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Floret Sterility in Rice in a Cool Environment[1]

J. E. Board, M. L. Peterson, and E. Ng[2]

ABSTRACT

Floret sterility induced by low temperatures of 15 C or below at meiosis (10 to 15 days before heading) is a major factor in reducing yields of *Oryza sativa*, var. *japonica*, L. in California. The objective of this study was to reduce sterility by manipulating genotypic environmental interactions. Field experiments employing differences in plant height, maturity, and water level were conducted at the Davis Rice Research Facility. Microclimatic studies were also conducted to determine temperature profiles within the canopy. Sterility was compared among nine cultivars with similar genetic origin but differing in plant height and maturity. Those that were short-statured and/or early-maturing exhibited significantly less sterility than tall and late cultivars. All cultivars in a water depth study showed less sterility in deep water (15 to 25 cm) than in shallow water (5 to 15 cm). Mean differences were significant at the 0.05 level. The beneficial effect of earliness in reducing sterility was caused by the weather patterns of the rice-growing region in the Sacramento Valley. The probability of receiving temperatures below 15 C at meiosis was considerably reduced as maturity was shortened. Increased water depth and decreased plant height reduced sterility by placing the panicle in closer proximity to water. Field water temperature at the coldest part of the night was usually 5 to 6 C warmer than air temperature. The microclimatic study demonstrated that absence of substantial nocturnal wind caused a temperature inversion at night between the mid-canopy level (50 cm above soil surface) and the top of the canopy. Temperature also increased from mid-canopy to water level because of the warming effect of the water. Thus mid-canopy is the coldest part of the vertical profile in a rice field.

Additional index words: Microclimate, *Oryza sativa*, Temperature profile, Water depth, Plant height, Canopy temperature, Temperature stress, Water temperature, Meiotic stage, Early maturity.

COOL night temperature is a major cause of floret sterility (blanking) in California rice (*Oryza sativa*, var. *japonica*, L.). Surveys of 40 fields in six counties in 1971 showed an average of 12.5% sterility with a range from 3.8 to 25.5%. In 1972, sterility in 59 fields averaged 12.8% and as high as 35% in some fields (Peterson et al., 1974). Cool temperature injury to rice has also been reported in Japan, Australia, Bangladesh, Colombia, Indonesia, Kashmir, Korea, Nepal, Pakistan, Peru, Sri Lanka, and Taiwan (Kaneda, C. 1972. Terminal report on studies on the breeding for cold resistance. International Rice Research Institute Los Banos, Philippines). Cool temperature injury in the tropics has increased with dry season culture made possible by water storage systems.

Scientists in Japan have been studying cold-induced sterility for almost a century. During the 1930's, meiosis was identified as the cold sensitive stage (Terao et al., 1941). Meiosis occurs about 10 to 15 days before heading. This stage can be identified by the vertical alignment of the collars of the flag leaf and penultimate leaf (Matsushima, 1967). Japanese scientists have also found that the critical temperature for inducing sterility differs among cultivars and among conditions of cold treatment. Satake (1969) estimated the critical temperatures were 15 to 17 C in a resistant cultivar and 17 to 19 C in a susceptible one. The symptoms, critical temperatures, and timing of injury in Japan and California are similar. Peterson et al. (1974) and Lin and Peterson (1975) have described the problem of low temperature-induced floret sterility in California as occurring 10 to 15 days before heading when night temperatures fall to 15 C or below.

The present studies were conducted in 1976 and 1977 at the Rice Research Facility at the Univ. of California, Davis. This location is ideal to study low temperature-induced floret sterility because it is situated in one of the coolest areas in California where rice is grown. The specific objectives were to determine the effects of plant height and water depth on the incidence of floret sterility and on the temperatures of the panicle, canopy, water, and ambient air. Plant height and water depth variables were selected because of higher nocturnal water temperature relative to air temperature.

MATERIAL AND METHODS

Plant Height and Maturity

Nine closely related cultivars and selections (hereafter called cultivars) differing in plant height and maturity were evaluated for sterility in the field. 'Calrose' and 'CS-M3' (Mastenbroek and Adair, 1970) are widely grown cultivars that are essentially identical in yield, adaptation, maturity, and quality. 'Calrose 76,' 'D18,' and 'D31' are mutants from Calrose produced by ^{60}Co irradiation (Rutger et al., 1976). 'ED7' is a spontaneous early mutation from Calrose 76. 'SD7' and '070' are respectively F_8 and F_6 selections from the cross CS-M3 × Calrose 76. The selection identified as '75/31236-3' is an F_4 selection from the cross SD7 × D18 which was still segregating for maturity in 1976. This entire group of plant types therefore came from Calrose or from crosses between Calrose derivatives and CS-M3. Calrose is also a parent of CS-M3. General adaptation of all nine is very similar. Plant height and days from seeding to heading are presented in Table 1.

