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HIGH-TEMPERATURE STRESS IN RICE

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HIGH-TEMPERATURE STRESS IN RICE[1]

ABSTRACT

When rice is exposed to air temperatures higher than 35°C, heat injuries occur. Clear varietal differences are observed for high temperature injuries at different growth stages. The rice plant appears to be most sensitive to high temperature at flowering. The second most sensitive stage is about 9 days before flowering. High temperature during anthesis induces high percentages of spikelet sterility. The occurrence of sterility can be attributed to disturbed pollen shedding and impaired pollen germination but not to inactivated pistil.

Early morning anthesis is considered one way to avoid high temperature stress. Oryza glaberrima flowers open 3 hours earlier than IR36, O. sativa. Some O. sativa and O. glaberrima crosses have anthesis earlier than IR36.

Studies of the genetics of high temperature-induced sterility indicate that heat tolerance has a fairly high heritability and that most genetic variation is additive.

There are clear varietal differences in high temperature-induced sterility at anthesis. Both heat-tolerant and early-maturing varieties can be found from the existing variety stocks.

A comparison between phytotron and field experiments confirmed that the phytotron can be used for screening for heat tolerance.

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Sato (1960) provides clear evidence of occurrence of high sterility in rice attributable to high temperature. Sato grew the variety Neang Meas in pots at the rice experiment station throughout the year in Battambang, Cambodia, and subjected the plants to a short day. Plants flowered every month of the year and 100% sterility was found in the plants that flowered in April, which coincided with the peak in the monthly maximum temperature (Fig. 1). Development of the panicle, spikelets, and pollen grains seemed normal. Sato suggested that the sterility was caused by poor dehiscence of the anthers and desiccation of the stigmas by high temperature and dry environment.

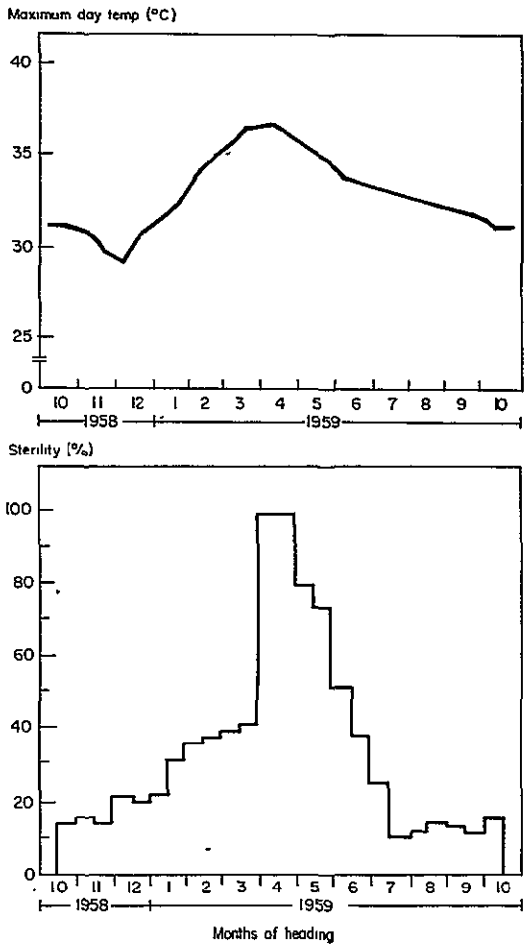

Fig. 1. Maximum day temperature and percentages of sterility of rice crops that flowered in different months of the year (Sato 1960).

On the Central Plain of Thailand, Osada et al (1973) observed high percentages of empty (sterile) grains in the dry season. They attributed the empty grains to high temperatures at flowering. Varietal differences were conspicuous. The percentage of sterility ranged from less than 10% for IR8, RD1, and Taichung Native 1 to 40-50% for BKN6624-46-2, a Thai selection, and C4-63G, a Philippine variety. In the rainy season, however, such varietal differences were no longer recognized; most varieties had a normal (6-13%) percentage of empty grains.

High sterility under high-temperature regimes has also been reported from studies using controlled environment facilities. Moriya and Nara (1971) observed high percentages of sterility and partially filled grains when the rice plant was exposed at flowering to a daily mean temperature of 31.5°C (daily maximum was 36°C, and daily minimum 27°C). Similarly, Sato et al (1973) and Kusanagi and Washio (1974) observed high percentages of sterility at 35/30°C and impaired ripening at 33/25°C daily maximum-minimum temperatures.

OCCURRENCE OF HIGH-TEMPERATURE PROBLEMS

High percentages of sterility in rice will occur if temperatures exceed 35°C at anthesis and last more than an hour. High temperature-induced sterility has been observed in the dry season crop in Cambodia, Thailand, and India; in the first rice crop in Pakistan; and in the crops in Iran, Iraq, Egypt, Saudi Arabia, tropical African countries, and the United States (Table 1). High temperature-induced sterility is currently not a major problem in Southeast Asia because most rice is grown in the rainy season. It will, however, become a constraint to rice production as areas of rice grown in the dry season with irrigation increase.

TYPE OF HIGH-TEMPERATURE INJURY

When rice is exposed to temperatures higher than 35°C, heat injuries occur according to growth stages (Table 2). Clear varietal differences are observed for high-temperature injuries at different growth stages. The geographic origin of rice varieties is not related to susceptibility to heat stress. BKN6624-46-2, a selection from Thailand, is much more susceptible to high temperatures at the vegetative and anthesis stages than Fujisaka 5, a Japanese variety.

When rice is grown in a heated glasshouse during winter in the temperate regions, white leaf tips, chlorotic bands and blotches, and white bands and specks often develop on the leaves. These symptoms are similar to those caused by high temperatures during cloudy weather in the IRRI Phytotron (Table 2).

Table 1. Reported observations of sterility in the field attributed to high-temperature injury.

Country where sterility was observed	Reference
Thailand	Osada et al (1973)
Cambodia	Sato (1960)
India	Mann and Kanwar (1972)
Pakistan	IRRI (1977)
Iran	Moafizad and Chaudry (1977)
Iraq	Chao (1959), Ito (1963), El-Shamma (1967), Al-Najar (1968)
Saudi Arabia	Chang et al (1978)
Egypt	Sato (1967)
Mauritania	Trinh (1976), Dingle and Trinh (1976)
Senegal	Dingle and Trinh (1976), Trinh (1978)
Mali	Dingle and Trinh (1976)
Niger	USDA (1968)
United Sates	Lehman (pers. comm.)

