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Salinity Effects on Seedling Growth and Yield Components of Rice

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ABSTRACT

Flood irrigation practices that are commonly used in California during the early stages of rice (*Oryza sativa* L.) establishment may contribute to salinity damage and eventually decrease yield. Knowledge of salinity effects on rice seedling growth and yield components would improve management practices in fields and increase our understanding of salt tolerance mechanisms in rice. Salinity sensitivity of rice was studied to determine salinity effects on seedlings and yield components. Plants of rice cultivar M-202 were grown in a greenhouse in sand and irrigated with nutrient solutions of control and treatments amended with NaCl and $CaCl_2$ (2:1 molar concentration) at 1.9, 3.4, 4.5, 6.1, 7.9, and 11.5 dS m^{-1} electrical conductivity. Shoot dry weights of seedlings were measured at five harvests in the first month after seeding. Seedling growth was significantly reduced by salinity at the lowest salinity treatment, 1.9 dS m^{-1}. At 1.9 and 3.4 dS m^{-1}, significant reduction of seedling growth occurred at longer cumulative thermal time than at higher salt levels. Seedling survival was significantly reduced when salinity was 3.40 dS m^{-1} and higher. Highly significant linear responses of grain weight per plant, grain weight per panicle, spikelet number per panicle, and tiller number per plant to salinity were observed. There was a common lowest salt level for fertility and pollen germination beyond which they were significantly reduced by salinity. Harvest index was significantly decreased when salinity was at 3.40 dS m^{-1} and higher. Tiller number per plant and spikelet number per panicle contributed the most variation in grain weight per plant under salinity. Reductions in seedling survival, tiller number per plant, and spikelet number per panicle were the major causes of yield loss in M-202 under salinity. The compensation between spikelets and other yield components was confounded with salinity effects, but was believed to be minor relative to the reduction of spikelets due to salinity and, therefore, not sufficient to offset yield loss even at moderate salt levels.

Salinity is one of the major obstacles to increasing production in rice growing areas worldwide. In recent years, the use of recirculating water systems in rice production and the requirement for water holding in the fields without recirculating water systems have increased in areas of the USA because of environmental concerns related to the problems caused by drainage into receiving rivers after pesticide applications (Scardaci et al., 1996). The use of recirculating water systems coupled with regulations for water holding have reduced the hazard to the environment, but have also increased salinity levels in the standing water of rice fields. In a rice field survey in California, the electrical conductivity (EC) of field water during the water-holding period after pesticide application ranged from 0.5 to 3.5 dS m^{-1}, with the lowest EC values in the top basin and the highest in the bottom basin (Scardaci et al., 1996). In these salt-affected rice growing areas, substantial loss in seedling establishment, leaf chlorosis, and final yield reduction were observed (Scardaci et al., 1996; Shannon et al., 1998).

Rice is rated as an especially salt-sensitive crop (Maas and Hoffman, 1977; Shannon et al., 1998). The response of rice to salinity varies with growth stage. In the most commonly cultivated rice cultivars, young seedlings were very sensitive to salinity (Pearson and Bernstein, 1959; Kaddah, 1963; Flowers and Yeo, 1981; Heenan et al., 1988; Lutts et al., 1995). Yield components related to final grain yield were also severely affected by salinity. Panicle length, spikelet number per panicle, and grain yield were significantly reduced after salt treatments (Sajjad, 1984; Heenan et al., 1988; Cui et al., 1995; Khatun et al., 1995). Salinity also delayed the emergence of panicle and flowering (Khatun et al., 1995) and decreased seed set through reduced pollen viability (Khatun and Flowers, 1995; Khatun et al., 1995). In contrast, rice was more salt tolerant at germination than at other stages (Narale et al., 1969; Heenan et al., 1988; Khan et al., 1997). Seed germination was not significantly affected up to 16.3 dS m^{-1}, but was severely inhibited when salinity increased to 22 dS m^{-1} (Heenan et al., 1988). The suppression of germination at high salt levels might be mainly due to osmotic stress (Narale et al., 1969; Heenan et al., 1988).

Although there are extensive studies of salinity effects on rice, our understanding of the quantitative effects of salinity on rice and critical thresholds of responses, especially with respect to modern, commonly used cultivars, is still limited. The determination of salinity-sensitivity parameters, for example, thresholds of salinity effects on rice seedling growth and yield components and the interrelationships among yield components under salinity stress, will help to develop better management practices for growing rice under salinity and improve our understanding of the mechanisms of salt tolerance in crops. The objectives of this study were to determine the effects of salt levels and stress durations on seedling growth under controlled conditions, to analyse the salinity sensitivity of different yield components, to identify the most important yield component(s) causing the reduction of grain yield, and to determine the possible compensations between yield components that could completely or partially offset the yield loss under moderate salinity.

MATERIALS AND METHODS

Plant Materials

A medium-size grain, early maturity, and semidwarf rice cultivar, M-202, was used. The seed was obtained from C. Johnson (California Cooperative Rice Research Foundation, Biggs, CA). Like most other common cultivars in California, M-202 has been rated as very sensitive to salinity (Shannon et al., 1998).

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Abbreviations: DAP, days after planting; EC, electrical conductivity; PI, panicle initiation.