Plots were sown in 1.5 m rows on 1 May 1976 in a randomized block design with 12 replications using standard seeding (5 g of seed per 1.5 m row) and fertilizer rates. Seedings were made in dry soil and the fields alternately flush irrigated and drained until seedlings were well-established. Water depth was then maintained continuously at about 15 cm. Days to heading and plant heights were recorded. Because of developmental variability among panicles and among spikelets on a panicle the time of meiosis was considered to be an 11-day period 5 to 15 days before heading. Sterility determinations were made at maturity by randomly harvesting 10 panicles per row. The 10-panicle sample was then threshed and bulked. Sterile florets were separated from fertile florets by use of a seed cleaner. The sterility percentage was then determined by use of the following formula:

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[1] Contribution from the Dep. of Agronomy and Range Science, Univ. of California, Davis, CA 95616. Received 23 July 1979.

[2] Postdoctoral research agronomist, professor of agronomy, and former postdoctoral research agronomist, Univ. of California, Davis, CA 95616 (senior author is currently assistant professor of agronomy, Louisiana State Univ., Baton Rouge, LA 70803).

$$\% \text{ sterility} = 100 \left[\frac{\text{Nsf}}{(100)\,\frac{\text{Ws}}{\text{Wff}} + \text{Nsf}}\right]$$

where:

Nsf = number of sterile florets in the sample
Ws = weight of all fertile florets
Wff = mean weight of 100 fertile florets.

Water Depth and Plant Height

The water depth study compared sterility in shallow (5 to 15 cm) and deep (15 to 25 cm) water plots (3.05 m × 6.1 m) sown with rice in standing water on 6 May 1977. The water levels were maintained throughout the life of the rice plants. A split-plot design with four replications and water depth as whole plots was used. The eight cultivars used as subplots are described in Table 2 (Carnahan et al., 1975; Carnahan et al., 1978). Air and water temperatures were recorded. During the summer, the Davis location experiences diurnal air temperature variations of about 25 C with pre-dawn temperatures sometimes declining to 10 C or lower during the sensitive period. Maximum daily temperatures in the 32 to 38 C range occur in late afternoons. Water temperatures are less variable ranging daily from 18 to 22 C.

Panicle locations were estimated from excised culms sampled at random. Panicle height above the soil was measured throughout the critical development period starting about 2 weeks before heading. Regression equations were used to estimate panicle location at meiosis in relation to soil and water surface. Anthers were observed under the microscope to estimate the percent of spikelets at meiosis on a particular panicle. This procedure is necessary since within any single panicle there is approximately a 7-day range in development of the spikelets. One hundred panicles per plot were randomly harvested at maturity to determine sterility percentages. The previously described procedure was used to determine sterility.

Table 1. Sterility, low air temperature exposure, and plant characteristics of nine closely related cultivars or genotypes.

Characteristics and cultivar or genotype	Sterile florets*	Days to heading	Plant height	Hours < 15.5 C at meiosis
	%	No.	cm	No.
Tall and late				
CS-M3	39 a	118	120	46
Calrose	26 b	118	111	46
Tall and early				
D18	17 c	106	110	46
Short and late				
75/31236-3	25 b	115	95	54
070	21 c	117	90	53
SD7	19 c	119	92	46
Calrose 76	17 c	119	92	46
Short and early				
ED7	19 c	108	91	56
Medium and very early				
D31	14 d	100	106	14

* Means with different letters differ significantly at the 0.05 level according to Duncan's New Multiple Range Test.

Table 2. Characteristics of rice cultivars included in the water depth and plant height experiment.

Cultivar†	Grain type‡	Plant height	Days to heading
		cm	No.
Calrose	M	99	116
Calrose 76	M	76	118
CS-M3	M	102	117
M7	M	78	118
M9	M	80	111
S6	S	101	110
SS6	S	80	108
ESD7-2	M	81	108

† SS6 is a short stature mutant from S6; ESD7-2 and SS6 are not released cultivars. ‡ M = medium grain; S = short grain.