EFFECT OF HIGH TEMPERATURE ON RICE GROWTH DURING VEGETATIVE STAGE

When rice is exposed to high air temperatures during the vegetative stage, plant height, tiller number, and dry weight may be considerably reduced (Table 3). At 35/25°C, the total dry weight of IR747B2-6 was only one-sixth that at 30/25°C. At 45/25°C leaves became discolored and desiccated in 2 days, gradually dried from the tip to the base, and died 9 days after treatment.

High water temperature also retards rice growth. The temperature of the irrigation water from deep wells at IRRI is sometimes as high as 45°C. Plants growing in water constantly above 38°C died a few days after transplanting. Plants outside but adjacent to the lethal zone developed narrow white or striped leaves. When the average day time temperature of irrigation water was increased from about 27°C to 34°C, grain yield per hill decreased sharply as shown in Figure 2.

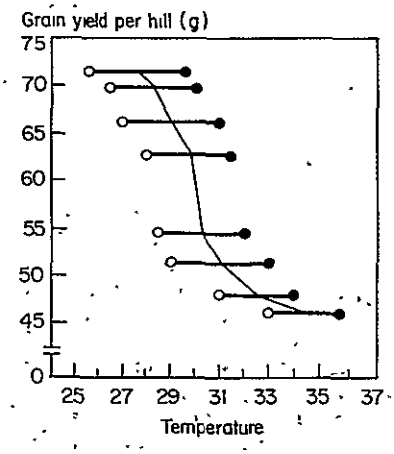

Fig. 2. Average day temperature of irrigation water and grain yield per hill of the dry-season rice crop. The open o and the solid o denote the temperature range (IRRI /1964/.

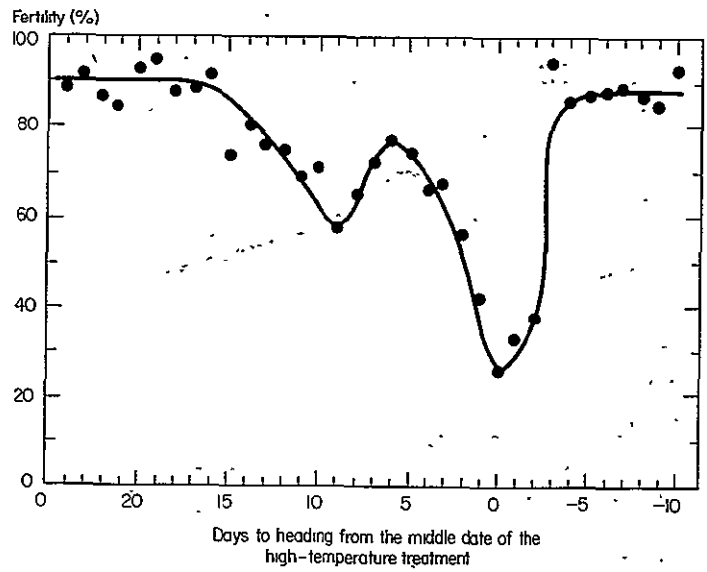

Fig. 3. Fertility of the spikelets of BKN6624-46-2 subjected to high temperature (35°C) at different stages of panicle growth for 5 days. Source: Satake and Yoshida (1978).

EFFECT OF HIGH TEMPERATURE DURING REPRODUCTIVE STAGE

The rice plant appears to be most sensitive to high temperature at flowering and the second most sensitive stage is about 9 days before flowering (Fig. 3). The second most sensitive stage corresponds to the most sensitive stage for low temperature. When the plants are subjected to high temperature earlier than 15 days before flowering or later than 3 days after flowering, high temperature does not affect spikelet sterility. When the plants are subjected to high temperature during the reproductive growth stage, white-tipped panicles are observed.

Table 2. Symptoms of heat stress and varietal differences in rice observed in the IRRI phytotron (IRRI 1975).

Growth stage	Symptoms	Susceptible varieties
Vegetative	White leaf tip	IR26, Calrose,
	Chlorotic bands and blotches	BKN6624-46-2
	White bands and specks	
	Reduced tillering	
	Reduced height	
Reproductive	White spikelets, white panicles	IR24, Calrose,
	Reduced spikelet numbers	
Anthesis	Sterility	C4-63G, H4, Calrose,
		Pelita I/1, Basmati-370,
		BKN6624-46-2
Ripening	Reduced grain filling	TN1, IR24, IR26, H4,
		Fujisaka 5, C4-63G,
		Pelita I/1

Table 3. Effect of high day temperature on the vegetative growth of IR747B2-6.[a/]

Plant characteristics	Day/night temperature (°C)			
	30/25	35/25	45/25	25/25
Plant height (cm)	60.6	34.2	22.9	x[b/]
Tiller number/plant	46.0	24.0	6.0	x
Shoot dry weight (g)	11.10	1.65	0.26	x
Root dry weight (g)	1.78	0.41	0.05	x
Total dry weight (g)[c/]	12.88	2.06	0.31	x
Root weight/total weight	0.14	0.20	0.16	x
RGR (g·g/wk)	1.5	1.0	0.5	x

[a/] Patel (1976): Plants were treated during 1 to 5 weeks after sowing. [b/] Plants died 9 days after treatment.
[c/] Initial dry weight: 0.03 g/plant.

In 1977, white-tipped panicles were widely observed in Palawan, Philippines. Both spikelets and rachis were white. The symptom was conspicuous on improved varieties such as C4-63G and IR26; no such symptom was found on traditional varieties. The symptom indicated cessation of panicle growth at early stages of panicle development. The white spikelet was about 3-5 mm long, which corresponds to the most active elongation period of spikelet during the reproductive growth stage.

With the above information, a detailed experiment was conducted to examine the effect of high temperature on panicles (IRRI 1980). When the plants

were subjected to 38/27°C and 41/27°C at 70 days after sowing (when panicle length was about 2 mm), about 20-25% white spikelets were observed (Fig. 4). This symptom induced by the high temperatures was identical to that observed in Palawan. At 35/27°C, however, only a few spikelets were white. In a separate experiment, the same variety had 38% spikelet sterility when the plants were subjected to 35/27°C at flowering. Thus, the critical temperature for white-tipped panicle is higher than that for sterility at flowering.

