special spikelets, gram.

*Auricle distance (cm)

distance and percent of dry weight of special spikelets.

Tetrad occurred at 10.3% in Jinheung, 27.7% in IR36, 19.4% in Suweon 264, 19.2% in Suweon 258, 15.5% in Milyang 29 and 28.0% in Lengkwang, with dry weight of special spikelets at auricle distance + 9 cm as 100% (this stage is 3-4 days before heading except Lengkwang).

4. Effect of low temperature treatment on flowering date

The 4-day and 7-day treatments differed in the number of days during which flowering date was delayed (Fig. 4). In the 4-day treatment, the flowering date of Jinheung was delayed 5 days; IR36, a susceptible variety, 7 days; and Lengkwang, a resistant variety, 7 days. In the 7-day treatment, Jinheung was delayed 7 days; IR36, 11 days; and Lengkwang, 8 days.

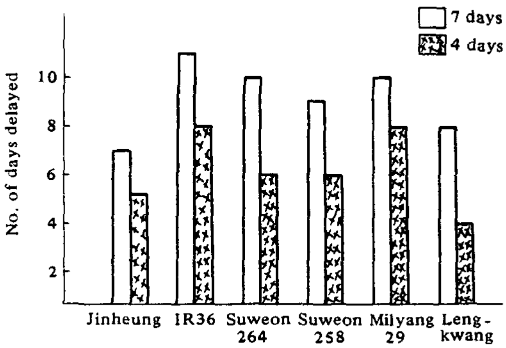

Fig. 4. Flowering date delayed by the low temperature treatment (days).

On the other hand, in indica-japonica varieties, flowering date was delayed about 7 days in the 4-day treatment, and 9-10 days in the 7-day treatment.

5. Effect of low temperature treatment on percentage of degenerated spikelets.

Figure 5 shows the percentage of degenerated spikelets at the tetrad stage as effected by the low temperature treatment. In variety, Jinheung and Lengkwang at 4 and 7 days treatment, there was little variation in the percentage of degenerated spikelets.

In IR36 at 4-day and 7-day treatment, the percentage of degenerated spikelets was very high. On the other hand, in indica-japonica crosses the percentage of degenerated spikelets was low at 4 days treatment, although at 7 days treatment the percentage was very high, as in IR36 (Table 6).

Table 6. Percentage of degenerated spikelets at the tetrad by the low temperature treatment.

Variety	No. of spikelet			Rate of degeneration	
	Control	4 days	7 days	4 days	7 days
Jinheung	54.0	50.8	49.5	5.9	8.3
IR36	101.2	88.3	75.8	12.7	25.1
Suweon 264	98.0	92.3	73.7	7.9	24.8
Suweon 258	153.6	145.2	113.7	5.5	26.0
Milyang 29	145.6	135.6	114.5	10.1	21.4
Lengkwang	134.4	132.7	130.7	1.8	2.7

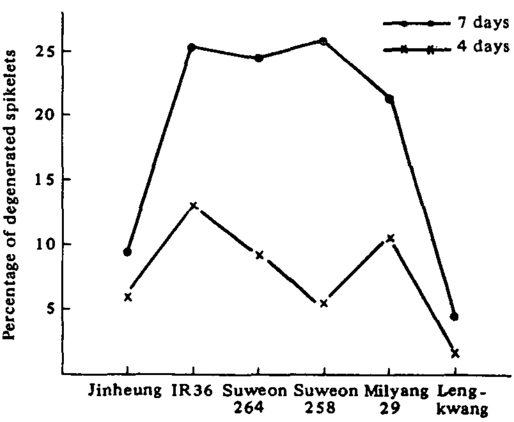

Fig. 5. Percentage of degenerated spikelets at the tetrad by the low temperature treatment.

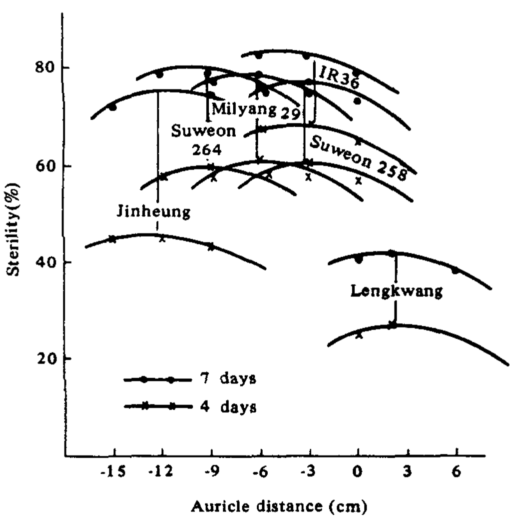

Fig. 6. Relationship between auricle distance and sterility of special spikelets by low temperature (15/15°C) treatment.