Microclimate

Microclimate studies were conducted in a 60 × 30 m (north to south and east to west, respectively) plot. The east half of the plot was sown to a tall rice cultivar, Calrose, and the west half to the short stature mutant, Calrose 76. Temperature data were recorded at half hour intervals throughout the day and night on a Hewlett Packard Data Acquisition System with 30 sensors using 0.13 cm diam thermistors. Five channels recorded temperatures on a mast at 0.25, 0.5, 1, 2, and 4 m above the soil surface. Other channels recorded various temperature regimes including panicle temperature and air temperature at various locations in and above the rice canopy. Radiative heat gain was eliminated by the application of white epoxy to the temperature probes. The temperature mast was continuously aspirated. Field data were recorded from 9 to 31 August, the most sensitive period to cool temperature for the two cultivars used. Water depth in the field and plant height were recorded during the experimental period.

RESULTS AND DISCUSSION

Plant Height and Maturity

Floret sterility and hours of exposure to cool temperatures of the nine cultivars are presented in Table 1. Hours of exposure to sub-optimal temperatures recorded during the critical stage depends entirely on weather patterns and therefore is a variable that cannot be controlled for field trials. Similarity of origin and adaptation of all nine cultivars greatly reduced the direct genetic differences in susceptibility to sterility. The main differences among these nine cultivars were in days to heading and plant height.

Greatest sterility occurred with the tall late cultivar, CS-M3, and least with the medium stature but very early D31. Because of its earliness, D31 received much less low temperature at meiosis than any other cultivar and therefore had much less sterility. The other seven cultivars separated into two significantly different sterility classes. Calrose and 75/31236-3 demonstrated similar sterility. Calrose, with 26% sterility, is tall and late. Cultivar 75/31236-3, having 25% sterility, is short-statured, but received 8 hours more low-temperature exposure than Calrose during meiosis. The remaining five cultivars exhibited 17 to 21% sterile florets. All were either shorter and/or earlier maturing than Calrose and 75/31236-3. Although a limited number of cultivars was used, a trend is evident that earliness and/or short stature reduces sterility among this group of closely-related cultivars.

Earliness as a factor in reducing sterility is related to the average weather pattern characteristic of the rice growing region of the Sacramento Valley (Board et al., 1979). As the season progresses beyond late July the chance of receiving injurious nightly temperatures increases. The Davis Rice Research Facility receives colder temperatures than the rest of the Sacramento Valley due to cool marine breezes from the San Francisco Bay region. The probability of night temperatures below 13 C is about 50% in the last half of July, and thereafter the probability increases steadily to about 70% by late August. Therefore early cultivars such as D31, which reach the meiotic stage between 15 and 30 July, should have a better chance of escaping cold temperature injury.

Water Depth and Plant Height

The differences for individual cultivars are shown in Fig. 1. Collectively, the mean sterility for all eight cultivars in deep water (17.8%) was significantly less at the 0.05 level than in shallow water (22.2%). Individually, significant reductions in sterility in deep water were achieved only in the case of M9. There also was a trend for sterility to decline with decreases in plant height. In shallow water, Calrose 76, a short-stature cultivar, had significantly less sterility (15%) at the 0.05 level than its taller isogenic counterpart, Calrose, which had over 20% sterility. Similarly, in the shallow water, comparison between closely related CS-M3 and M7, the taller cultivar had 25% sterility compared to 21% for the shorter cultivar. Thus, the tendency for short-stature to reduce sterility was again demonstrated. SS6 and S6 performed differently compared to the other cultivars in the test. Neither reduction in plant height nor increased water level reduced sterility. Possibly, these cultivars could be more susceptible to sterility induced by causes other than cold temperature. The beneficial effect of deep water and reduced plant height on fertility is probably attributed to minimum water temperatures 5 to 6 C higher than air temperatures at night. Other researchers have had similar findings. Nishiyama et al. (1969) reported that plants grown in deep water at normal temperature (23 C) showed less sterility than plants grown in shallow water when air temperatures were low. In the Davis water depth study, mean minimum water and air temperatures at panicle height during the meiotic period were 17.3 and 11.0 C, respectively, in shallow water and 18.9 and 13.6 C for deep water. Since the critical temperature for inducing sterility is in the 15 C range, it is probable that the warmer temperature in deep water could have a beneficial effect on floret fertility.

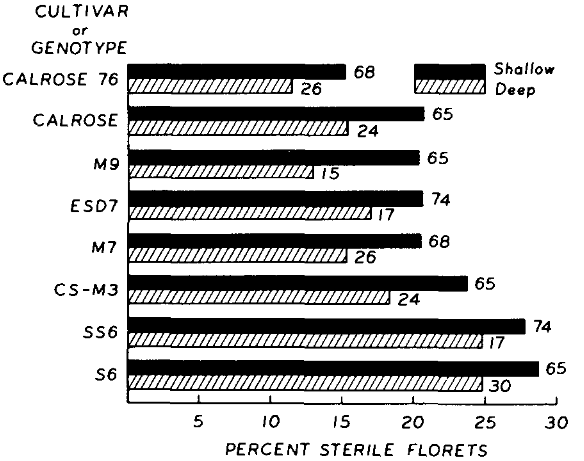

Fig. 1. Percent sterile florets among eight rice cultivars grown in deep and shallow water in the field. Numbers to the right of the bars give the number of hours below 15.5 C at meiosis.