Plant Culture

Two experiments were conducted in the greenhouse at Riverside, CA (33°58′24″ N, 117°19′12″ W) between May and November 1997. The plants were cultured in nutrient solution (Yoshida et al., 1971) in sand tanks (122 by 61 by 46 cm deep) filled with white silica sand (#12, Cisco Inc., CA)[1] with an average bulk density of 1.4 g cm^{-3}. Nutrient solution pH was maintained between 5.5 and 6.5 by adding H_2SO_4 twice a week. Nutrient solutions were changed once in the middle of the growing season. Nutrition status of plants was monitored by visual observations. Irrigation solutions were prepared in 1100-L reservoirs and pumped to provide irrigation to the sand tanks. Overflow irrigation was returned through drainage by gravity to the reservoirs. Each reservoir provided irrigation to six sand tanks (replicates) three times daily for 30 min per irrigation cycle. Rice seed was sterilized in $HgCl_2$ (0.5g L^{-1}) for 2 min, rinsed with formaldehyde (16 mL L^{-1}) and methanol (4 mL L^{-1}) for 15 min, and then rinsed and soaked in distilled water for 24 to 48 h. Seeds were planted in nine rows per tank. The rows were spaced 12 cm apart with 15 seeds per row. Sowing depth was <1 cm. Water depth was controlled at 1 to 2 cm during the first week and at 6 to 8 cm thereafter. Hourly mean temperatures were integrated across the 24 h and summed to give cumulative thermal time (°C d, Logan and Boyland, 1983). Air temperature ranged from 25 to 33°C during the day and 18 to 23°C during the night. Humidity ranged from 40 to 85%. Light averaged 1050 μmol m^{-2} s^{-1} with a minimum of 200 and a maximum 1400 μmol m^{-2} s^{-1} at noon. A mixture of NaCl and $CaCl_2$ (2:1 molar concentration) were added to the nutrient solutions 5 d after seeding. The stress remained continuous till harvest. Electrical conductivities of nutrient solutions were measured with an EC meter on alternate days. A control (i.e., nutrient solution without NaCl and $CaCl_2$) was prepared. A randomized block design was used with five replicates for each salt treatment in the first experiment and six replicates in the second experiment.

Plant Harvest

In the first experiment, seeds were planted 22 May 1997. The survived seedlings were harvested at cumulative thermal times of 276 [i.e., 11 d after planting (DAP)], 349 (i.e., 14 DAP), 420 (i.e., 17 DAP), 495 (i.e., 20 DAP), and 566°C d (i.e., 23 DAP), assuming a base temperature of 0°C. Seedling dry mass accumulation was measured at these time intervals. Plants were not grown to maturity in the first experiment.

In the second experiment, seeds were planted on 17 July 1997. The survived seedlings were harvested at cumulative thermal times of 289 (i.e., 12 DAP), 365 (i.e., 15 DAP), 469 (i.e., 19 DAP), 550 (i.e., 22 DAP), and 622°C d (i.e., 25 DAP), assuming a base temperature of 0°C, for measurements of seedling dry mass accumulation. The seedling survival rate was only measured in the second experiment at 622°C d. or 25 DAP. The dead plants were removed and the remaining plants in each sand tank were thinned to 12 cm between rows and 10 cm between plants. Plants were harvested in November 1997 for yield component analysis. Plants at different salt levels were harvested sequentially when seed on primary tillers matured (i.e., the kernels were yellow and could no longer to be dented by the thumbnail).

Methods of Measurements for Salinity Sensitivity at Different Growth Stages

Seedling survival rate was measured in three rows of seedlings [germinated from 15 (no. row^{-1}) × 3 (rows) = 45 seeds], which were randomly chosen from each replicate. The seedling survival rate was calculated as the percentage of live seedlings from germinated plants. At each harvest at seedling stage, 15 seedlings of each replicate were randomly sampled from surviving plants. After roots were removed, shoots of seedlings were dried in a forced-air oven (70°C) for 1 wk. The dry weights of seedlings were measured using an electronic balance with milligram precision.

Main culms of all surviving plants were tagged before tillering. After harvest, main culms and panicles on main culms were separated from the other culms and panicles. Plants were bagged individually after roots were removed. Shoot dry weights of main culms and all tillers were measured after oven drying at 70°C for 1 wk. Panicles on main culms were counted and weighed. Panicles on tillers were also weighed. The following yield components were determined: primary branches per panicle, panicle length, spikelet number per panicle, fertility, 1000-kernel weight, and grain dry weight per panicle. Among them, fertility was defined as the percentage of filled spikelets relative to the total number of spikelets per panicle. Tiller number per plant and grain dry weight per plant were also measured. Tiller number per plant was determined on all tillers with emerged heads. All matured panicles (i.e., kernels were too hard to be dented by the thumbnail) were hand-threshed and weighed for grain dry weight per plant. The immature panicles were not weighed. Harvest index was calculated as grain dry weight per plant divided by the total aboveground biomass, which was the sum of grain dry weight per plant and shoot dry weight per plant.

Most yield components were only measured from the panicles on main culms because of the consideration of nonuniform maturity among tillers and plants and the labor involved in making the measurements. Some information on other panicles such as those on young tillers was sacrificed by this method; however, the results obtained from these measurements still represent, in a general sense, the salinity effects on all yield components.

