イネの小胞子初期冷温処理による雄性不稔(28)

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Male Sterility Caused by Cooling Treatment at the Young Microspore Stage in Rice Plants

XXVIII. Prevention of cool injury with the newly devised water management practices —— effects of the temperature and depth of water before the critical stage

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Abstract : Potted rice plants were grown in the phytotron with different water temperature and water depth during the period from the spikelet differentiation stage to just before the young microspore stage, and then cooled at 12°C for 3 days at the young microspore stage to test their cool tolerance. The degree of cool tolerance at the young microspore stage was greatly varied with the temperature and depth of water before the critical stage. It was enhanced with raising the water temperature up to 25°C and with increased water depth up to 10cm. Effect of the deep water irrigation as countermeasures against cool injury were experimented under the severe cool-temperature conditions in the phytotron. Yield-decrease due to cool air temperature during the critical stage was remarkably reduced by keeping the water depth at 10cm before the critical stage, and it's effect was larger than that of the former deep water irrigation of 20cm during the critical stage. Preventive effect of cool injury by combining the deep water irrigation before and during the critical stage was not additive but synergistic. Based on these results, we proposed the water management with a depth of 10cm during the period from the spikelet differentiation stage to the young microspore stage as a newly devised countermeasure against cool injury.
Key words : Cool injury, Cool temperature, Rice, Sterility, Water management.

イネの小胞子初期冷温処理による雄性不稔　第28報　新水管理法による冷害防止：佐竹徹夫・李　善龍・小池説夫・刈屋国男（農林水産省北海道農業試験場）
要　旨：ポットで土耕栽培のイネを，穎花分化期から小胞子初期までの期間（前歴期間）ファイトトロン自然光室（昼24／夜19°C）内で水温と水深を変えて栽培し，小胞子初期に冷温処理（12°C 3日間）を行って耐冷性を検定した．小胞子初期のイネの耐冷性は前歴水管理によって大きく変動し，水温25°Cまでは水温を高くするほど，水深10 cmまでは水深を深くするほど，耐冷性が向上した．つぎにファイトトロン内のきびしい冷温条件（前歴期間の気温18°C，水温21°C，および小胞子初期5日間の気温15°C，水温18°C）の下で，深水灌漑による冷害防止効果を実験した．前歴期間10cmの深水灌漑を行うと小胞子初期の冷気温による減収が著しく軽減され，その効果は従来から唱導されてきた危険期20 cmの深水灌漑のそれよりも大きかった．また前歴深水と危険期深水を組合せた場合の冷害防止効果は，相加的ではなく相乗的であった．以上の結果に基づき，冷害防止のための新しい水管理法として，穎花分化期から小胞子初期までの期間における10cmの深水灌漑を提唱した．
キーワード：不稔，イネ，水管理，冷温，冷害．

Kakizaki and Kido[2] reported for the first time that sterility in rice was induced most easily by cool temperature at the meiotic division stage of pollen mother cells. Sakai[8] pointed out that sterility was definitely reduced by deep water irrigation in 1941 with a cool summer and proposed the deep water irrigation with a depth of 15 cm during the meiotic division stage as countermeasures to prevent sterility due to cool air temperature. This is based on the facts that water temperature in paddy fields around the booting stage is generally 2—5°C higher than air temperature and that 80% of the susceptible spikelets at the meiotic division stage were distributed up to a height of 15cm above ground level.

Since Sakai's report was published, attention has been focused only on the deep water irrigation around the meiotic division stage as countermeasures against cool injury. Weather

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conditions before the critical stage were not so noticed, because sterility was hardly caused by only a spell of cool temperature before the meiotic division stage. Ito[1] demonstrated, however, that moderate pre-cooling increased the sterility caused by cool temperature at the critical stage, although the sterility hardly increased by the moderate pre-cooling only. Furthermore we found that the degree of sterility caused by cooling at the young microspore stage was greatly changed with water temperature during the period from the spikelet differentiation stage to just before the cooling[9]. This finding gave us a key to reconsider the water management practices as countermeasures against cool injury.