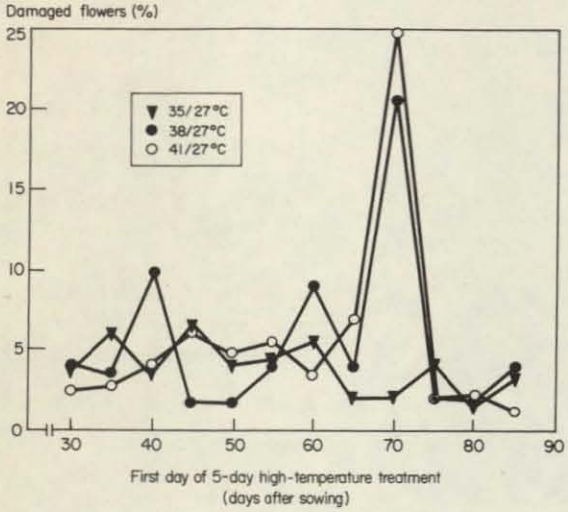

Fig. 4. Effect of high temperature on occurrence of damaged spikelets (IRRI 1980).

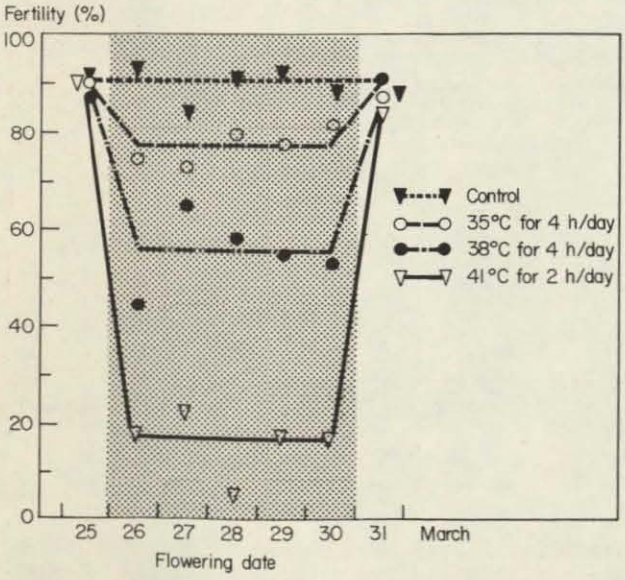

Fig. 5. Fertility of the spikelets that flowered on the days before, during, and after high-temperature treatments. The variety IR747B-2-6 was subjected to high temperature for 5 consecutive days (26-30 March). Source: Satake and Yoshida (1978).

In Palawan, the daily maximum air temperature is unlikely to exceed 38-41°C. The temperature near the soil surface, however, can be 40°C or higher under strong sunshine, even when the air temperature is about 35°C. Therefore, it is possible that the high soil temperature can inhibit spikelet growth if the growing panicle is near the soil surface at the critical stage.

EFFECT OF HIGH TEMPERATURE AT ANTHESIS

As previously discussed, the rice plant is most sensitive to high temperature at flowering. A further examination of the stage sensitive to high temperature revealed that high temperature on flowering day causes sterility, and high temperature, except 41°C, for 5 consecutive days before or after flowering day does not disturb fertilization of spikelets provided the temperature on flowering day is below the critical high temperature (Fig. 5).

Sato et al (1973) studied the response of Norin No. 17, a japonica variety, to high temperature at flowering by subjecting the plants to 35/30°C for 3 consecutive days. They found that spikelets that flowered on the third day of the high-temperature treatment had high percentages of sterility whereas those that flowered on the first and second day were hardly affected by high temperature. Their findings disagree with those of Satake and Yoshida (1978), who found that any spikelet that flowered during high-temperature treatments had high percentages of sterility. These findings were further confirmed by studying the sensitive time of spikelets to high temperature on flowering day. High temperature during anthesis had a decisive effect on the incidence of sterility (Fig. 6). High temperature after anthesis had less effect on sterility. High temperature before anthesis had considerably less effect on sterility than the above. At both 38 and 41°C, the fertility percentage of spikelets that flowered an hour before the high-temperature treatment or earlier was normal. In rice, the pollen tube extends into the embryosac 30 minutes after anthesis, and fertilization is completed within 1.5-4.0 hours after anthesis (Cho 1956). Hence, spikelets that flowered at 29°C an hour earlier were already near completion of fertilization. These considerations suggest that spikelets at anthesis time are the most sensitive to high temperature, and that reproductive processes occurring within an hour after anthesis, such as dehiscence of anther, pollen shedding, germination of pollen grains, and elongation of pollen tubes, are disturbed by high temperature.

Causes of nonfertilization

Several lines of evidence show that sterility under high temperature is caused by disturbed pollen shedding and impaired pollen germination but not by inactivated pistil.

First, artificial shedding of healthy pollens on the stigmas of spikelets subjected to high tem-

perature during anthesis time increases the spikelet fertility to a normal level or nearly so (Fig. 7). The percentage of spikelet fertility of BKN6624-46-2 was about 35% when subjected to 35°C for 8 hours and increased to about 85% by artificial pollen shedding. Similarly, the percentage of spikelet fertility of IR747B-2-6 was about 3% when subjected to 38°C for 8 hours and increased to about 65%. These results suggest that the major cause of nonfertilization at 35°C for BKN6624-46-2 and at 38°C for IR747-2-6 is disturbed pollen shedding or decreased viability of pollen grains, and the ability of the pistil to be fertilized is normal. Failure of artificial pollen shedding to improve the spikelet fertility of IR747B-2-6 at 41°C could be attributed to impaired germination of pollen grains on the stigma. As will be shown later, pollen grains of N22 can germinate at 41°C but those of IR747B-2-6 cannot. Furthermore, the fact that the fertility of spikelets subjected to 41°C for 5 days before anthesis was increased by artificial pollen shedding (Fig. 7c) indicates that the ability of the pistil to be fertilized remained unaffected by the high temperature.

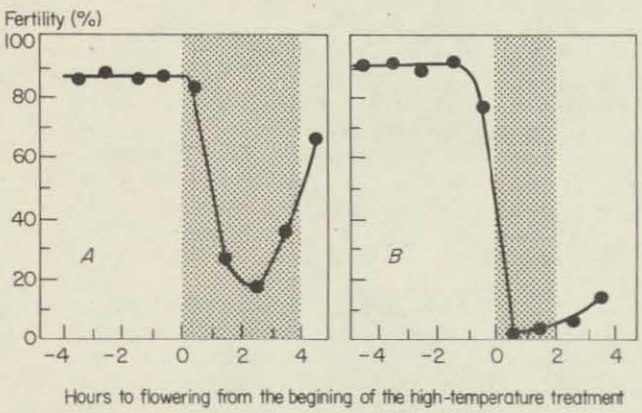

Fig. 6. Fertility of the spikelets of IR747B-2-6 that flowered in the hours before, during, and after high-temperature treatments. The treatments were 38°C for 4 h (A) and 41°C for 2 h (B). High temperature is indicated by the shaded area. Source: Satake and Yoshida (1978).