For measurements of pollen viability, two plants from each replicate were randomly chosen. About one hundred pollen grains in each of two plants were scored for both pollen stainability and in vitro germination. Pollen grains were stained with 0.9% (w/v) thiazolyl blue in 54% (w/v) sucrose (Khatun and Flowers, 1995). Fresh pollen grains were collected on microscope slides in a drop of fresh stain solution and scored for stainability after 5 to 10 min. For in vitro pollen germination, pollen grains were germinated in agar medium, as described by Brewbaker and Kwack (1963), with the following components: 1.6×10^{-3} *M* H_3BO_3, 1.3×10^{-3} *M* $Ca(NO_3)_2$, 8.1×10^{-4} *M* $MgSO_4$, 1×10^{-3} *M* KNO_3, 2.7×10^{-5} *M* EDTA, 20% (w/v) sucrose, and 0.5% (w/v) agar, at pH 5.5. Fresh pollen grains were collected on agar in petri dishes immediately after anthesis and cultured at 37°C for 20 min before observation under a light microscope at 100× magnification.

The yield measurements of each salt treatment were compared and grouped with Tukey's multiple comparisons (Ott, 1993). Regression relating seedling survival rates to salinity levels was analysed with a quadratic regression model. All statistical analyses were carried out with the SAS system (SAS Institute, 1994).

Interrelationships among Yield Components

The relative importance of yield components to grain yield (i.e., grain weight per plant, GWL) was evaluated based on the equation of GWL as the product of tiller number per plant (TP) and grain weight per panicle (GWP). Since GWP is the direct function of spikelet number per panicle (SP), fertility (FT), and 1000-kernel weight (TW), the equation can be expressed as

[1] Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA.

Table 1. Means and standard errors of shoot dry weights of survived rice seedlings harvested at different cumulative thermal times after planting at different salt levels (Exp. 1).

	Thermal time (°C d)†				
Salt	276 (11 DAP)	349 (14 DAP)	420 (17 DAP)	495 (20 DAP)	566 (23 DAP)
dS m^{-1}	mg plant^{-1}				
Control	15.8 ± 0.8a‡	20.2 ± 0.8a	32.2 ± 1.2a	63.5 ± 3.0a	123.6 ± 7.1a
1.9	13.9 ± 0.7ab	17.5 ± 0.9ab	28.1 ± 1.5ab	46.3 ± 3.1b	83.8 ± 5.0b
3.2	13.5 ± 0.7ab	18.5 ± 0.8ab	23.5 ± 1.5bc	46.8 ± 3.2b	70.2 ± 4.7bc
4.6	12.9 ± 0.6b	15.4 ± 0.9bc	20.3 ± 1.6cd	39.8 ± 2.9bc	62.3 ± 4.3cd
6.2	11.4 ± 0.5b	14.1 ± 0.9c	22.9 ± 1.2bc	36.8 ± 2.6bc	52.2 ± 3.3cd
8.1	11.5 ± 0.6b	15.5 ± 0.7bc	19.9 ± 0.9cd	34.2 ± 2.1c	54.5 ± 3.3cd
11.7	12.1 ± 0.4b	13.3 ± 0.5c	17.2 ± 0.8d	30.9 ± 1.5c	45.3 ± 2.4d

† Cumulative thermal time was summed from hourly mean temperatures that were integrated across the 24 h.
‡ Means within columns followed by the same letter are not different at $P = 0.05$ according to Tukey multiple comparisons.

$$GWL = TP \times SP \times FT \times TW$$

The relative importance of yield components to grain yield was analyzed using multiple linear regression. The significance of yield components was determined by stepwise regression analysis, that is, based on the order of their addition into the multiple regression model.

Tiller number per plant depended on plant density (Counce et al., 1989; Wu et al., 1998), which was determined at vegetative stages. Spikelet number per panicle was determined at panicle initiation, fertility at booting and early anthesis, and 1000-kernel weight at filling stage (Yoshida et al., 1981; Hoshikawa, 1989). It is clear that these yield components are sequentially and successively formed in the order of tiller number per plant, spikelet number per panicle, fertility, and 1000-grain weight. There was a compensatory relationship between two successively formed yield components, with a certain level of competition within a population. The potential value of a newly formed yield component decreased as the previously formed yield component increased (Siband et al., 1999). A ratio between two successively formed yield components, newly formed yield component/earlier-formed yield component, was used to study the interrelationships among these yield components under salinity. When density was fixed, in populations of equal spaced plants, the changes of the ratios were expected to be a combination of salinity effects and a possible compensation between the two successively formed components.

RESULTS

Salinity Levels and Controls

In the first experiment, the EC readings of salinity treatments were averaged through the duration of salinity stress to six salt levels: 1.9 (1.7–2.0), 3.2 (2.8–3.5), 4.6 (4.2–4.9), 6.2 (5.6–6.7), 8.1 (7.4–8.5), and 11.7 (11.2–12.1) dS m^{-1}. In the second experiment, the EC readings of salinity treatments were averaged through the duration of salinity stress, continuous stress through harvest, to six salt levels: 1.9 (1.6–2.0), 3.4 (3.1–3.7), 4.5 (4.1–4.8), 6.1 (5.8–6.7), 7.9 (7.5–8.3), and 11.5 (10.5–12.1) dS m^{-1}. The EC of controls was 0.87 dS m^{-1} in the first experiment and 1.15 dS m^{-1} in the second experiment.