In the present study, experiments were designed to 1) determine the water temperature and water depth before the critical stage which are necessary for full enhancement of cool tolerance in rice, and 2) evaluate the effects of the new water management practices on the prevention of cool injury under the severe cool temperature conditions in the phytotron.

Materials and methods

Abbreviation :

WT : water temperature, WD : water depth, AT : air temperature, p : previous period (from the spikelet differentiation stage to just before the young microspore stage), c : critical stage (young microspore stage), For example, water temperature during the previous period is abbreviated as WTp, water depth during the critical stage as WDc, air temperature during the previous period as ATp, and so on.

Experiment 1. Changes in cool tolerance by the WTp

Two varieties differing in degree of cool tolerance, Hayayuki (high tolerance) and Norin 20 (medium tolerance) were used. Twenty seeds were directly sown in a circular pattern in each 4-liter plastic pot and grown in the naturally lit room with day/night temperature regime of 24/19°C. Each pot was provided with 0.9g each of N, P and K. Tillers were removed at the 7th leaf stage and only panicles from uniform main stems were used for experiments. Water temperature in the pot was controlled only during the previous period to 5 levels in the range from 18 to 30°C by submerging the pot into water bath in the growth room controlled at 24/19°C, with a WD of 10cm. Plants were cooled at 12°C for 3 days at the critical stage just after the WTp treatments and then transferred back to the growth room. Control plants were not subjected to cool temperature at the critical stage. Spikelet fertility was measured for all the spikelets of each panicle at maturity.

In the experiment above, WT was kept constant throughout the day and night. On the other hand, the effects of WTp with different combination of day and night temperatures were examined for 13 treatments in Table 1, keeping the WD at 10cm.

Experiment 2. Changes in cool tolerance by the WDp

Rice variety Hayayuki was grown as in the previous experiment in the naturally lit room at 24/19°C until the spikelet differentiation stage. During the previous period, plants were grown in the water of 25°C with 4 different WD of 1, 5, 10 and 15cm, in the naturally lit room with day/night air temperature regime of 20/20°C, and then cooled at 12°C for 3 days at the critical stage. After the cooling treatment plants were transferred back to the growth room at 24/19°C and spikelet fertility was investigated for all the spikelets of each panicle at maturity.

Experiment 3. Single and combined effect of deep water irrigation before and during the critical stage on the prevention of cool injury

Ten seeds of rice variety Kitahikari (medium tolerance) were directly sown in a circular pattern in each 4-liter plastic pot. Each pot was provided with 0.9g each of N, P and K. Plants were grown in the naturally lit room with day/night AT regime of 26/19°C until the spikelet differentiation stage and then plants were subjected to 18/18°C during the previous period and 15/15°C for 5 days at the critical stage. Water temperature was controlled to 2 levels of 21 and 24°C combined with WD of 3 and 10cm during the previous period and at 18°C combined with WD of 3, 10 and 20cm for 5 days at the critical stage.

Water temperature was set at 3 and 6°C higher than AT on the basis of an estimation, as will be described later, that the WTp was 3.1—5.6°C higher than the ATp in the ordinary year in Hokkaido. As a result, 17 treatments with different combination of AT, WT and WD were conducted as shown in Fig. 5. Duration of the previous treatments subjected to 18°C AT differed with the combination of WT and WD as shown in Fig. 5. After the cooling treatment at the critical stage plants were transferred back to the growth room at 26/19°C and the grain yield components were investigated at maturity.

Results

The WTp and WDp which are required to fully enhance cool tolerance at the critical stage

Fig. 1 shows the spikelet fertility in rice grown at the different WTp. The percentage of fertility decreased with decreasing WT in the range of WTp below 22—25°C even without cooling at the critical stage. Changes in cool tolerance with the WTp were evaluated with the fertility index calculated with the following equation.

$$\text{Fertility index } (\%) = \frac{\arcsin\sqrt{\text{Fertility}(\%) \text{ in the cooled}}}{\arcsin\sqrt{\text{Fertility}(\%) \text{ in the control}}} \times 100$$

As shown in Fig. 2, the fertility index increased linearly with rising the WTp in the range of 18—25°C and the curve became a plateau between 25 and 30°C in both varieties, although it was always high in Hayayuki than in Norin 20 over the whole range of WTp.