Second, the number of pollens on a stigma varied among the 3 varieties even at 29°C; it was generally more than 200 and was often too high to count in N22 but was mostly about 50-200 in IR747B-2-6 and 30-150 in BKN6624-46-2 (see Fig. 8). For convenience, spikelets that flowered during the high-temperature treatment were classified into 3 groups according to the number of pollen grains on a stigma -- spikelets with more than 20 pollen grains, those with 1 to 19 pollen grains, and those with none. Varietal difference in the percentage of well-pollinated spikelets with more than 20 pollen grains on a stigma was clear even at 29°C (Fig. 9). The percentage of well-pollinated spikelets decreased as temperature increased and the varietal difference in that percentage became more conspicuous.

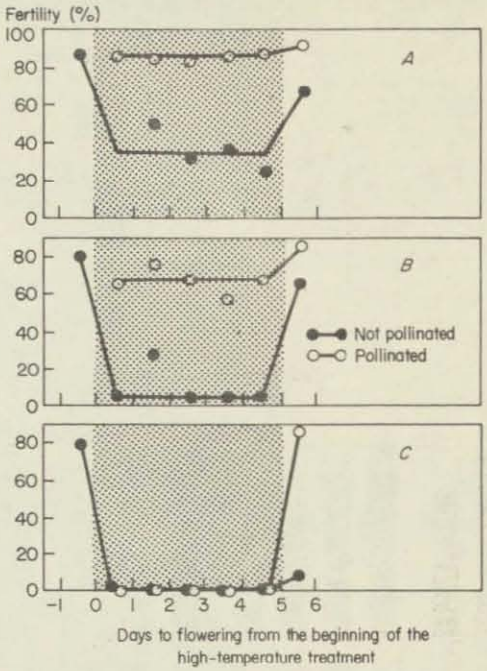

Fig. 7. Effect of artificial pollen shedding on the fertility of spikelets subjected to high temperature during anthesis. Treatments were: 35°C for 8 h for BKN6624-46-2 (A), 38°C for 8 h for IR747B-2-6 (B), and 41°C for 4 h for IR747B-2-6 (C). Source: Satake and Yoshida (1978).

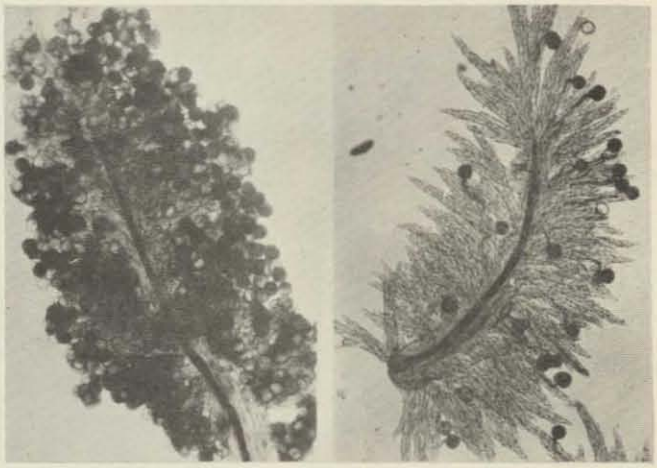

Fig. 8. Varietal difference in the number of pollen grains on a stigma. Left: N22, Right: BKN6624-46-2.

Third, germination of shed pollen grains is impaired by high temperature. Enomoto et al (1956) reported that the critical high temperature for pollen germination ranges from 41° to 45°C. Satake and Yoshida (1978) found large differences in the number of spikelets with more than 10 germinated pollen grains among varieties and at different temperatures (Fig. 10). In rice, more than 10 germinated pollen grains on a stigma are needed for

normal fertilization(Togari and Kashiwakura 1958). At 41°C, N22 had some germinated pollen grains but IR747B-2-6 had no germinated pollen grains. Abnormal shape of clustered pollen grains that failed to germinate at 41°C was clearly observed under a microscope (Fig. 11). The percentage of spikelets with more than 10 germinated pollen grains on a stigma was identical with the percentage of spikelet fertility.

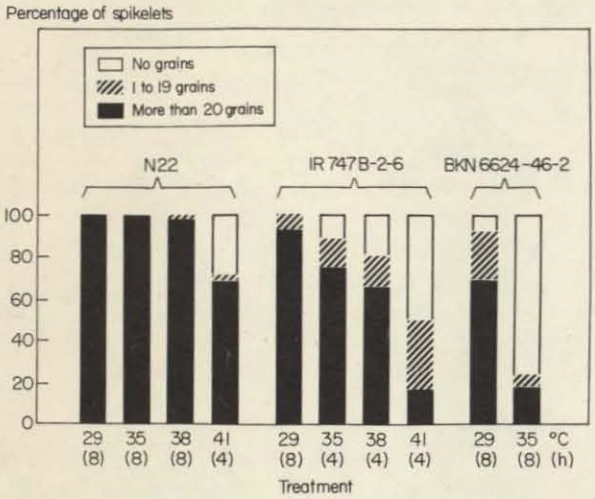

Fig. 9. Proportion of the spikelets grouped by the number of shed pollen grain on a stigma of spikelets that flowered during high-temperature treatments. Source: Satake and Yoshida (1978).

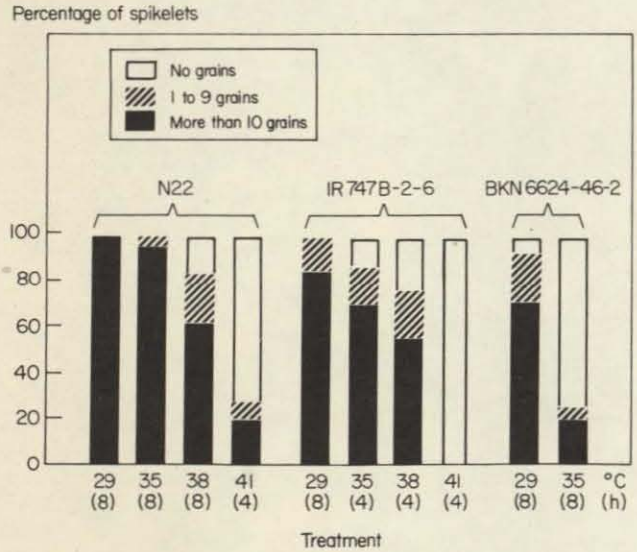

Fig. 10. Proportion of the spikelets grouped by the number of germinated pollen grain on a stigma of spikelets that flowered during high-temperature treatments. Source: Satake and Yoshida (1978).