6. Effect of low temperature treatment on spikelet sterility.

1) Sterility in relation to cooling duration.

Figure 6 shows the sterility of special spikelets at the most sensitive stage, at tetrad, due to low temperature treatment. There are clear differences in sterility between the 4-day and the 7-day treatments. These differences were also observed in different varieties.

In the 7-day treatment except in Lengkwang all varieties showed very high sterility. Furthermore, there was not much difference in sterility between varieties other than Lengkwang.

It appears that critical limit for temperature is over. However, in the 4-day treatment the sterility of each variety was very clear. In Jinheung, sterility was 46.8%; IR36, 67.6%; Suweon 264, 60.9%; Suweon 258, 60.0%; Milyang 29, 62.2%; Lengkwang, 27.8% (Table 7).

Compared to susceptible variety IR36, sterility in Jinheung, about 20%; in Lengkwang, 40% dif-

Table 7. Percentage of sterility of the special spikelets on the low temperature treatment at the tetrad.

Variety	Control (29/21°C)	4 days (15/51°C)	7 days (15/15°C)
Jinheung	10.8	46.8	75.7
IR36	5.0	67.6	82.4
Suweon 264	6.6	60.9	79.1
Suweon 258	6.8	60.0	76.3
Milyang 29	5.1	62.2	78.9
Lengkwang	4.9	27.8	44.1

*Sterility (%)

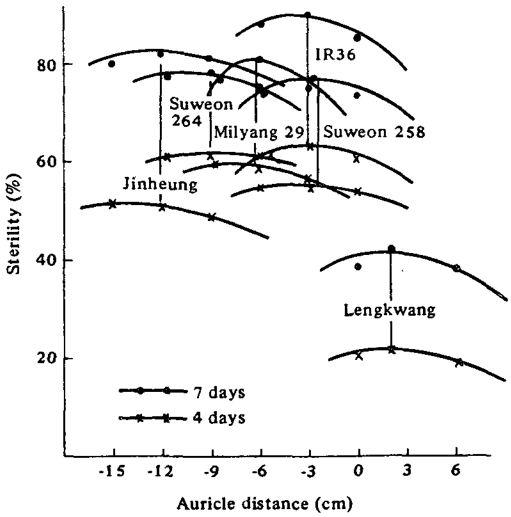

Fig. 7. Relationship between auricle distance and sterility of panicle by low temperature (15°C/15°C) treatment.

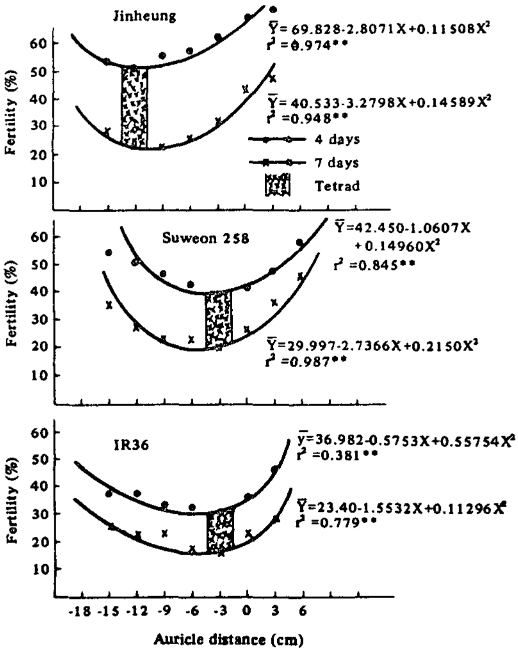

Fig. 8. Relationship between fertility of the special spikelets and auricle distance due to low temperature (15/15°C) treatment.

Table 8. Percentage of sterility on tne low temperature at the tetrad in different varieties.

Variety	Control (29/21°C)	4 days (15/51°C)	7 days (15/15°C)
Jinheung	18.4	51.2	82.4
IR36	6.2	63.5	90.5
Suweon 264	9.7	60.6	79.0
Suweon 258	15.5	55.4	76.5
Milyang 29	17.1	58.3	80.5
Lengkwang	11.0	21.8	42.4

*Sterility (%)

ferent. But all indica-japonica crosses about 5-7% different. This means that the indica-japonica crosses are susceptible to low temperature.