Table 1 shows the fertility index of rice grown at the different regimes of day/night WTp. The fertility index increased with increasing the daily average WTp. It was, however, higher in rice grown with different day/night WTp regimes than those grown with constant day/night WTp, if the daily average WTp was equal. In other words, cool tolerance was further strengthened when daytime WTp was high enough even if low WTp lasted for long hours during the night.

Fig. 3 shows the effect of WDp on fertility. The percentage of fertility increased with an increase of the WTp in the range of 1—10cm, but did not increase further in the range of 10—15cm. Fertility of rice grown at a depth of 5cm for the first half of the previous period and 10cm for the latter half was almost the same as that of rice grown at a depth of 10cm throughout the whole period.

Fig. 4 shows the time course of the height of panicles from ground level when plants were grown at the WDp of 10cm. From the figure, the period during which panicle's position was lower than the height of water surface was about 5 days in rice grown at a depth of 5cm, 7 days in that of 10cm and 8 days in that of 15cm. Thus, the deeper the WDp the longer the period during which panicle growth was affected directly by WT because of the position below the water surface.

Prevention of cool injury by the water management before and during the critical stage

Table 2 shows the yields and yield components in 17 experimental plots. The yields dispersed in the wide range of 4—46g/pot, correspointing to 9—98% of the control (C_0). The air temperature conditions given were so severe that the yield decreased to only a 9% level (C_1T_1) of the control when plants were grown at 21°C WTp and 18°C WTc, with a depth of 3cm throughout the period. Even if the AT and WT conditions were the same, the yield increased to a 28% level of the control by only keeping the WDp at 10cm (C_2T_1), to a 17% level by only keeping the WDc at 20cm (C_1T_3) and to a 55% level by combining them (C_2T_3). Thus, the single effect of the WDp (evaluated as $28-9=19\%$) on the prevention of cool injury was larger than that of the WDc (evaluated as $17-9=8\%$) and the combined effect of the WDp and WDc (evaluated as $55-9=46\%$) was substantially great, being rather synergistic than additive. Higher yields were obtained when the WTp was controlled

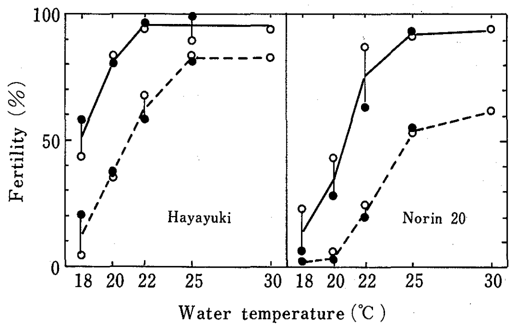

Fig. 1. Changes in the percentage of ferility in rice grown with different water temperature before the critical stage.

Water temperature was controled with a depth of 10cm under air temperature conditions of 24/19°C. Experiments were conducted in 1983(○) and 1984 (●).

—○●—Control (24/19℃).

---○●---Cooled (12℃, 3 days).

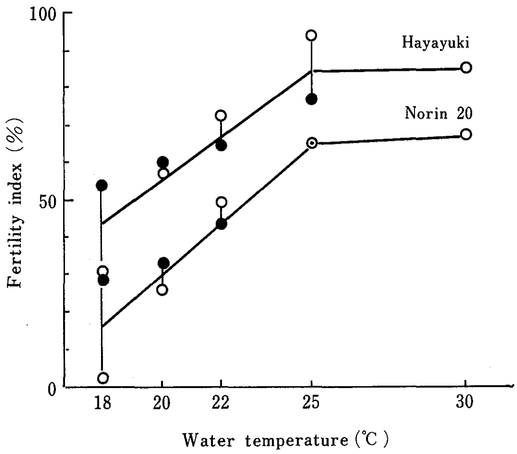

Fig. 2. Changes in the fertility index in rice grown with different water temperature before the critical stage.

