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The Difference in Sterility due to High Temperatures during the Flowering Period among Japonica-Rice Varieties

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Abstract : The objectives of this study are to compare the floret sterility induced by a high temperature given in the daytime during the flowering period among nine japonica rice varieties, and to clarify the mechanism of the high-temperature-induced sterility. Nine japonica rice varieties were subjected to 35.0, 37.5 or 40.0°C day- temperature conditions (1000-1600) for six consecutive days using sun-lit phytotrons, and the percentage of fertility, pollination and germinated pollen grains on the stigmas were examined. The temperature that caused 50% sterility varied with the variety, and a difference of approximately 3.0°C was observed between the most tolerant and susceptible varieties. Under the 37.5°C day-temperature condition, the percentage of florets with 10 or more germinated pollen grains was roughly coincident with the percent fertility, but under the 40°C day-temperature condition, it was higher than the percent fertility. Many of the florets with less than 10 germinated pollen grains had less than 20 total pollen grains on their stigmas under both temperature conditions. From these results, we concluded that sure pollination under high-temperature conditions is an important factor and that the high-temperature tolerance of the processes following pollen germination is also required for fertility under excessively high temperature conditions.

Key words : Flowering period, High temperature, Japonica rice, Pollen, Pollination, Sterility.

Increasing concentrations of greenhouse-effect gases such as carbon dioxide in atmosphere may cause global warming (Hansen et al., 1984). Such an environmental change would affect rice growth and yield. Some scientists have attempted to assess the effects of warm temperature and high carbon dioxide in the atmosphere on the yield of rice using simulation models (Baker et al., 1992; Bachelet and Gay, 1993; Horie, 1993; Horie et al., 1996). In particular, Horie et al. (1996) issued stern warning on the effect of high temperature at the flowering stage; the anticipated high temperature would induce floret sterility, negate the positive effects of the elevated CO_2 concentration and increase the instability of the rice yield even in temperate regions. Various experimental and observational lines of evidence have been reported for the occurrence of the floret sterility induced by air temperature of over 35°C at flowering (Osada et al., 1973; Sato et al., 1973; Satake and Yoshida, 1978; Matsushima et al., 1982; Horie et al., 1996; Morokuma et al., 1996; Matsui et al., 1997a; Matsui et al., 1997b). The floret sterility seems to be the key issue to assess the effect of the environmental change on the rice yield and to form the countermeasures.

In tropical Asian and African countries, the high temperature-induced floret sterility occasionally affects the rice yield (Osada et al., 1973; Satake and Yoshida, 1978). Osada et al. (1973), Satake and Yoshida (1978), and Matsushima et al. (1982) reported the difference in susceptibility to a high temperature among indica-rice varieties which were mainly cultivated in tropical Asian countries. These findings suggest the importance of adoption of the tolerant varieties in the high-temperature areas and the possibility of genetic improvement of high-temperature tolerance. On the other hand, we have only limited information about the difference in sterility among varieties under high-temperature conditions among japonica-rice varieties which were dominant in the temperate regions. Although high temperature-induced sterility has not been a serious problem for the rice production in the temperate region so far, the high-temperature tolerance in japonica rice varieties needed to be investigated for sustained stable rice production under the higher environmental temperatures anticipated in the future.

Physiological analysis of high-temperature-induced sterility has been also done by several researchers using indica-rice varieties. Osada et al. (1973) found that the main cause of the sterility is a failure of fertilization. Satake and Yoshida (1978) studied the relationship between pollination and fertility under high-temperature conditions, using three varieties selected from tropical Asian countries. They pointed out that the percentage of spikelets with more than 10 germinated pollen grains on each sigma was almost identical with the percent spikelet fertility, and concluded that the direct cause of sterility induced by a high temperature was the disturbance of pollen shedding and the decreased number of germinated pollen grains on a stigma. However, their data showed that some florets having 10 or more germinated pollen grains were not nessesarily fertile at a high temperature

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Table 1. The percent fertility of the nine japonica-rice varieties under 37.5 and 40.0°C day-temperature conditions.