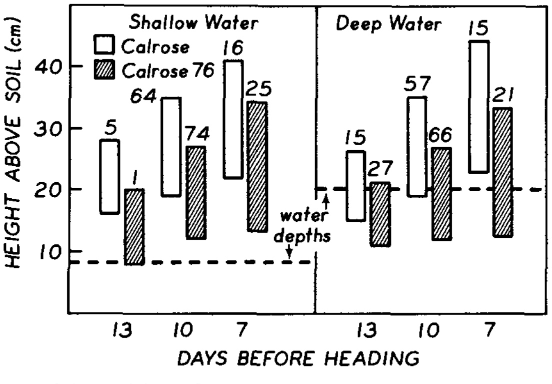

Fig. 2. Panicle position above soil and water of a tall (Calrose) rice cultivar and its short-stature mutant (Calrose 76) during meiosis. Figures above bars are estimated percent of florets at meiotic stage. Bar length represents panicle length.

Panicle location with respect to air and water temperatures was determined to further explain the results. These are presented in Fig. 2 for Calrose and Calrose 76. Panicle length as well as location in relation to the surface of the soil and mean water level are shown. These locations are shown for the pair of cultivars at 13, 10, and 7 days before heading. The figures above each panicle symbol are the percent of the florets estimated to be at the meiotic stage. The panicles entered the meiotic stage at about 13 or 14 days before heading and had nearly completed meiosis by 7 days before heading. The most active meiotic period was 10 days before heading. In shallow water, panicles of both cultivars were above the water but the short stature cultivar, Calrose 76, was closer to it. In deep water, Calrose 76 panicles were almost completely submerged at the start of meiosis and nearly half submerged near its completion. The tall Calrose panicles were nearly half submerged at the start and above the water level near the end of meiosis. The upper halves of all panicles reach the meiotic stage earlier than the lower halves. The sterility percentages for the treatments and cultivars shown in Fig. 2 were: shallow water—Calrose, 21%, Calrose 76, 15%; deep water—Calrose, 15%, Calrose 76, 11%.

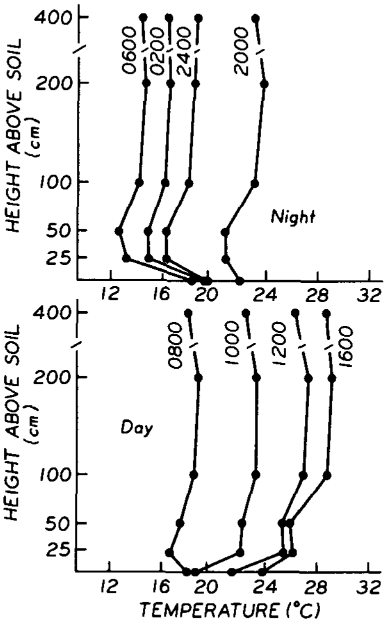

Fig. 3. Night and day air temperature profiles at various heights within and above the rice canopy at various hours.

Microclimate

The microclimate studies in 1977 were in an adjacent rice paddy with water depths of about 15 cm. Temperature profiles in Calrose 76 and Calrose were comparable (Calrose profile shown in Fig. 3). Beginning at 0800 hours, a slight temperature inversion of about 1 C is indicated between mid-canopy (50 cm) and canopy height (100 cm); water and air temperatures (400 cm) are similar at this time. As the day advanced large changes in these initial conditions occur with water temperature increasing less than air temperature. The inversion between mid-canopy and canopy height increased from 1 C to almost 3 C by the afternoon. Radiation attenuation by the canopy and the presence of a relatively cool body of water (2 to 3 C colder than canopy air temperature) kept lower and middle canopy air (25 and 50 cm above the soil, respectively) temperatures several degrees lower than air temperature at canopy height. The temperatures at 100 and 200 cm follow the same daily pattern while a lag of 1 C was evident at 400 cm.