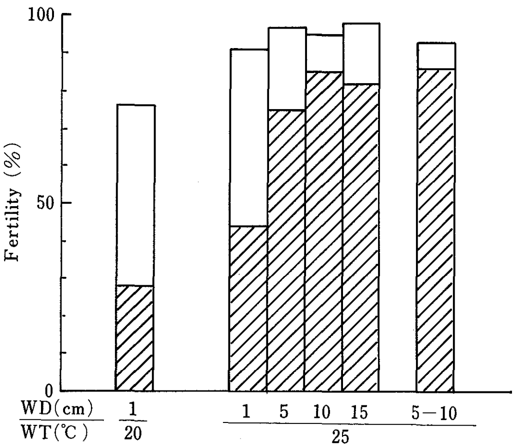

Fig. 3. Changes in the percentage of fertility in rice grown with different water depth before the critical stage.
Water depths were controlled at a water temperature of 25°C under the air temperature conditions of 20/20°C.

Table 1. Effects of the different combination of the day and night WTp on the fertility index.

Daily average WTp	Daytime WTp	Night WTp	Fertility* C	Fertility* T	Fertility index
°C	°C(hrs)	°C(hrs)	%	%	%
26	26	26(12)	88	88	100
22	22(12)	22(12)	79	74	95
	24(12)	20(12)	80	77	97
	26(8)	20(16)	75	76	101
20	20(12)	20(12)	81	50	70
	22(12)	18(12)	79	57	78
	24(8)	18(16)	78	67	89
	26(6)	18(18)	77	65	88
	24(12)	16(12)	81	65	84
	26(9.6)	16(14.4)	78	69	91
18	18(12)	18(12)	45	21	65
	24(6)	16(18)	70	34	63
	26(4.8)	16(19.2)	63	36	70

* C : Control (24/19°C), T : Cooled (12°C, 3 days).

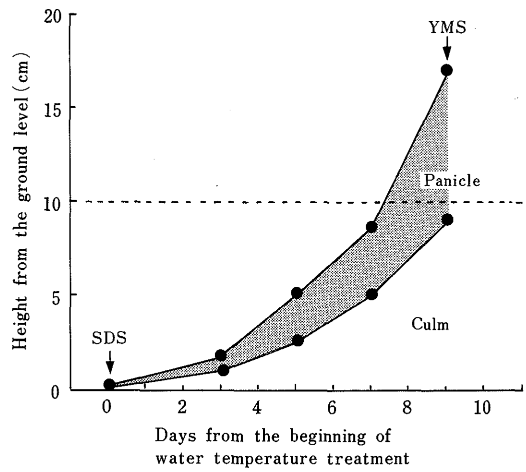

Fig. 4. Time course of the position of panicles above ground level during the water temperature treatment at 25°C with a depth of 10cm.
SDS : Spikelet differentiation stage.
YMS : Young microspore stage.

at 24°C (6°C higher than the ATp): the yield ratio in the single treatment of 10cm WDp and 20cm WDc and that in the combined treatment of them were 74% (C_4T_1), 70% (C_3T_3) and 89% (C_4T_3), respectively, whereas the yield ratio was only 36% (C_3T_1) in plants grown with a depth of 3cm throughout the treatment period. The WDc of 10cm was insufficient to prevent cool injury. Raising the WTp from 21°C to 24°C resulted in a remarkable increase of yield. The yield of rice grown at 24°C WTp with 3cm WDp was higher than that at 21°C WTp with 10cm WDp.