Thus, the major cause of nonfertilized spikelets induced by high temperature varies with variety -- impaired germination for N22, and insufficient pollen shedding for IR747B-2-6 and BKN6624-46-2. Between these two, pollen shedding appears to be the primary cause for varietal differences in heat tolerance. The reason for such varietal difference appears to relate to the dehiscence characteristic of the anther, which is illustrated in Figure 12. In N22, dehiscence of anthers starts right after the glume opens and is completed when the anthers still remain inside the glume on short filaments. Thus, pollen grains of N22 can easily be shed onto the stigma. In IR747B-2-6, dehiscence of anthers starts when the anthers are about to emerge from the glume, and is completed when anthers stand on somewhat longer filaments, just above the glume, or the anthers droop over the lip of the glume on long, sagging filaments. BKN6624-46-2 has a dehiscence characteristic of anther similar to that of IR747B-2-6. Furthermore, many anthers remain closed at high temperature, resulting in poor pollen shedding on the stigma.

Fig. 11. Pollen germination on a stigma at 35 and 45°C. Upper photo shows normal germination at 35°C and lower photo shows failure of germination at 41°C.

It is clear that the position of the anther relative to the glume at dehiscence time and the degree of dehiscence are important characteristics for high temperature-tolerant varieties.

Relation between temperature at flowering and spikelet fertility

The percentage of fertility of spikelets as affected by different temperatures is shown in Figure 13.

For convenience two critical temperatures (CT) can be defined to characterize varietal response to high temperature -- the temperature when the percentage of spikelet fertility begins to fall below

80% (CT 80) and the temperature when the percentage of spikelet fertility is decreased to 50% (CT 50). From Figure 13, CT 80 was estimated at 36.5°C for N22, 35°C for IR747B-2-6, and 32°C for BKN6624-46-2. Thus, the difference in CT 80 between the heat-tolerant variety N22 and the heat-susceptible selection BKN6624-46-2 is more than 4°C. Likewise, CT 50 was estimated at 39°C for N22, 36.5°C for IR747B-2-6 and 33.5°C for BKN6624-46-2. At 41°C, the percentage of spikelet fertility of all 3 varieties was zero.

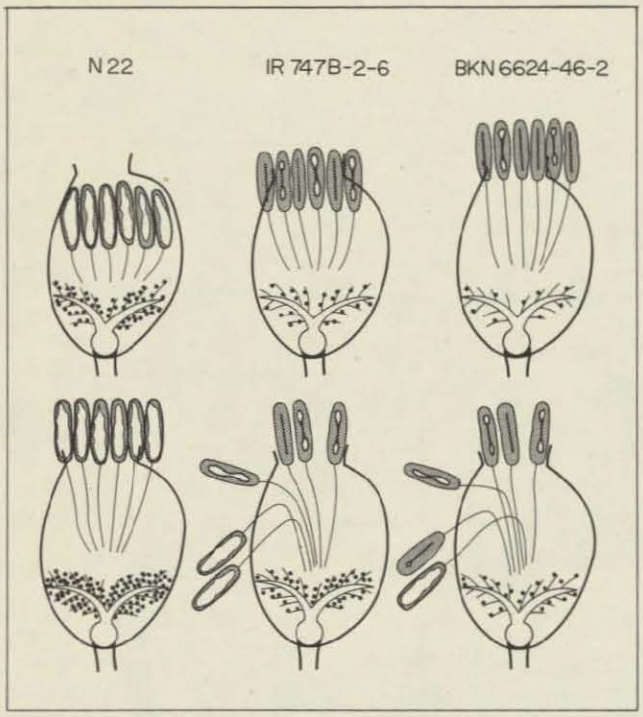

Fig. 12. Schematic diagram of varietal difference in anther dehiscence under high temperatures. Source: Satake and Yoshida (1978).

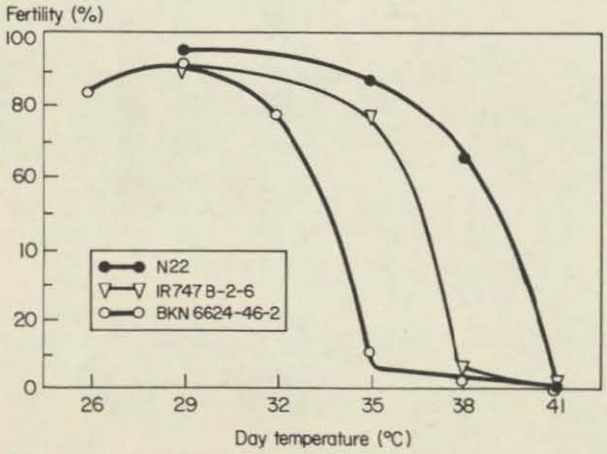

Fig. 13. Fertility of the spikelets that flowered at different day temperatures. Day temperature was kept for 8 h and night temperature was fixed at 21°C in each treatment. Source: Satake and Yoshida (1978).

The results shown in Figure 13 were obtained from 8 hours of high temperature per day. In a natural environment, however, it is unlikely that the high temperature lasts for 8 hours. In Figure 14, the duration of high temperature was varied from 2 to 8 hours/day for 5 consecutive days. From this figure, the critical temperature duration to induce 20% sterility was estimated at 38°C for 4 hours for N22, 38°C for 2 hours, and 35°C for 8 hours for IR747B-2-6, and 38°C for 2 hours and 35°C for 4 hours for BKN6624-46-2. At 41°C even the 2-hour treatment induced high percentages of sterility in the 3 varieties and hence the critical temperature duration was difficult to estimate. From Figure 14 it appears that 35°C can discriminate heat-susceptible BKN6624-46-2 from the 2 other rices and 38°C can discriminate heat-tolerant N22 from the others. The 41°C temperature is too high to detect any difference in heat tolerance among the 3 varieties.

The effect of night temperature at flowering on sterility is shown in Figure 15. In this experiment, night temperature was varied from 21°C to 33°C with a constant day temperature of 35°C for 8 hours a day. Night temperatures from 21°C to 30°C did not affect spikelet fertility but 33°C clearly decreased the percentage of fertility when it persisted for 16 hours. Such high night temperature for long duration may seldom occur, even in the tropics, and hence it is unlikely that high night temperature at flowering would induce a high percentage of sterility.