Figure 7 shows sterility of the whole panicle at the most sensitive stage, at tetrad, due to low temperature treatment.

The special spikelets and the whole panicle showed the same tendency in sterility, although in the whole panicle sterility was a little lower (Table 8).

2) Relationship between fertility of the special spikelets and auricle distance.

In this experiment, a close relationship was observed between fertility and auricle distance

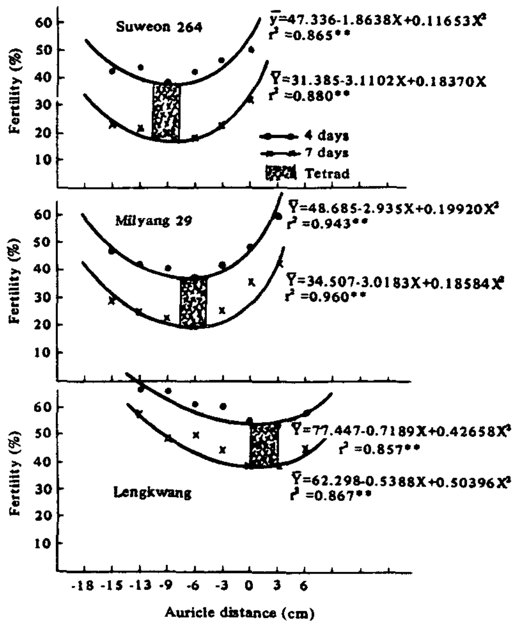

Fig. 9. Relationship between fertility of the special spikelets and auricle distance due to low temperature (15/15°C) treatment.

(Fig. 8,9)

The lowest fertility for the special spikelets was at the tetrad stage and the first contract phase.

In Jinheung, the lowest fertility for the special spikelets occurred at the auricle distance -12 cm; in IR36, -3 cm; in Suweon 264, -9 cm; in Suweon 258, -3 cm; in Milyang 29, -6 cm; and in Lengkwang, +1 to 2 cm.

Before and after the tetrad stage there was an increase in fertility. At tetrad, fertility was lowest and sterility, highest (Tables 9, 10).

3) Comparison between sterility of auricle distance at tetrad and auricle distance at zero.

Table 11 shows the relation between sterility of auricle distance at tetrad and auricle distance at zero. At 4 days treatment, in Jinheung sterility of special spikelets with the auricle distance at tetrad

Table 9. Relationship between auricle distance and sterility of special spikelets in low temperature (15°C/15°C) at 4-day treatment.

Auricle distance	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Lengkwang
Control	10.8	5.0	6.6	6.8	5.1	4.9
-18	45.8	-	-	-	-	-
-15	47.9	61.1	55.6	-	51.8	-
-12	46.8*	58.3	54.8	50.0	57.1	8.9
-9	45.2	64.4	60.9*	52.7	58.3	11.1
-6	42.6	63.9	59.3	58.0	62.2*	16.7
-3	38.9	67.6*	57.4	60.0*	59.3	18.0
0	29.6	61.1	51.8	56.7	51.4	25.1
(+1)						(27.8)*
3	-	52.3	44.4	52.8	40.0	22.2

*Tetrad
*Lengkwang ( ) Auricle distance +1-2
*Sterility (%)
*Auricle distance (cm)

Table 10. Relationship between auricle distance and sterility of special spikelets in low temperature (15°/15°C) at 7-day treatment.

Auricle distance	Jinheung	IR36	Suweon 264	Suweon 258	Milyang 29	Lengkwang
Control	10.8	5.0	6.6	6.8	5.1	4.9
-18	76.7	-	-	-	-	-
-15	74.4	75.0	76.7	-	70.4	-
-12	75.7*	79.8	77.8	72.2	75.0	23.3
-9	76.6	77.8	79.1*	76.1	76.7	31.5
-6	74.6	82.7	80.9	77.8	78.9*	29.6
-3	69.1	82 4*	77.8	76.3*	73.6	35.2
0	58.3	75.0	66.7	69.4	63.0	40.2
(+1)						(44.1)*
3	-	70.8	-	61.1	55.6	37.8

*Tetrad
*Lengkwang ( ) Auricle distance +1-2
*Sterility (%)
*Auricle distance (cm)