Salinity Effects on Seedling Growth

The results of the first and second experiments showed that salinity caused a significant reduction in seedling growth very soon after planting (Tables 1 and 2). In Exp. 1, significant ($P < 0.05$) growth reduction occurred at 276°C d when salinity was 4.6 dS m^{-1} and higher (Table 1). In Exp. 2, significant ($P < 0.05$) reduction of seedling growth occurred at 289°C d when salinity was 4.5 dS m^{-1} and higher (Table 2). As the duration of salinity stress increased, significant reduction in seedling growth occurred at lower salt levels. In Exp. 1, a significant reduction in seedling growth was first observed at 276°C d when salinity was 4.6 dS m^{-1}. At 3.2 dS m^{-1}, a stress period of 420°C d resulted in a significant reduction in seedling growth. At 1.9 dS m^{-1}, the lowest salinity treatment, a stress period of 495°C d resulted in a significant reduction in seedling growth compared with the control (Table 1). In Exp. 2, a significant reduction in seedling growth was first observed at 289°C d when salinity was 4.5 dS m^{-1}. After 365°C d, salinity treatments at 1.9 and 3.4 dS m^{-1} resulted in a significant reduction in seedling growth compared with the control (Table 2).

The percentage of seedling survival rate was significantly ($P < 0.05$) reduced at 3.4 dS m^{-1} and higher compared with the controls in Exp. 2 (Table 3). A qua-

Table 2. Means and standard errors of shoot dry weights of survived rice seedlings harvested at different cumulative thermal time after planting at different salt levels (Exp. 2).

	Thermal time (°C d)†				
Salt	289 (12 DAP)	365 (15 DAP)	469 (19 DAP)	550 (22 DAP)	622 (25 DAP)
dS m^{-1}	mg plant^{-1}				
Control	12.6 ± 0.6a‡	20.8 ± 0.8a	40.5 ± 1.8a	123.9 ± 6.7a	232.4 ± 14.8a
1.9	11.5 ± 0.4ab	15.0 ± 0.5b	24.7 ± 1.4b	76.5 ± 5.0b	161.4 ± 12.2b
3.4	11.1 ± 0.4abc	14.2 ± 0.6b	21.1 ± 1.0b	67.7 ± 4.5b	136.1 ± 9.7bc
4.5	10.8 ± 0.4bc	13.5 ± 0.5b	16.7 ± 0.6c	45.8 ± 3.6c	109.2 ± 9.1c
6.1	9.8 ± 0.3cd	10.5 ± 0.4c	12.5 ± 0.5c	20.4 ± 1.7d	42.4 ± 4.8d
7.9	8.9 ± 0.3d	10.3 ± 0.4c	12.6 ± 0.6c	16.0 ± 0.9d	24.5 ± 2.5d
11.5	8.7 ± 0.3d	10.7 ± 0.3c	12.7 ± 0.5c	18.5 ± 1.3d	25.2 ± 2.4d

† Cumulative thermal time was summed from hourly mean temperatures which were integrated across the 24 h.
‡ Means within columns followed by the same letter are not different at $P = 0.05$ according to Tukey multiple comparisons.

Table 3. Means and standard errors of seedling survival rates, shoot dry weights of main stem, harvest index, and pollen viability at different salt levels.

	Salt levels (dS m^{-1})						
	Control	1.9	3.4	4.5	6.1	7.9	11.5
	%						
Seedling survival, %‡	98.3 ± 1.3a†	91.5 ± 3.0ab	79.4 ± 2.0bc	68.3 ± 5.5cd	58.3 ± 6.7de	56.0 ± 1.8de	50.7 ± 2.9e
Shoot weight g main culm^{-1}	4.11 + 0.11a	4.12 + 0.12a	3.64 + 0.11a	3.75 + 0.14a	2.89 + 0.13b	2.91 + 0.11b	2.20 + 0.09c
Harvest index§	0.49 + 0.01a	0.47 + 0.01a	0.41 + 0.01b	0.39 + 0.01bc	0.36 + 0.01c	0.29 + 0.01d	0.21 + 0.01e
Pollen stainability, %	76.9 ± 2.5a	70.6 ± 3.8a	65.1 ± 3.0a	43.9 ± 5.9b	28.2 ± 3.7c	20.3 ± 2.7cd	11.3 ± 2.8d
Pollen germination, %¶	51.8 ± 5.7a	52.7 ± 5.5a	49.8 ± 4.1a	51.9 ± 2.8a	29.2 ± 5.0b	15.0 ± 3.9bc	8.5 ± 3.0c

† Means within rows followed by the same letter are not different at $P = 0.05$ according to Tukey multiple comparisons.
‡ Seedling survival was measured at 622°C d. The survival rates are the percentages of live seedlings from germinated plants.
§ Harvest index was calculated as the grain weight per plant divided by the total aboveground biomass per plant.
¶ Pollen grains were stained in thiazolyl blue solutions (see Materials and Methods). Pollen stainability was calculated as the percentage of light red or red pollen grains among the total observed. The germination percentage was calculated based on number of germinated pollens among the total observed.

dratic equation was determined to best predict the response of seedling survival rates to salinity by stepwise analysis (Fig. 1). The confidence intervals of seedling survival rates were 81.1 to 74.4% at 3.4 dS m^{-1} salt level and 104.1 to 93.0% at control salt level. Note that the seedling survival rates were almost linearly decreased by salinities <6.2 dS m^{-1} (Fig. 1). Then the responses became curvilinear between 7.9 and 11.5 dS m^{-1}.