The temperature-rise pattern also affects spikelet fertility (Fig. 16). The percentage of spikelet fertility was only 11% when temperature was raised by the one-step control and maintained at 41°C between 1000 and 1200 hours but was 50% when the high temperature hours were shifted to 1200-1400 hours by the same procedure. In the multistep control where the temperature was raised by 3°C/hour, reached 41°C at 1200 hours, maintained at that temperature until 1400 hours, and dropped by 3°C/hour to the base temperature (29°C), the percentage of spikelet fertility was 61%. In the multistep control, the plants were subjected to temperatures higher than the base temperature for longer duration than the one-step control, yet the percentage of spikelet fertility of those plants was higher than that of the others.

These results appear to indicate that the occurrence of sterility relates to the time of anthesis relative to the onset of the critical high temperature. In those treatments where lower percentages of sterility were observed, more spikelets must have completed anthesis before the onset of critical high temperature. This is because spikelet sterility is induced by high temperature at anthesis and because high temperature does not affect fertility if it comes 1 hour after anthesis.

AVOIDANCE OF HIGH TEMPERATURE-INDUCED STERILITY BY EARLY MORNING ANTHESIS

Among the 3 varieties, IR747B-2-6 flowered more than 30 min earlier than BKN6624-46-2 and N22 in

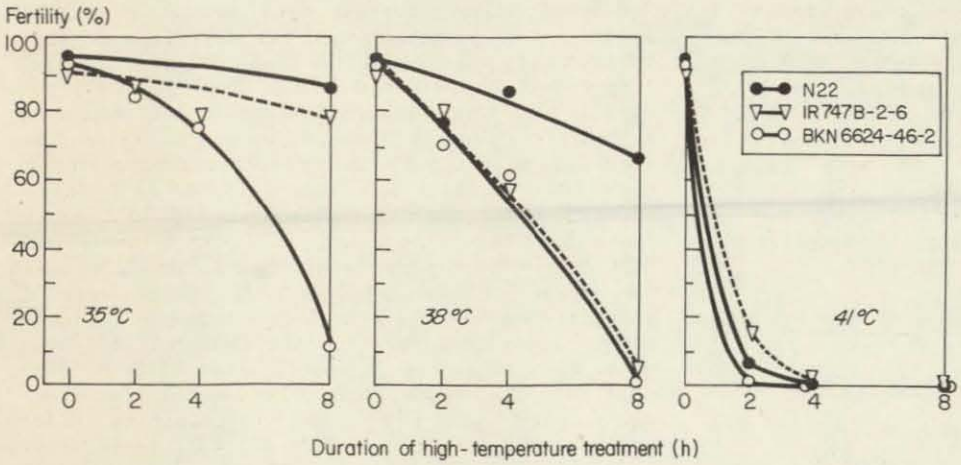

Fig. 14. Fertility of the spikelets subjected to different durations of different day temperatures. After the rice plants were subjected to high temperatures for specified number of hours, they were moved back to 29/21°C regime every day. Source: Satake and Yoshida (1978).

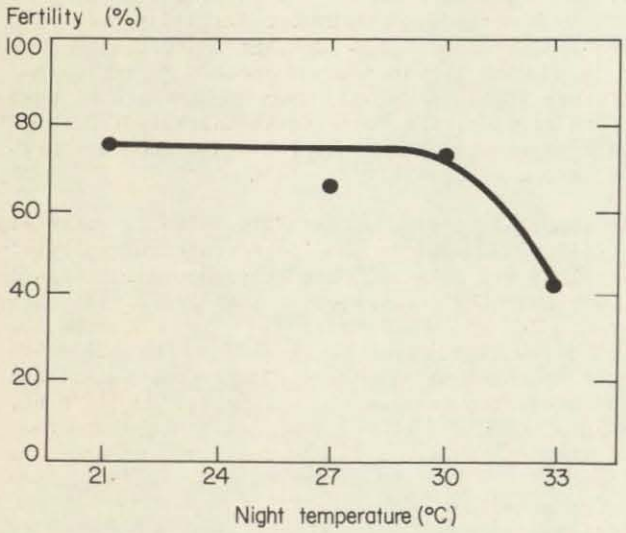

Fig. 15. Fertility of the spikelets of IR747B-2-6 subjected to different night temperatures for 5 flowering days. Day temperature was kept at 35°C for 8 h/day in each treatment. Source: Satake and Yoshida (1978).

the morning. Early morning anthesis is highly desirable because high temperature is avoided and hence high temperature-induced sterility is reduced.

Rice varieties usually open flowers about 1000-1200 hours (this depends on varieties, and climatic, edaphic, and cultural conditions; local time must also be taken into consideration). Air temperature goes up rapidly in the morning and exceeds the critical temperature (35°C) about 1000 hours in many high-temperature areas. Thus, the advancement of flower opening to early morning is one way to avoid high temperature-induced sterility.

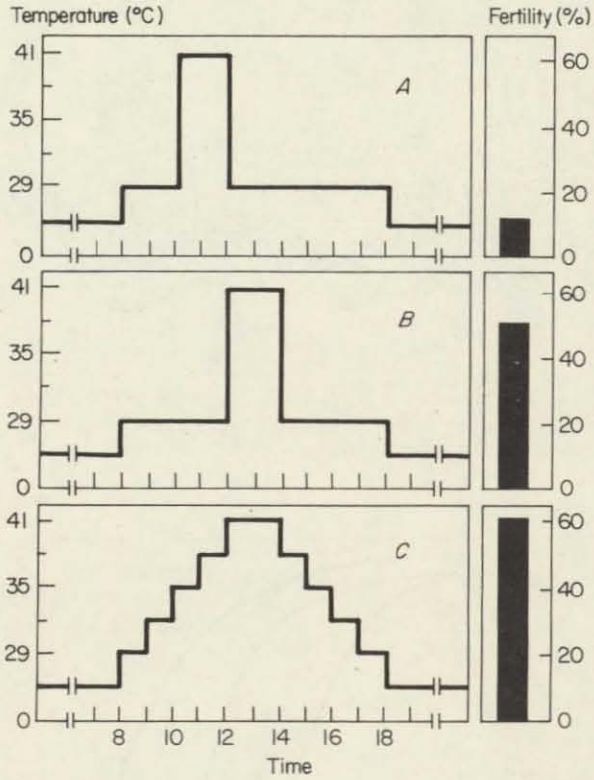

Fig. 16. Three different temperature-rise patterns and the fertility of spikelets of IR747B-2-6 that flowered in these regimes. Fertility is indicated by the shaded area. Source: Satake and Yoshida (1978).