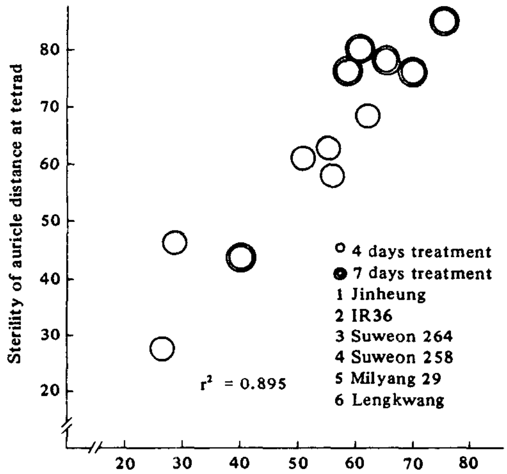

Fig. 10. Correlation between sterility of special spikelet of auricle distance at tetrad and auricle distance at zero due to low temperature treatment.

Table 11. Relationship between sterility of special spikelets of auricle distance at tetrad and distance at zero due to low temperature (15°/15°C) treatment.

Variety	Auricle distance at tetrad (cm)	Sterility of Special Spikelets: (4 days treatment) Auricle distance at tetrad	Auricle distance at zero	Differences	7 days treatment: Auricle distance at tetrad	Auricle distance at zero	Differences
Jinheung	-12	46.8	29.6	17.2	75.7	58.3	17.4
IR36	-3	67.6	61.1	6.5	82.4	75.0	6.6
Suweon 264	-9	60.9	51.8	9.1	79.1	66.7	12.4
Suweon 258	-3	60.0	56.7	3.3	76.3	69.4	6.9
Milyang 29	-6	62.2	51.4	10.8	78.9	63.0	15.9
Lengkwang	+1	27.8	25.1	2.7	44.1	40.2	3.9

Table 12. Relationship between sterility of special spikelets of auricle distance at tetrad and distance at zero due to low temperature (15/15°C) treatment.

Variety	Auricle distance at tetrad (cm)	Sterility of whole panicle					
		4 days treatment			7 days treatment		
		Auricle distance at tetrad	Auricle distance at zero	Differences	Auricle distance at tetrad	Auricle distance at zero	Differences
Jinheung	-12	51.2	40.4	10.8	82.6	62.4	20.0
IR36	-3	63.5	59.3	4.2	90.5	85.5	5.0
Suweon 264	-9	60.6	53.2	7.4	79.0	61.3	17.7
Suweon 258	-3	55.4	51.5	3.9	76.5	72.0	4.5
Milyang 29	-6	58.3	43.1	15.2	80.5	61.7	18.8
Lengkwang	+1	21.8	20.2	1.6	42.4	36.9	5.5

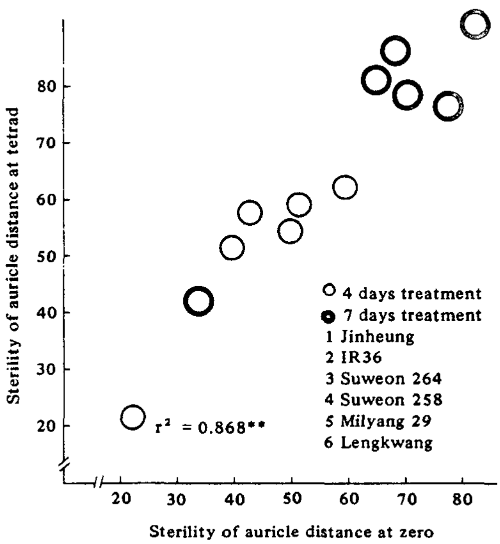

Fig. 11. Correlation between sterility of per panicle of auricle distance at tetrad and auricle distance at zero due to low temperature treatment.

and auricle distance at zero had a difference of 17.2%; in IR36, 6.5%; in Suweon 264, 9.1%; in Suweon 258, 3.3% Milyang 29, 10.8%; in Lengkwang, 2.7% (Table 12).

Likewise, in Jinheung formation of tetrad stage is earlier, so sterility of auricle distance at tetrad and auricle distance at zero was very different. But in Lengkwang formation of tetrad stage is auricle distance +1 cm, so sterility of auricle distance at tetrad and auricle distance at zero had only a difference of 2.7%. Thus, as shown in Fig. 10,11, when the formation of tetrad stage is near the auricle distance at zero, there is a high correlation between sterility of auricle distance at tetrad and auricle distance at zero (Fig. 10, 11). At 7 days treatment, the same tendency was observed.

DISCUSSION

In rice, it is important to find out the most sensitive stage to sterile-type cool injury of rice. There have been many studies on the sensitive stage due to low temperature.