The night-time profile shows a temperature inversion between mid-canopy and canopy height. Mid-canopy air temperatures were 1.2 to 3.0 C lower than canopy height temperature. At nightfall, irradiation losses occurred from the leaves at the top of the canopy. Leaf cooling reduced the temperature of the immediate atmosphere and the denser cool air moved into the canopy. Lack of turbulence resulted in an air inversion between mid-canopy and canopy height levels. However, this trend was counteracted by the warming effect of water on lower canopy air temperatures. Air temperatures declined much more than water temperature as the night advanced. The small decline in water temperature is probably explained by the high specific heat of water combined with the insulating influence of the rice canopy. At 2000 hours, canopy air temperature was only 1 C lower than water temperature. By early morning (0400 to 0600 hours), this difference was 5 C. Consequently, water acted as a heat source during the night, lessening the decline in lower canopy air temperatures. Thus, the temperature inversion was arrested at about the 50 cm height. Throughout most of the night, lower and middle canopy air temperatures were similar. However, during the coldest part of the night (0400 to 0600 hours) the decline in lower canopy air temperature was less than mid-canopy temperatures. At this time, middle canopy temperatures were 0.5 to 0.6 C less than lower canopy air temperatures.

Inversion conditions result from the minimal air movement in the Davis area during most nights. On occasional windy nights, turbulence is generated and the inversion disrupted. Therefore, temperatures in and immediately above the canopy tend to equalize. The profile on a typical non-windy night exhibits strong inversion conditions with mid-canopy air temperatures about 1 to 1.5 C less than canopy-level air temperature (Fig. 4). The presence of an air inversion within the upper canopy has significant microclimatic consequences. Turbulent mixing of heat, CO_2, and water vapor between upper and super canopy levels is limited. Mid-canopy air temperatures are therefore several degrees colder than ambient temperatures. Canopy air temperature would be warmer if nocturnal winds were a common occurrence at Davis during the summertime. Obviously, this would not be the case if the winds were severely cold. However, the prevailing nocturnal winds at Davis generally are moderate marine breezes. Temperature probe studies have confirmed that panicle temperature is essentially the same as air temperature in the canopy adjacent to the panicle.

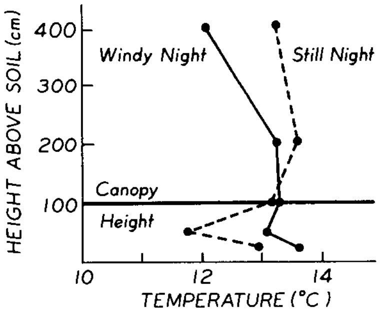

Fig. 4. Comparison of mean temperature profiles in rice on windy and still nights. Temperature points are means from 0400 to 0700 hours.

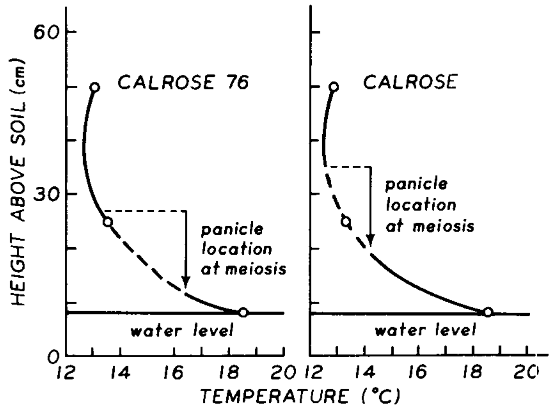

Fig. 5. Panicle locations in relation to temperature profile of a tall cultivar (Calrose) and its short-stature mutant (Calrose 76).

The beneficial effects of lower plant height and higher water level is probably explained by the interaction between panicle location and canopy temperature profile shown in Fig. 5. Panicle location at meiosis (as determined by collar alignment) has been superimposed on the temperature profile at that same time. Although the Calrose 76 panicle is only 8 cm lower than the Calrose panicle, the former is in a warmer location. These results offer a plausible explanation for lower sterility observed with the short-stature cultivar, Calrose 76, as contrasted with the tall cultivar Calrose. Increasing water level provides essentially the same effect by placing the developing panicle nearer the water line where temperatures are warmer.

In conclusion, these studies have shown that cold-induced floret sterility in rice in California can be reduced by using early-maturing or short-stature cultivars and increasing the water level. Earliness reduces sterility because the probability of receiving injurious temperatures increases as the season progresses.

Short stature and increased water level reduce sterility by lowering panicle location at meiosis within the temperature profile. Water temperature is about 5 to 6 C warmer than air temperature during the coldest part of the night. Air temperature within the canopy is characterized by decreasing canopy air temperature from water level to 50 cm above the canopy and increasing temperature from this level to canopy height. Thus, panicle location at meiosis within the lower canopy will have warmer temperatures than at the mid-canopy level. This favorable location can be achieved either by reducing plant height and/or increasing the water level.

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