The flowers of Oryza glaberrima, an African-cultivated rice species, open in the early morning (IRRI 1978). This characteristic of O. glaberrima can be incorporated into O. sativa (Fig. 17). The

earliest flower opening line in the O. sativa and O. glaberrima crosses had a peak of 0900-1000 hours, about 1 hour earlier than that of IR36. The flowering peak of O. glaberrima occurred at 0700-0800 hours, 3 hours earlier than that of IR36.

Even an hour advancement in the flower opening time may have a significant effect on sterility, because air temperature rises at a rate of 3°C/hour or more around 1000 hours.

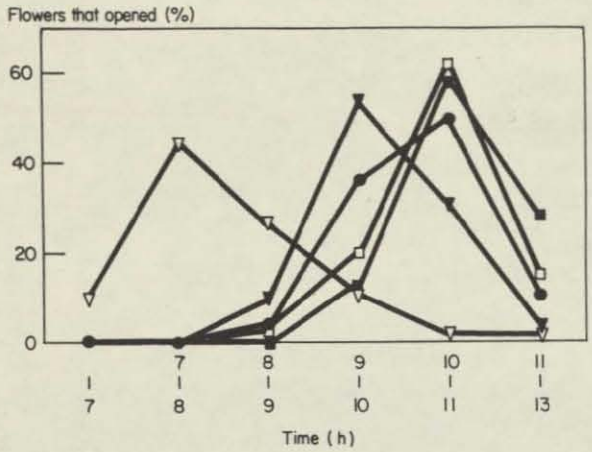

Fig. 17. Flower opening time of Oryza glaberrima x O. sativa hybrids, O. glaberrima, and IR36. Source: Nishiyama and Blanco (1980).

GENETICS OF HIGH TEMPERATURE-INDUCED STERILITY TOLERANCE

A diallel-cross experiment of six rice lines has shown that general and specific combining abilities for heat tolerance are highly significant. The general combining ability and specific combining ability variance for the six parents are shown in Table 4. Although IR2006-P12-12-2-2 has a good general combining ability, it has a high specific combining ability variance, indicating the presence of nonadditive genetic variance. N22 has a good general combining ability for heat tolerance but it would probably not be an ideal donor for this trait because of its poor plant type and the high amount of genetic sterility in its hybrid progeny. IET4658 and IR2006-P12-12-2-2 should prove good donors for heat tolerance in a breeding program.

The heritabilities for heat tolerance in the diallel cross were 76% for the broad-sense heritability and 71% for the narrow-sense. This indicates that heat tolerance has a fairly high heritability and that most genetic variation is additive. The cross IR52/IR2006-P12-12-2-2 was studied further by growing the parents, F_1, F_2, both backcrosses, and the F_3 generation in the phytotron and subjecting them to 35/27°C during flowering. Nonallelic genetic interaction for percentage of filled grains was low. The narrow-sense heritability was calculated as 81.91%. This again indicates that it should not be difficult to select for heat tolerance provided that the environmental variation is low.

In the above six diallel parents and two F_1 hybrids, heat tolerance was found highly associated with the number of pollen grains on the stigma (Fig. 18). Tolerant genotypes shed more pollen grains on the stigma at both normal and high temperatures than susceptible genotypes. In the susceptible genotypes the amount of pollen shed on the stigma was markedly reduced at high temperature. The correlation coefficients of the number of pollen grains per stigma at 29/21°C and 38/27°C with percent fertility (transformed) at 38/27°C were 0.94, and 0.98, respectively. It thus appears that differences in the pollination ability of the genotypes could be distinguished even at the control temperature (29/21°C). These genotypic differences can be attributed to two important characteristics -- the position of the anther relative to the glume at dehiscence time and the degree of dehiscence.

Table 4. General combining ability effects and specific combining ability variance for heat tolerance of the six diallel parents.[a/]

Parents	General combining ability	$\sigma^2 S_i$
Tolerant		
N22	6.80	15.16
IR2006-P12-12-2-2	4.08	18.07
IET4658 (UPR96-1-1-1)	3.02	3.33
Susceptible		
IR28	-3.40	7.09
IR1561-228-3-3	-4.92	9.49
IR52	-5.58	14.76

Heritability: narrow sense, $h^2_N = 0.71$, broad sense, $h^2_B = 0.76$. [a/] MacKill (1981).

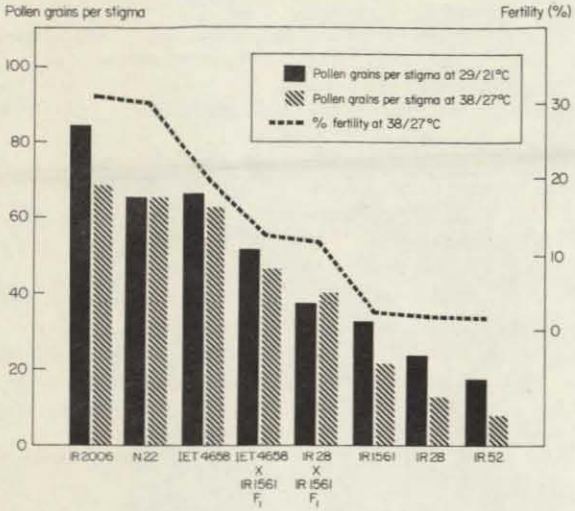

Fig. 18. Mean number of pollen grains per stigma at 29/21°C and 38/27°C and percentage of fertility at 38/27°C for the 6 diallel parents and 2 F_1 hybrids (D. J. MacKill, 1981).

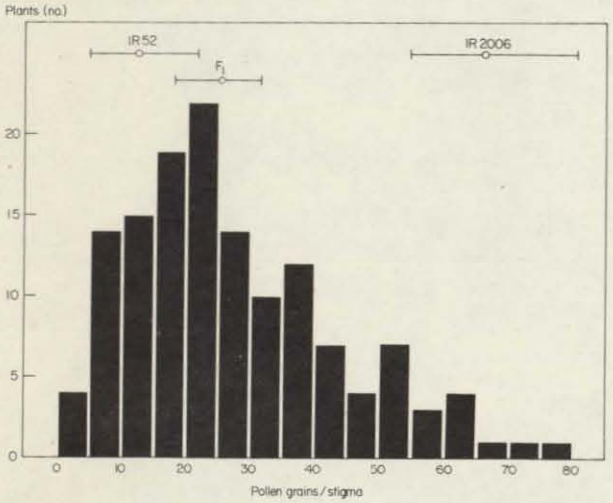

Fig. 19. Distribution of pollen grains per stigma for F_2 plants from the cross IR52/IR2006-P12-2-2. Plants were treated at 35/27°C for 10 days during flowering. The mean and range of the parents and F_1 are shown (D. J. MacKill, 1981).