Anthesis had been believed to be the only sensitive stage to cool induced sterility until the middle of 1930's. Later, another sensitive stage, the booting stage, was found by some researchers (Enomoto, 1933; Kakizaki and Kido, 1938; Terao *et al.*, 1940). In the early 1940's the meiotic stage of pollen mother cell was considered to be the most sensitive during the booting stage, because some cytological abnormalities were observed in meiosis through optical microscopes (Terao *et al.*, 1940; Sakai, 1943). Recently, Satake and Hayase (1970) found that the most sensitive stage is just after meiosis, that is, the tetrad and the early microspore stage. They denoted this stage as the young microspore stage. They further found a secondary sensitive stage just before meiosis (Satake and Hayase, 1974).

In the earlier studies the procedure of estimating the sensitive stage consisted of comparing sterility of panicle with the same heading date. Even in the panicles with the same heading dates there is a difference of 1 day in maturity between the earliest and the latest heading; and within the same panicle there is a great variation in maturity (7 days) between the apical and basal portion of spikelets. Satake and Hayase (1970) adopted auricle distance instead of heading date. However, actual determination by ocular inspection of the most sensitive stage (the tetrad-1st contraction phase) to low temperature is very difficult.

Since the objective of the study was to identify the most sensitive stage (the tetrad-1st contraction phase) to low temperature in the field, analysis of several methods was done on the following bases: (1) relation between auricle distance and pollen developmental stage in special spikelets; (2) relation between palea length and auricle distance; (3) relation between pollen developmental stage and palea length, and (4) relation between dry weight of special spikelets and auricle distance.

By these methods, each pollen developmental stage can be identified in the microscope with respect to different auricle distances, but this method is very difficult in the field. The percentages of dry weight of special spikelets at tetrad stage were very different between varieties (Table 5) compared to those at auricle distance +9 cm (3-4 days before heading except in Lengkwang).

Since dry weight at tetrad is very different between varieties, it can not be used for identification of tetrad. Table 3 shows the relation between pollen developmental stage and elongation of palea length. In all varieties the most sensitive stage occurred at tetrad when the elongation of palea length was about 50-60% compared to the flowering stage (final palea length) as 100 percentage. This result will be helpful in identifying the tetrad stage in the field.

Figure 3 shows a straight line relation, observed between panicle distance and palea length until the final palea length. It means that pollen developmental stage can be estimated by the use of auricle distance as reported by Satake (1976).

As pointed out in a number of research studies, temperature is one of the major factors affecting rice production. Rice plants have optimum temperature ranges for their different growth stages. Usually for each growth stage of rice, optimum temperature range is about 25 to 30°C. However, sometimes the temperature drops lower than the optimum in each phase as influenced by weather condition. Delay in the growth stages also delays flowering.

In the temperate zone flowering is often delayed. The temperature for ripening is very low because of low temperature in late fall, so ripening is very poor. The weight of grain is decreased and this results in decreased yield. Likewise, the delayed-type of cold damage delays the growth of rice plants (Enomoto, 1941; Matsushima, 1964) and prevents them from maturing. The result is a decrease in yield and deterioration of grain quality. During the growth of rice, there are three sensitive stages to low temperature: (1) from rooting stage to start of tillering stage, (2) before and after initial panicle formation stage (25-35 days before heading), and (3) before and after heading (Enomoto, 1933, 1937; Fuku and Kondo, 1939; Terao and Kondo, 1942; Takeshima, 1962; Satake and Hayase, 1970).

In this experiment on indica-japonica varieties, at 7 days treatment the delay in flowering was close to that of susceptible variety IR36, but at 4 days treatment, close to that of Jinheung (Fig. 4). In indica-japonica varieties when the low temperature treatment is about 4 days, then there is little or no delay but with more than 7 days at 15/15°C, there is delay in flowering. This result is similar to the finding of Lee (1979).

Several researches reported the decreased number of spikelets due to low temperature treatment at the initial panicle formation and the booting stage. Fuku and Kondo (1939) observed that number of spikelets decreased due to low temperature (3 day at 14.5°C, 5 days, 6.5 days and 10 days at 17°C) at the vegetative growth stage and at the spikelet formation stage, but they considered the latter factor more important. Terao (1940, 1941) reported decrease in number of spikelets due to low temperature (10 days at 17°C) during panicle formation.