Increase of the WTp, WDp and WDc resulted in increase of the spikelet fertility and 1000 grain weight. The spikelet number per pot rather increased as the WTp, WDp and WDc decreased because of the increase of late developed tillers. The yield correlated with the spikelet number ($r=-0.61^{**}$), fertility ($r=0.99^{**}$) and 1000 grain weight ($r=0.93^{**}$).

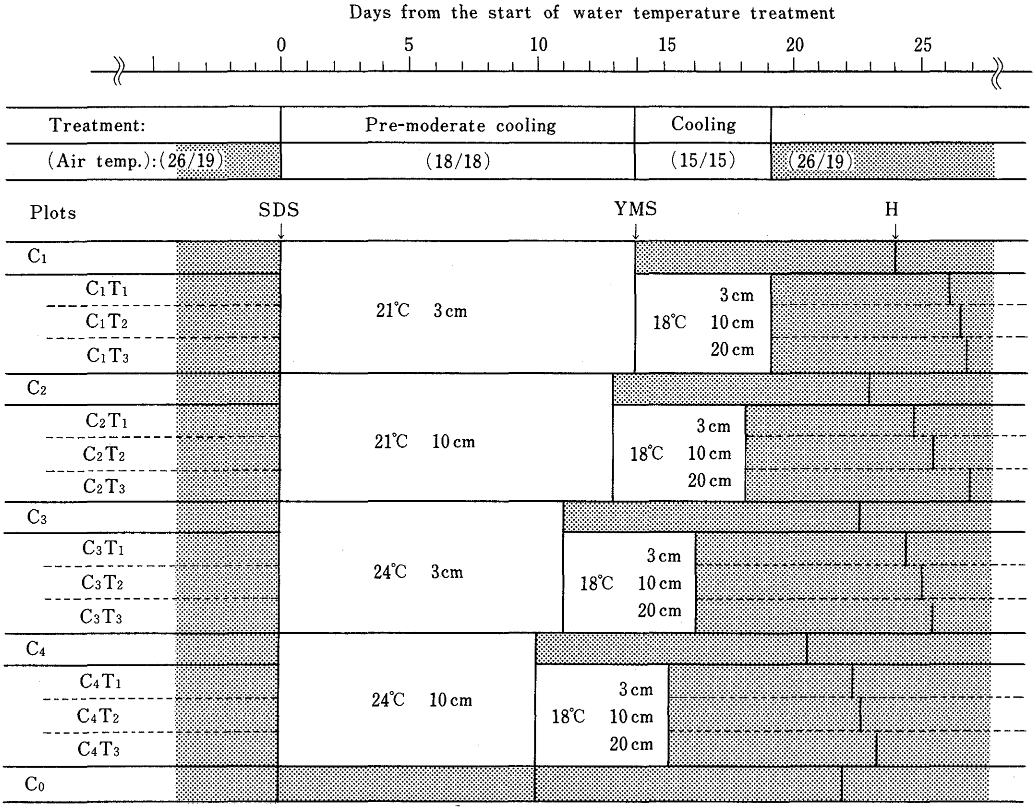

Fig. 5. Combination of air temperature, water temperature and water depth in 17 experimental plots.
SDS : Spikelet differentiation stage.
YMS : Young microspore stage.
H : Heading stage of main culms.
Water temperature and water depth are shown in the figure.

The contribution ratio of the yield components on the yield was analysed by the method of stepwise foreword regression. The following multiple regression equation was obtained among the yield (Y), spikelet number (X_1), spikelet fertility (X_2) and 1000 grain weight (X_3).

$$Y=0.014X_1+0.47X_2+1.41X_3-62.79 \quad (R=0.99^{**})$$

$$b'_{YX_1 \cdot X_2X_3}=0.18^{**}, \quad b'_{YX_2 \cdot X_1X_3}=0.99^{**}, \quad b'_{YX_3 \cdot X_1X_2}=0.14^{**}$$

The multiple correlation coefficient and the standard partial regression coefficient of the yield with the yield components were highly significant. The standard partial regression coefficient of the percentage of fertility to the yield ($b'_{YX_2 \cdot X_1X_3}$) was 5.5 and 7.1 times higher compared with that of spikelet number ($b'_{YX_1 \cdot X_2X_3}$) and 1000 grain weight ($b'_{YX_3 \cdot X_1X_2}$), respectively. This means that the variation of yield was resulted mainly from that of the percentage of fertility.