Genetic differences in the number of pollen grains per stigma were further confirmed by examining individual F_2 plants and their parents (Fig. 19). This trait is apparently controlled by more than one gene, because few of the F_2 plants were as high as the parent IR2006-P12-12-2-2. The skewness of the distribution suggests that some nonallelic gene interaction is present. The phenotypic and genetic correlation coefficients for the number of pollen grains per stigma and percentage of filled grains were 0.62 and 0.68, respectively. This again indicates the importance of pollen shedding for heat tolerance.

Table 5. Examples of heat-tolerant and heat-susceptible varieties.

Designation	Fertility (%) at 35°C
Tolerant varieties	
Agbede	88
Carreon	90
Dular	86
N22	84[a/]
OS4	86
PI 215936	88
Sintiane Diofor	86
Susceptible varieties	
Basmati-370	4
BKN 6624-46-2	6[a/]
C4-63G	5[a/]
H4	2
Pelita 1/1	7
IRRI varieties	
IR5	19
IR8	66
IR20	67
IR22	39
IR24	62
IR26	58
IR28	50
IR29	42
IR30	27
IR32	48
IR34	39
IR36	74
IR38	37
IR40	48
IR42	62
IR43	46
IR44	36
IR45	47
IR46	17
IR48	47
IR50	67
Cold-tolerant varieties	
C-21	0
Dourado Agullia	0
Lengkwang	0
Pratao	0
Silewah	0
Somewake	18
Sorachi	27
Thangone	1

[a/] Mean value of several measurements.

VARIETAL DIFFERENCES IN HIGH TEMPERATURE-INDUCED STERILITY

There are clear varietal differences in high temperature-induced spikelet sterility (Table 5). Tolerant varieties have fertility percentages

higher than 84% while susceptible ones have less than 10%. In our work on high-temperature tolerance both in the phytotron and the heat-prone areas, we use C4-63G and BKN6624-46-2 as susceptible checks and N22 as a tolerant check. Among IRRI varieties, IR36, IR8, IR20, and IR50 appear to be tolerant of high temperature. These results are in good agreement with those reported by Osada et al (1973) that BKN6624-46-2 and C4-63G suffered high percentages of empty grains when grown in the hot part of the dry season in Thailand whereas IR8 maintained a normal fertility percentage. In many heat-prone areas, low temperature is a problem at early stages of rice growth. There is also a report that cold-tolerant varieties might be tolerant of high temperature (National Hokkaido Agricultural Experiment Station, unpubl.). For these reasons, we have tested the heat tolerance of 8 cold-tolerant varieties. All the cold-tolerant varieties tested are highly susceptible to high temperature at anthesis time (Table 5).

Early maturity is one of the requirements for rice varieties to be grown in the heat-prone areas. Early maturity fits into the rice cultivation system in the heat-prone areas and also economizes water use. It is not difficult to find varieties that are heat tolerant and early maturing (Table 6). In fact, in a field trial at Al-Hassa, Saudi Arabia, all the entries selected in the IRRI phytotron were heat tolerant and early maturing (see Table 6,7).

Table 6. Heat-tolerant, early-maturing lines.

Lines	Fertility (%)	Days to flower at Los Baños
IR9129-136-2	86	66
IR9209-26-2	85	67
IR9209-263-3	81	70
IR9224-117-2	83	72
IET 4094[a]	62	72
IET 4658	71	72
IET 4700	85	71
IET 4701	72	71
IET 5688	74	60
IET 5714	88	70
IET 5734	75	70
IET 6187	75	57
IET 6238	75	60

[a] IET is an abbreviation of Initial Evaluation Trial, All-India Coordinated Rice Project, India.

Table 7. Grain yield and percentage of fertility of some selected varieties/lines in Al-Hassa, Saudi Arabia, Saudi Arabia, 1980.[a]

Variety/line	Fertility (%)	Grain yield (t/ha)	Remarks
IET 4094	73	3.5	From India; selected in the Phytotron
IET 4658	80	4.3	"
IET 4700	61	3.6	"
IET 5688	74	2.8	"
IET 5734	50	2.2	"
IET 6238	70	4.3	"
N.T.U. No. 306	35	2.3	From Taiwan
Hovayzeh	33	0.7	From Southern Iran
C4-63 G	17	0.8	Susceptible check
Hassa No. 1	50	2.6	Local check

[a] Data were obtained by C. I. Lin (pers. comm.) in collaboration with IRRI.

FIELD EXPERIMENTS

As part of the International Rice Testing Program (IRTP), heat tolerance has been field tested at several sites -- Al-Hassa, Saudi Arabia; Mishkab, Iraq; Dokri, Pakistan; and Imperial Valley, USA.

In general, there is a good agreement between phytotron and field tests (Table 8). In the field trial, we normally include two check varieties -- N22 as the tolerant check and C4-63G as the susceptible check. At Al-Hassa, N22 and Hovayzeh, supposedly heat tolerant, had low percentages of fertility. The same varieties, however, had high percentages of fertility at Imperial Valley. Apparently, some factors other than heat tolerance affected the performance of the two varieties at Al-Hassa. On the other hand, C4-63G, a susceptible variety, did not have high sterility at Mishkab. This may suggest that high temperature was not the problem at Mishkab in that particular crop period. Many IET lines from India, which were selected for heat tolerance in the IRRI phytotron, performed well in Al-Hassa (Table 7). Grain yields of IET 4658 and IET 6238 was 65% higher than that of Hassa No. 1, a local check. The higher yields of the IET lines are attributed to higher degrees of heat tolerance as indicated by higher percentage of fertility.

Table 8. Agreement between phytotron and field tests (1979-80).[a]

Variety/ line	Al-Hassa, Saudi Arabia	Mishkab, Iraq	Imperial Valley, USA
IET 4094	0	0	0
IET 4658	0	0	0
Hovayzeh	X	-	0
N22	X	0	0
C4-63G	0	X	0

[a] Agreement with phytotron evaluation: 0 = Yes, X = No, - = not determined.

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Dr. Issam Al-Najjar, Mishkab Rice Research Station, Naijaf, Iraq.

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