Group	Variety	Place of breeding station*	Percent fertility 37.5 ℃**	40.0 ℃**
Tolerant	Akitakomachi	N	80.0	50.3
	Nipponbare	M	85.3	35.0
Moderate	Aichinokaori	M	78.2	19.8
	Yumehikari	W	74.3	22.9
	Akihikari	N	65.2	22.2
	Kinmaze	M	65.9	13.2
	Aoinokaze	M	58.4	19.9
Susceptible	Minamihikari	W	45.7	19.2
	Hinohikari	W	44.1	13.7

* N : North Japan, M : Middle Japan, W : West Japan.
** Day temperature (1000-1600).

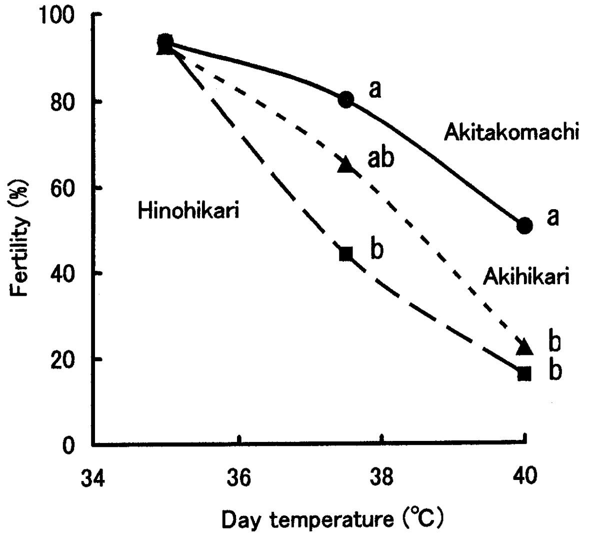

Fig. 1. The percent fertility of the florets flowered at various day-temperature conditions. Day temperature (6 hours from 1000 to 1600) was changed, night temperature (1800 -0800) being fixed at 26°C.
Symbols with the same letters are not significantly different at 5% level and at 1% level for 37.5 °C and 40.0°C day-temperature conditions, by Duncan's multiple range test (n=3).

of around 41°C; the percent fertility of the florets decrease to 0%, although 20% of florets had more than 10 germinated pollen grains on stigma under 41°C. This may indicate that an excessively high temperature affects the process after pollen germination and inhibits the fertilization.

In this report, we first clarified the difference in the high-temperature-induced sterility among nine japonica-rice varieties. Then, we explored the cause of the difference in the sterility among varieties on the basis of the observation of pollen grains deposited on the stigmas under 37.5 and 40°C day-temperature conditions.

Materials and Methods

Nine japonica rice varieties were used (Table 1). Seeds were sown so that their panicles would emerge late in August. Seedlings each at the 5.0-5.5 leaf stage were transplanted in a circular pattern into four L pots, 20 seedlings per pot, and grown under submerged soil conditions outdoors. Each pot was provided 0.4 g N, 0.4 g P_2O_5, 0.4g K_2O as a top dressing at about 45 days before heading. Tillers were removed as they appeared.

Sun-lit phytotrons at the National Institute for Environmental Studies (Aiga et al., 1982) were used for high-temperature treatments. The plants at the middle heading stage were exposed to 35.0°C, 37.5°C or 40.0°C for six hours (1000-1600) for six consecutive days. Night temperature (1800-800) was 26.0°C for all treatments. Relative humidity was 60% in the daytime (1000-1600) and 80% in the nighttime (1800-800). Air temperature and humidity from 800 to 1000 and from 1600 to 1800 were lineally changed. The treatments started and ended at 1800. Three pots per treatment were used for each variety. The flowering time of all varieties were 1030-1130, 1100-1215, and 1130-1300 under 35, 37.5, and 40°C day-temperature conditions, respectively.