It is feared that deep water irrigation may cause the decrease of lodging tolerance due to the hyper-elongation of lower internodes. Table 3 shows the length of the 3rd and 4th internode which are closely related to lodging tolerance. The 3rd internode lengthened with an increase of the WDc but rather shortened as the WDp and WTp was increased. On the contrary, uppermost internode lengthened as the WDp and WTp was increased. A definite tendency was not recognized in the length of the 4th internode. Similar result was obtained in Hayayuki too in the experiment 1 (Fig. 6): the length of the 3rd internode shortened with an increase of the WTp in the range of 18 to 25°C although that of upper internode rather lengthened.

Table 2. Yield and yield components.*

Plot	Grain weight (Y)	Spikelet number (X_1)	Fertility (X_2)	100 grain weight (X_3)
	g/pot(%)	/pot	%	g
C_1	24(51)	2000	52	22.8
C_1T_1	4(9)	2208	10	20.2
C_1T_2	6(13)	2215	13	21.2
C_1T_3	8(17)	2186	17	21.7
C_2	33(70)	1675	83	23.9
C_2T_1	13(28)	2370	25	21.8
C_2T_2	14(30)	2064	32	21.6
C_2T_3	26(55)	1980	58	22.7
C_3	44(94)	1970	94	23.6
C_3T_1	17(36)	2351	32	22.0
C_3T_2	21(45)	2295	42	22.0
C_3T_3	33(70)	2076	71	22.4
C_4	46(98)	1888	96	25.5
C_4T_1	35(74)	2100	72	23.4
C_4T_2	38(81)	2000	72	23.4
C_4T_3	42(89)	1938	90	24.1
C_0	47(100)	2118	88	25.1

* See Fig.5 for the different treatments.

Table 3. Length of 3rd and 4th internode.

WTp (°C)	WDp (cm)	WDc (cm) 3	10	20	WDc (cm) 3	10	20
		3rd internode (cm)			4th internode (cm)		
21	3	12.3	13.0	14.5	3.9	3.9	3.9
	10	11.8	11.7	14.3	4.1	4.7	4.8
24	3	10.7	12.1	14.4	3.3	3.4	3.7
	10	8.9	10.4	12.2	3.2	4.2	3.4

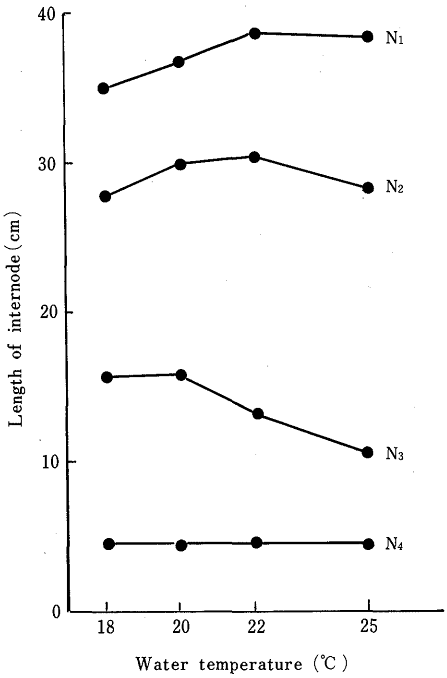

Fig. 6. Changes in the length of internode in rice grown with different water temperature before the critical stage. N_1-N_4 : 1st-4th internode.