Salinity Effects on Yield Components

All yield components investigated, except 1000-kernel weight, were significantly ($P < 0.05$) reduced at 6.1 dS m^{-1} and higher compared with the controls (Table 4). None of the components was significantly ($P < 0.05$) reduced at 1.9 dS m^{-1}. Spikelet number per panicle, grain dry weight per panicle, and grain dry weight per plant were significantly ($P < 0.05$) reduced at 3.4 dS m^{-1} and higher. Tiller number per plant was significantly ($P < 0.05$) reduced at 4.5 dS m^{-1} and higher. Primary branches per panicle, panicle length, and fertility were not significantly reduced except at salinity levels of 6.1 dS m^{-1} and higher. Kernel weight was not significantly reduced at any salt level tested. Instead, there was slight increase of kernel weight at 11.5 dS m^{-1}, although not significant when compared with the control. Linear regressions of salinity on the yield components were highly significant except for kernel weight (Fig. 2). When grain yield per plant was expressed as the product of tiller number per plant, spikelet number per panicle, fertility, and kernel weight, tiller number per plant, and spikelet number per panicle contributed the most variation to grain yield, while fertility and kernel weight contributed less, based on stepwise analysis (Table 5). The ratio of spikelets per panicle/tillers per plant decreased with the increase of salinity (Table 6). The ratios of fertility/spikelets per panicle and kernel weight/spikelets per panicle increased with the increase of salinity. The ratio of fertility/spikelets per panicle at 11.5 dS m^{-1} was 1.9 times that of the control. The ratio of kernel weight/spikelets per panicle at 11.5 dS m^{-1} was 3.4 times that of the control.

Salinity Effects on Other Relative Traits

Shoot dry weights of main culms were not significantly ($P < 0.05$) reduced by salinity until EC was 6.1 dS m^{-1} or higher (Table 3). Harvest indices were significantly ($P < 0.05$) reduced by salinity at 3.4 dS m^{-1} or higher (Table 3). The pollen viability based on staining was

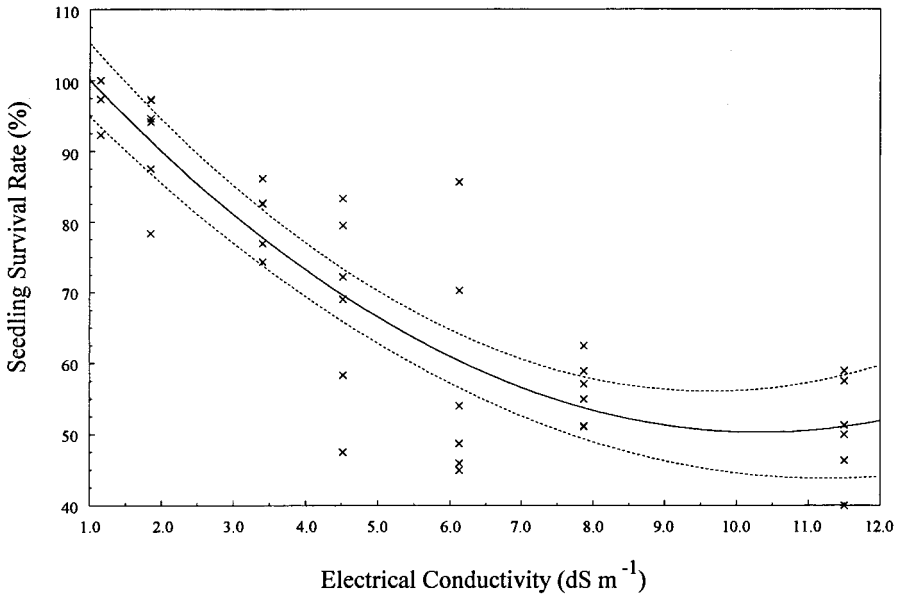

Fig. 1. Regression of salinity (measured by electrical conductivity [EC] of irrigation solutions) on seedling survival rate. Measurements of seedling survival rates at 622°C d (25 DAP) from six replicates are represented by the symbol (×). The solid line is the quadratic equation: survival rate (%) = 111.36 − 11.83EC + 0.57EC^2 ($F = 76.21$, df = 2, 39). The dashed lines are upper and lower confidence levels (95%).

Table 4. Means and standard errors of yield components measures at different salt levels.

Salt	Tiller	Primary branch	Panicle length	Spikelet	Fertility†	Grain weight		
dS m^{-1}	no. plant^{-1}	no. panicle^{-1}	cm	no. panicle^{-1}	%	g panicle^{-1}	g 1000^{-1}	g plant^{-1}
Control	15.7 ± 0.7a‡	13.4 ± 0.2a	20.8 ± 0.2ab	176.3 ± 4.7a	80.5 ± 1.7a	4.1 ± 0.1a	29.3 ± 0.4ab	34.3 ± 1.8a
1.9	13.9 ± 0.7ab	12.9 ± 0.2a	21.2 ± 0.2a	162.7 ± 5.3a	76.9 ± 2.0ab	4.0 ± 0.1a	30.6 ± 1.2ab	30.5 ± 1.4ab
3.4	13.1 ± 0.9abc	11.5 ± 0.3bc	18.5 ± 0.7c	136.9 ± 5.7b	74.1 ± 2.0ab	3.0 ± 0.2b	29.0 ± 0.4ab	24.2 ± 2.4bc
4.5	12.2 ± 0.9bcd	12.2 ± 0.3ab	19.6 ± 0.3bc	131.6 ± 5.1b	72.8 ± 2.6ab	2.6 ± 0.1b	27.9 ± 0.5ab	19.3 ± 1.9c
6.1	10.7 ± 0.7cd	10.6 ± 0.3c	18.2 ± 0.4c	96.8 ± 4.9c	70.1 ± 2.9b	1.9 ± 0.1c	27.0 ± 0.6a	12.5 ± 1.3d
7.9	9.9 ± 0.7d	10.4 ± 0.3c	18.1 ± 0.3c	93.2 ± 3.7c	52.2 ± 2.4c	1.4 ± 0.1c	28.7 ± 1.2ab	7.79 ± 0.7de
11.5	6.0 ± 0.4e	8.7 ± 0.3d	15.0 ± 0.4d	53.9 ± 3.5d	44.7 ± 3.0c	0.8 ± 0.1d	31.2 ± 1.3b	2.52 ± 0.2e