On the fourth day after the start of the high-temperature treatments, 37.5 and 40.0°C, the florets which flowered on that day were sampled at 1300, and the pollen grains on the stigma were observed under a microscope. The number of pollen grains deposited on each stigma and the number of germinated pollen grains on each stigma were counted after staining with Cotton Blue. More than 50 florets per treatment in each variety were used for this examination. The degree of fertility of all florets on the panicles, on which the florets started to flower on the first day of treatment, was measured at maturity, using more than four panicles (over 150 florets) per pot.

Results and Discussion

Table 1 shows the percent fertility of the nine varieties under the high-temperature conditions. The nine varieties were divided into three classes of tolerance; tolerant, moderate and susceptible varieties. The percent fertility of the nine varieties was not clearly related to the place where the varieties had been bred. Figure 1 shows the percent fertility of the typical three varieties under various day-temperature conditions. The temperature at which the percent fertility decreased to 50% was about 37.0°C for 'Hinohikari' (most susceptible of the nine varieties) and about 40.0°C for 'Akitakomachi' (most tolerant of the nine varieties). Thus, the difference in the sterility-inducing temperature was about 3°C between the two varieties.

Horie et al. (1996) predicted using the simulation model that, in the varieties with high-temperature tolerance similar to 'Akihikari', rice yield will decrease by 10 -40% in southern Japan under the future climate conditions predicted by the General Circulation Models of the earth's atmosphere, and that, in the variety more tolerant than Akihikari by 1.6°C, we can limit the yield decrease in the same area to 10%. The floret sensitivity to the high temperature damage is one of the most sensitive parameters for the prediction of rice yield. The present result

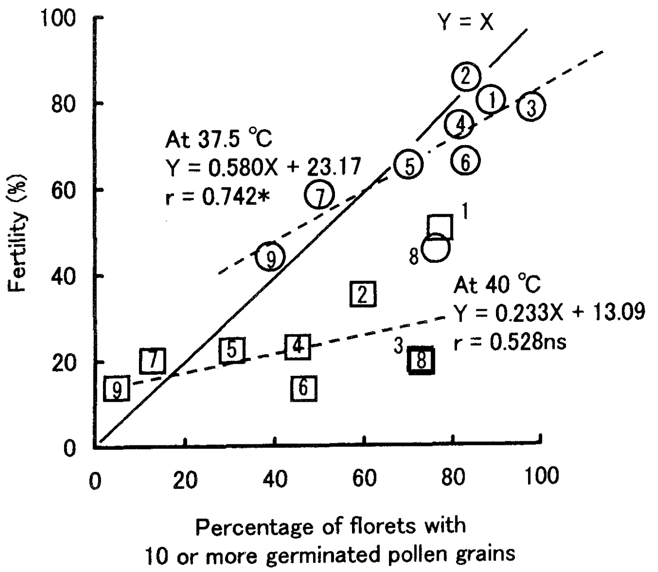

Fig. 2. The relationship between the percentage of florets with 10 or more germinated pollen grains on the stigma and the percent fertility.
Symbols : (□) 40.0°C, (○) 37.5°C. Numbers : (1) Akitakomachi, (2) Nipponbare, (3) Aichinokaori, (4) Yumehikari, (5) Akihikari, (6) Kinmaze, (7) Aoinokaze, (8) Minamihikari, (9) Hinohikari.

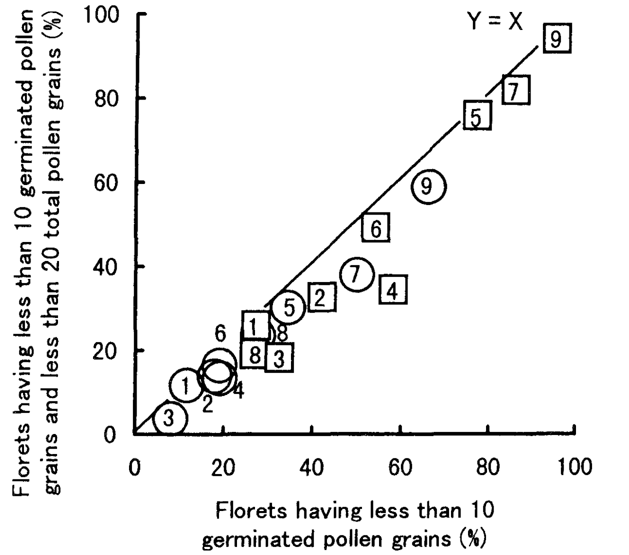

Fig. 3. The relationship between the percentage of florets with less than 10 germinated pollen grains and that of the florets with less than 10 germinated pollen grains and less than 20 total pollen grains.
Symbols and numbers are the same as those in Fig. 2.