Discussion

From the results of Figs. 2 and 3, the guide value of the WTp and WDp necessary for full enhancement of cool tolerance was determined as 25°C and 10cm, respectively. Increasing the WDp resulted in the prolongation of the period during which panicles grow at a position below the water surface (Fig. 4), and changes in cool tolerance with an increase of the WDp was in parallel with the increase of this period. This suggests that changes in cool tolerance with the WTp are caused by the temperature around panicles. This idea is supported by Matsushima et al.'s report[5] pointing out that growth of tillers was greatly affected by the temperature around the growing points but was not affected by the root temperature. Thus, it is practically enough to raise the water level gradually with the growth of panicles, without keeping the WDp at 10cm from the start (Figs. 3 and 4).

Noticeable effects of the deep water irrigation as countermeasures against cool injury were demonstrated in the experiment-3. Sakai[8] recommended the WDc at 15 cm to decrease spikelet sterility but later workers[3,6] pointed out that a depth of 20 cm was necessary to bear its full fruit. In the experiment-3 too, the preventive effect of spikelet sterility was deficient at a depth of 10 cm but sufficient at 20 cm.

On the other hand, water management with the WDp of 10 cm we proposed was superior than the former water management with the WDc of 20 cm in the following points : 1) the effect is larger, 2) its practice is easier, and 3) the lower internode becomes short. Moreover, a synergistic effect is expected when the WDp at 10 cm was combined with the WDc at 20 cm. Therefore, we think that the WDp at 10 cm should be widely practised as a fundermental water management practice in the cool region.

The reason why the 3rd internode shortened with raising the WTp up to 25°C (Table

Table 4. Average air temperature (ATp) and average water temperature (WTp) during the previous period in the ordinary year observed at 11 locations in northern Japan.

Location	Spikelet differentiation stage	ATp	WTp
Hokkaido		°C	°C
Kun-neppu	July, 4	18.2	23.8
Asahikawa	July, 4	20.1	23.2
Iwamizawa	July, 8	20.3	23.6
Sapporo	July, 12	19.1	22.5
Ohno	July, 15	21.1	—
Tohoku			
Kuroishi	July, 16	23.3	24.3
Towada	July, 18	22.8	24.2
Ohmagari	July, 13	23.6	—
Takizawa	July, 17	22.7	25.2
Furukawa	July, 17	24.3	—
Kohriyama	July, 17	24.7	25.3

The ATp and WTp were calculated as the average temperature for 15 days after the spikelet differentiation stage of midmaturing varieties in each locations.

3 and Fig. 6) is not clear, however, Matsushima et al.[4] also made mention of a similar result : the 3rd internode was the longest in rices grown at WT of 21°C than in rices grown in 18, 31 and 36°C water. This is very interresting phenomenon in relation to lodging tolerance in rice.

Cool tolerance was effectively enhanced by the raise of WTp, especially of the daytime WTp (Table 1). Several methods to raise WT in paddy fields have been tried[7]. Of these methods, only plastic wind break nets are now practically used in the strong wind area in Hokkaido[10]. Development of more effective method to raise WT with lower cost is required for stable rice production in the cool region.

From the discussion above, the effects of the WTp can be always expected when and where the ATp is below 25°C, because the WTp is usually higher than the ATp in the cool region. The ATp and WTp in the northern part of Japan were estimated from the average AT and WT in the ordinary year, which were observed at 11 Agricultural Experiment Stations (Table 4). The ATp in the ordinary year ranged from 18.2 to 21.1°C in Hokkaido and 22.7 to 24.7°C in Tohoku district, and the WTp was 3.1 to 5.6°C and 1.6 to 2.5°C higher than the ATp, respectively. As the ATp and WTp are considered to be lower than those in Table 4 in the year of cool summer, the careful water management before and during the critical stage is essential in such a cool region as Hokkaido and Tohoku districts.

As discussed above, weather condtions prior to the critical stage cause the variation in cool tolerance of rice plants. This fact is very important in relation to precise testing of cool tolerance of breeding lines and also to the mechanism of cool injury. Our great interest is now focused on the mechanism of changes in cool tolerance with the WTp. The details of this will be given in the next paper.

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* In Japanese.
** In Japanese, the title was tentatively translated by the present authors.
*** In Japanese with an English summary.