† Fertility was defined as the percentage of filled spikelets relative to the total number of spikelets per panicle.
‡ Means within columns followed by the same letter were not different at $P = 0.05$ according to Tukey multiple comparisons.

not significantly reduced except at 4.5 dS m^{-1} and higher, while the viability based on germination was not significantly reduced except at 6.1 dS m^{-1} and higher compared with controls (Table 3). Note that there was a steep decline in pollen stainability and germination when salinity was above 3.4 and 4.5 dS m^{-1}, respectively (Fig. 3). In contrast, a steep decline in fertility occurred when salinity was above 6.2 dS m^{-1} (Fig. 3).

DISCUSSION

Reduction in seedling growth and loss of stand due to salinity have been implicated as causative factors for yield losses in California rice production (Scardaci et al., 1996; Shannon et al., 1998). Our study indicated that salinity as low as 1.9 dS m^{-1} can significantly reduce seedling shoot dry weight and that salinity at 3.4 dS m^{-1} can reduce seedling survival (plant stand) in M-202, a common rice cultivar in California. The reductions in seedling survival rates and growth are major causes of the stand loss in salt-affected rice fields. The threshold value of salinity on seedling survival rate in M-202 is between 1.9 and 3.4 dS m^{-1}, although the exact value was difficult to determine because of the quadratic response of this variable to salinity and the variability due to the experimental conditions. The observed effects of salinity on seedling growth were a function of both salt level and time of exposure. At low salt levels (i.e., 1.9 and 3.4 dS m^{-1}) significant reduction of seedling growth occurred at higher cumulative thermal time than those seedlings at higher salt levels (i.e., 4.5 dS m^{-1} and higher). This indicated that plants affected by salts at low concentrations can tolerate salt stress for longer durations before significant reduction of seedling growth occurs.

Yield sink capacity is always one of the primary objectives in crop breeding for increasing crop yield. Yield sink capacity can be defined as the maximum size of the sink organs to be harvested (Kato and Takeda, 1996). The final grain yield can be described as the product of the number of panicles per unit area and panicle weight. The number of panicles per unit area depends on plant density and tillering ability of plants. The low threshold value of salinity on rice M-202 seedling survival rate at the early seedling establishment indicated a reduction in yield sink capacity under salinity by a reduction in plant density. It was also known that, under nonstressed conditions, there was a compensatory relationship between plant density and tillering, which maintained panicle density within a certain range of change in plant density (Counce et al., 1989; Hoshikawa, 1989; Counce and Wells, 1990; Gravois and Helms, 1992; Wu et al., 1998). The determination of this compensatory relationship between plant density and tillering under salinity stress requires further studies at the population level. However, the high sensitivity of tillering to

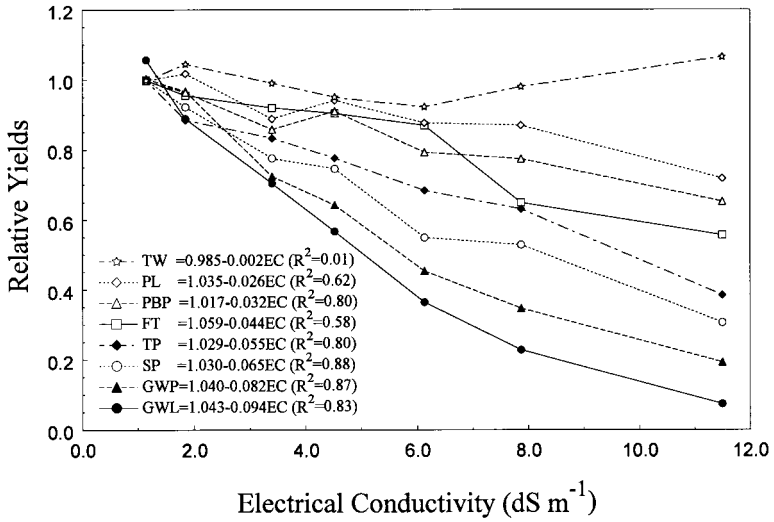

Fig. 2. Regressions of salinity on relative yields based on yield components. Relative yield were calculated from observations for yield components divided by the mean values of the controls. TW, 1000-kernel weight; PL, panicle length; PBP, primary branch per panicle; FT, fertility; TP, tiller number per plant; SP, spikelet number per panicle; GWP, grain weight per panicle; GWL, grain weight per plant; EC, electrical conductivity.

Table 5. Contributions of yield components to grain yield in rice under salinity. Grain weight per plant was the product of tillers per plant (TI), spikelets per panicle (SP), fertility (FT), and 1000-kernel weight (TW).