demonstrates the importance of variety selection for the anticipated future climate conditions, and suggests that we can considerably mitigate the high-temperature damage in rice yield by the cultivation of high-temperature-tolerant varieties.

Since the high temperature affects the fertilization of the florets only on their flowering day (Satake and Yoshida, 1978), we hypothesized that the percent fertility of florets flowered on any day during the treatment periods was almost constant. In order to examine the direct cause of sterility in this experiment, we, therefore, compared the percent fertility of panicles which start to flower on the first day of the treatment period (such panicle finish the flowering within the treatment period (six days)) with the percentage of the florets having 10 or more germinated pollen grains on the stigma at the fourth day of the treatment periods. The percent fertility roughly coincided with the percentage of the florets having 10 or more germinated pollen grains on the stigma in plants exposed to 37.5°C (Fig. 2). Since more than 10 germinated pollen grains are required for sound fertilization (Togari and Kashiwakura, 1958; Satake and Yoshida, 1978; Sawada,1978; Matsui et al., 1997a), we can regard the decrease in the number of germinated pollen grains on the stigma as the primary cause of the sterility at 37.5°C. In plants exposed to 40.0°C day-temperature, the rate of increase in the percent fertility against the percentage of florets with 10 or more germinated pollen grains was lower than that in plants exposed to a 37.5°C day-temperature and the percent fertility was considerably lower than the percentage of florets with 10 or more germinated pollen grains in many varieties. This indicates the possible existence of a high-temperature-sensitive process following the pollen germination. Akitakomachi and 'Nipponbare', which showed a relatively high percent fertility against the percentage of florets with 10 or more germinated pollen grains (Fig.2) among varieties examined, may have tolerance in these processes. Yamada (1964) showed that the high temperature of 38°C impedes elongation of pollen tubes in rice and that there is a difference in the tolerance to high temperatures in pollen tube elongation among the varieties. Further research will be required for the investigation of pollen tube elongation in high-temperature-tolerant varieties like Akitakomachi and Nipponbare.

Many of the florets with less than 10 germinated pollen grains on the stigma had less than 20 pollen grains on it (Fig. 3) and florets with 10 or more germinated pollen grains on the stigma always had 20 or more pollen grains on it. These results suggest that the high temperature decreases the number of germinated pollen grains per stigma mainly through poor pollination in japonica rice, as was the case in indica rice varieties (Satake and Yoshida, 1978). In particular at 37.5°C level, we can conclude that the direct cause of sterility is poor pollination. Mackill et al. (1982) reported that the number of pollen grains per stigma at the flowering time under the control temperature is highly associated with the fertility and the number at a high temperature and showed that the pollination trait can be improved by breeding. The improvement of pollination trait by breeding would be effective to increase the percent fertility under a 37.5°C day-temperature condition. Many of the florets with less than 10 germinated pollen grains had less than 20 pollen grains under the 40°C day-temperature condition indicates that, even under this temperature condition, the primary cause of the occurrence of florets with less than 10 germinated pollen grains was poor pollination.

Satake and Yoshida (1978) reported that the major cause of floret sterility varied among indica varieties; it is poor germination of pollen grains on a stigma for a high-temperature-tolerant variety while it is poor shedding of pollen grains on the stigma for susceptible varieties. Our results showed that high-temperature induced floret sterility mainly through the poor pollination under the 37.5°C day-temperature condition and that, under the 40°C day-temperature condition, a high temperature also affected the process after pollen germination and inhibited the fertilization. These results suggest that the improvement of high-temperature tolerance in the process after the pollen germination as well as that in the pollination process is required for high percent fertility at the 40°C day-temperature condition.

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