In this study, the percentage of degenerated spikelets at the tetrad stage due to low temperature treatment was low at 4 days treatment and high at 7 days treatment. This means more than 7 days treatment is harmful. In other studies, sterility is observed from the 20th to the 25th days after heading. Through this study, it can be suggested that in selecting varieties resistant to low temperature, the number of degenerated spikelets must be considered.

Sterility is one of the important factors in cold damage during the panicle formation and the heading stage. It is called sterile-type cold injury. This damage is very different at each growth phase, among varieties, with different cultural methods, duration of low temperature, and environmental condition. The critical temperature for sterile type cool injury is 15°±15°C (Nishiyama *et al.*, 1969; Sasaki *et al.*, 1973). The inhibition of cell plate formation during meiosis and the dilatation of tapetal cells occur approximately below 15°C (Sakai, 1937, 1949). On the other hand, high temperature above 30°C inhibits fertilization (Matsushima and Manaka, 1959). Sterility is induced when the cooling treatment is confined to the panicle. This is the reason why deep-water irrigation covering the level of panicle is an effective method of protection against sterility (Sakai, 1949).

As shown in Fig. 6, in all varieties at the 7 days treatment, sterility of the special spikelets was more than 80% at the most sensitive stage of treatment (15/15°C). This result, however, cannot be used for recognition of difference in varieties. On the other hand, at the 4 days treatment, in Jinheung sterility of the special spikelets was 46.7% and susceptible variety IR36, 67.8%. Indica-japonica varieties had about 60% sterility, very close to IR36, showing susceptibility to low temperature. Lee (1979) pointed out that the japonica variety Jinheung was more tolerant to low temperature than indica-japonica varieties during the whole ripening stage at 17°C for 10 days. Similar result have been reported by other researchers (Heu, 1978; Chung, 1979; Ahn, 1973).

Figure 9 shows the relation between fertility of the special spikelets and auricle distance as affected by low temperature. All varieties had the lowest fertility of special spikelets at the most sensitive stage, at tetrad. This result is in agreement with the report of Satake and Hayase (1970). As shown in Table 11, comparison between sterility of the auricle distance at tetrad and auricle distance at zero. When testing for sterile type to cold injury, actual determination of the most sensitive stage to low temperature is not easy. So in many cases, auricle distance zero or heading stage has been used. But formation of the tetrad and auricle distance are different in all varieties. So it is suggested that in order to get the right sterility data, the tetrad stage must be considered. However, when the formation of tetrad stage is near the auricle distance at zero, then it is a possible use either auricle distance zero or heading stage.

摘　　要

水稻 Indica×Japonica品種을 中心으로 類型이 다른 品種을 供試 低溫에 敏感한 時期를 外的으로 손쉽게 判別할 수 있는 方法과 減數分裂期에 있어서 低溫의 影響을 究明하고자 phytotron을 利用하여 精密試驗을 試圖한 結果를 要約하면 다음과 같다.

1. 水稻生育期間中에서 低溫에 가장 敏感한 Tetrad phase는 葉耳間長이 振興은 - 12 cm, IR 36-3cm 水原 264號 - 9cm, 水原 258號 - 3cm, 密陽 29號 - 6 cm, Lengkwang+ 1 cm 였다.

2. 本試驗結果 Tetrad phase는 모든 品種에서 內穎(palea)의 길이가 最大에 達하는 開花期를 100로 하였을때의 50 - 60% 伸長되었을 때 나타나고 있었다.

3. 低溫에 依한 穎花의 退化率은 15 ℃에서 統一型品種 및 印度型品種에서는 대단히 높았으나 Japonica品種(振興)과 Indica品種(Lengkwang)에서는 比較的 낮었다.

4. 水稻減數分裂期에 있어서 繼續 15 ℃로 7日以上 低溫處理는 水稻의 低溫에 限界溫度를 넘어서 耐

冷性의 品種間 差異를 區別하기 어려웠으나 4日間의 低溫處理에서는 品種間 差異가 뚜렷하여 不稔率이 振興 ; 46.8%, IR 36 ; 67.6% 水原 264號 ; 60.9% 水原 258 ; 60.0% 密陽 29號 ; 62.2%, Lengkang 27.3%였다.

5. 花粉母細胞의 發育段階의 Tetrad-1st contraction phase에서의 低溫은 稔實率을 가장 낮게 하였으며 이 時期를 前後로 멀어질수록 稔實率은 높아졌다.

6. 內穎의 길이는 穎花分化에서 開花期까지 直線的으로 伸長하였고 葉耳間長의 伸長과는 正의 相關關係가 認定되었다.

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