Yield components	Contribution to total variation in yield (R^2)†
TI	71.4
SP	71.1
FT	38.0
TW	1.1
TI + SP	86.8
TI + SP + FT	89.1
TI + SP + FT + TW	89.9

† The relationship between grain weight per plant and other yield components was determined by stepwise regression analysis. The yield components with highest R^2 values were the first to add to the regression model. The next yield components were added to the model at $P = 0.05$.

Table 6. Relationships between two successively formed yield components under salinity stress.

	Salt (dS m^{-1})						
	Control	1.9	3.4	4.5	6.1	7.9	11.5
SP/TI†	12.3	11.7	10.7	10.8	9.3	9.5	9.2
FT/SP	0.43	0.47	0.54	0.58	0.73	0.56	0.83
TW/SP	0.17	0.19	0.21	0.22	0.28	0.31	0.58

† SP, spikelet number per panicle; TI, tiller number per plant; FT, fertility; TW, 1000-kernel weight. The ratios of two successively formed yield components were calculated from each observation of late-formed component divided by each observation of early-formed component. The order of the formation in yield components was assumed to be TI, SP, FT, and TW.

salinity in M-202 indicated a limited tillering ability of rice plants under salinity stress. Yield sink capacity per plant was defined as the product of tiller number per plant, spikelet number per panicle, fertility, and kernel weight (Kato and Takeda, 1996). In M-202, tiller number per plant and spikelet number per panicle were the most salinity-sensitive yield components, showing highly significant linear responses to salinity (Fig. 2). These two yield components contributed the most variation to grain yield under salinity stress, based on stepwise analysis (Table 5). It was concluded that the reductions in seedling survival rate, tiller number per plant, and spikelet number per panicle were the major causes of yield loss in M-202 under salinity.

The yield components of tiller number per plant, spikelet number per plant, fertility, and kernel weight were believed to have their own critical development periods that can affect the final grain yield. Different relationships between these sequentially and successively formed yield components allow the calculation of maximum yield. A compensatory relationship between two successively formed yield components has been observed in maize (*Zea mays* L.). The newly formed yield component decreased when the earlier formed component increased (Siband et al., 1999). These phenomena have been observed in rice crops under nonstressed conditions. Generally, the correlations between tiller number per plant and spikelet number per plant, and between spikelet number per plant and fertility and kernel weight are negative (Counce and Wells, 1990; Kato and Takeda, 1996). In wheat (*Triticum aestivum* L.), a complete or partial compensation between spikelets and kernels was observed which resulted in a nonsignificant reduction in final kernel number under moderate salinity (Maas and Grieve, 1990; Grieve et al., 1992; Maas et al., 1996). The removal of some spikelets increased fertility on remaining spikelets in rice (Matsushima, 1970). In the analysis of interrelationships between these yield components under salinity stress, the compensation was difficult to observe because of the confounding effects with salinity. For example, as the earlier-formed yield component, tiller number per

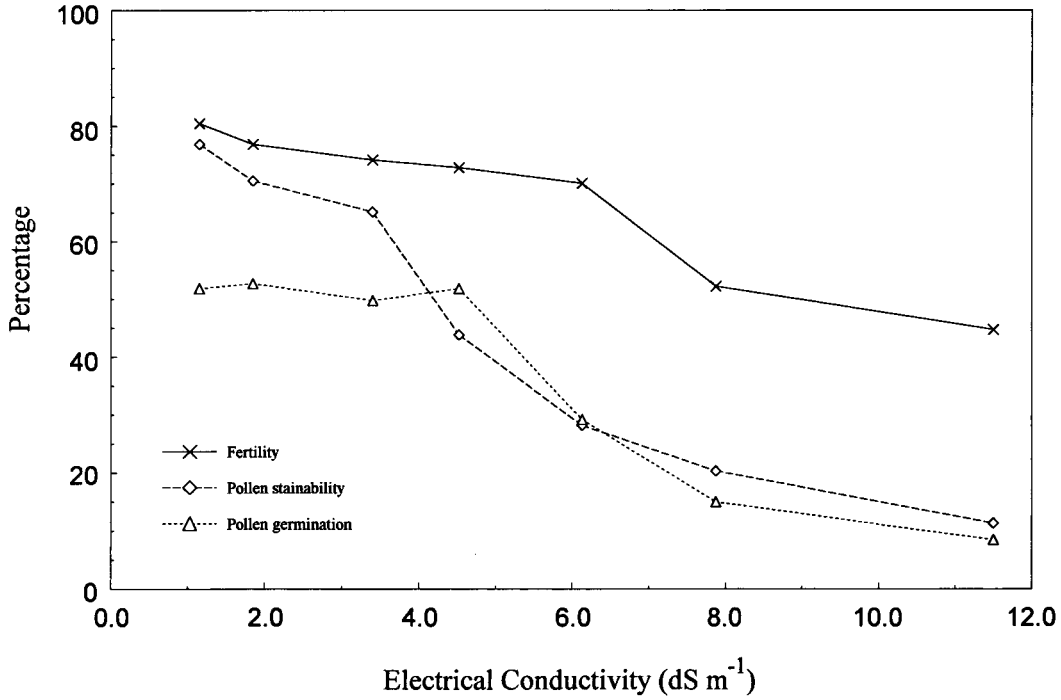

Fig. 3. Means of pollen viability and fertility.

plant, decreased, the expected compensation was an increase in spikelet number per panicle. However, salinity stress at PI reduced spikelet number per panicle. In M-202, the ratio of spikelets per panicle/tillers per plant decreased with the increase of salinity (Table 6). This indicated that the compensation between tiller number per plant and spikelet number per panicle was limited and that the effect of salinity on spikelet number per panicle was more pronounced than that on tiller number per plant. In contrast, the ratio of fertility/spikelets per panicle increased almost two times, and the ratio of kernel weight/spikelets per panicle increased more than three times with the increases of salinity. There could be two explanations for these results. First, the compensation by increasing fertility and kernel weight upon the reductions in the earlier-formed yield component, spikelet number per panicle, was significant. Second, the salinity effect on spikelet number per panicle was more pronounced than that on fertility and kernel weight. The overal effects on fertility resulted from the confounding effects of the compensation between yield components and the reduction due to salinity stress at the booting and anthesis stages. It appeared that the salinity effect on fertility was less pronounced than that on pollen viability (Fig. 3). Although the exact threshold value of salinity effect on pollen germination was difficult to determine because of its nonlinear response to salinity, the threshold values of salinity on pollen germination and fertility were both between 4.5 and 6.1 dS m^{-1} (Tables 3 and 4). The close thresholds of salinity effects on these two variables do not indicate a strong compensation on fertility. There might a compensation by increasing kernel weight upon the reduction in spikelets, although the multiple comparisons of mean values were not significant (Table 4). However, a strong compensation between these two components does not seem possible because of the enclosed hull in rice, which limits the increase of grain size (Matsushima, 1957). Therefore, the changes in the ratios with the increase of salinity were mainly caused by the different sensitivity of these yield components to salinity. It was obvious that plants were more sensitive to salinity at PI than to salinity at later reproductive stages. It was concluded that the compensation between the successively formed yield components was minor relative to the reduction of spikelets per panicle due to salinity. The highly significant linear responses of grain weight per panicle and grain weight per plant to salinity (Fig. 2) added evidence that the compensation between these yield components was not sufficient to offset yield loss due to salinity even at moderate salt levels.

Rice panicles consist of primary ranchi-branches, secondary branches differentiated from primary branches, and flower primordia that develop into spikelets on these branches (Hoshikawa, 1989). There is only one flower structure in each spikelet that will develop into a rice kernel after fertilization and filling (Yoshida, 1981). The loss of potential spikelets are due to the degeneration of primary and secondary branches and flower primordia. The measurement of potential spikelet number is difficult since the degeneration of branches occurs rapidly after their initiation (Hoshikawa, 1989). In rice M-202, the number of primary ranchi-branches and panicle length were significantly reduced by salinity at 6.1 dS m^{-1} or above, but not at salinities below that level, while spikelet number per panicle was significantly reduced at 3.4 or above (Table 4). The higher salinity threshold values of primary branches and panicle length compared with spikelet number per panicle suggest that the degeneration of primary branches on panicle and the reduction in panicle length were not major causes for the reduction of spikelets at moderate salinity. Cui et al. (1995) observed the salinity-induced reduction in both primary and secondary ranchi-branches on panicles in sand-cultured rice plants that were treated with salinity at panicle initiation. In their study, secondary branches degenerated at 0.1% NaCl (≈2.0 dS m^{-1}), while primary branches did not degenerate until NaCl concentration was increased to 0.5% NaCl (≈8.5 dS m^{-1}). Further experiments are needed to determine the threshold value of salinity on secondary ranchi-branches in order to confirm the morphological causes of reduction in spikelets on the panicle.

The loss of potential spikelets has been attributed to a competition for carbohydrate supply between vegetative growth and developing panicles (Murty and Murty, 1982) and among spikelets within panicle (Yoshida, 1976). Low radiation at the early reproductive stage (Evans and De Datta, 1979; Patro and Sahu, 1986) and drought and submergence damage (Hoshikawa, 1989) may exacerbate this competition. In wheat, a complete compensation between spikelets and kernels under moderate salinity was observed on the main spike and was explained by the presence of additional florets in spikelets that were usually aborted under nonstressed conditions, but were stimulated due to redistribution of carbohydrate supply upon reduction in spikelets under salinity (Grieve et al., 1992). In contrast, there are no additional florets in spikelets in rice. The redistribution of carbohydrate among spikelets upon the reduction in spikelets under salinity might partially compensate for loss of yield sink capacity by improving fertility and kernel weight among the remaining spikelets. However, the elongation of the culm, which occurs at the same time as panicle differentiation and development, could be highly competitive for carbohydrate supply (Mohapatra and Sahu, 1991). In M-202, shoot dry weight of the main culm was not significantly different from that of controls at moderate salinity (i.e., at or below 4.5 dS m^{-1}) (Table 3). The relatively normal growth of shoots under moderate salinity could have competed for the extra carbohydrate supply and constrained its distribution to the remaining spikelets. The decreased harvest index with the increase of salinity (Table 3) was consistent with this hypothesis. Although the mechanisms of salinity effects on translocation of carbohydrate and assimilates among rice organs remain speculative, it is clear that salinity reduced yield sink sites (i.e., spikelets on panicles) on main culms and restricted the intraplant competition of yield sink organs for carbohydrate supply. It is hypothesized that, under salinity, an increase in planting density will result in an increase in the num-

ber of main culms, while tillers will decrease. Harvest index will further decrease because of the reduced competition of yield sink sites on main culms for carbohydrates and shading effect at high density. Therefore, the management option of increasing planting density might not be effective in dealing with yield loss under salinity. Further studies will be needed to test this hypothesis.

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