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Time of Salt Stress Affects Growth and Yield Components of Irrigated Wheat

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ABSTRACT

Salt tolerance of wheat (*Triticum aestivum* L.) is known to change during different stages of growth. The effects of salinity on growth and yield components of wheat at different stages of growth were determined in a 2-yr field plot study at Brawley, CA. Four salinity levels were imposed on a Holtville silty clay [clayey over loamy, montmorillonitic (calcareous), hyperthermic Typic Torrifluvent] by irrigating with waters salinized with NaCl and $CaCl_2$ (1:1 w/w). Electrical conductivities of the irrigation waters were 1.4, 10.0, 20.0, and 30.0 dS m^{-1} in 1989, and 1.4, 8.0, 16.0, and 24.0 dS m^{-1} in 1990. The three irrigation treatments were (i) salinity imposed throughout the growing season, (ii) saline irrigation initiated after terminal spikelet differentiation (TSD), and (iii) saline irrigation discontinued at TSD. Growth and yield components measured were straw yield, total above ground biomass, number of spikelets per spike, number of kernels per spike, individual kernel weight, number of tillers per plant, and number of tiller spikes. Continuous salinity throughout the growing season significantly reduced all growth and yield components. Salinity imposed prior to TSD reduced the number of spikelets per spike and the number of tillers per plant, whereas salinity imposed after TSD significantly reduced only kernel number and weight. In general, the effect of salinity appears to be most pronounced on the yield components that are growing or developing at the time the salt stress is imposed. Total grain yields were maintained when moderately saline irrigation waters were substituted for good quality water during part of the growing season.

As water resources suitable for irrigation become less abundant throughout the world, water currently considered too saline will have to be used to meet agricultural needs. Also, growers in many areas of the western USA are being asked to reduce the volume of drainage water that leaves their fields. These waters include surface runoff water and the water that had percolated through the soil profile. Large areas of once productive soils throughout the world have already been taken out of cultivation due to waterlogging (Eckholm, 1975). While subsurface drainage systems have been installed in some areas to reduce waterlogging and to allow leaching of salts from the crop root zone, the problem of disposal of saline agricultural drainage water still exists.

Recent studies have shown that saline agricultural drainage waters can be used successfully to grow crops without detrimental long-term consequences to either crops or soils (Rhoades, 1989; Rhoades et al., 1989). In this management scheme, salt-sensitive and salt-tolerant crops are grown in rotation by irrigating sensitive crops with good quality water and tolerant crops with saline water after seedling establishment.

Salt tolerance of many crops varies with growth stage (Maas and Grieve, 1994). Results of greenhouse experiments have shown that sorghum [*Sorghum bicolor* (L.) Moench] (Maas et al. 1986), wheat (*Triticum aestivum* L.) (Maas and Poss, 1989a), and cowpea [*Vigna unguiculata* (L.) Walp.] (Maas and Poss, 1989b) were most sensitive during the vegetative and early reproductive stages, less sensitive during flowering, and least sensitive during the grain-filling stage. Therefore, it may be possible to irrigate with saline water during the more tolerant stages of growth and use low-salinity water only during the sensitive stages of growth. A field study by Grattan et al. (1987) showed that irrigating with 8 dS m^{-1} water from first flower to harvest had no significant effect on yields of melon (*Cucumis melo* L.) and tomato (*Lycopersicon esculentum* Mill.) compared with irrigating with 0.2 dS m^{-1} water.

Since organs contributing to various growth and yield components of wheat develop at different phenological stages (Evans et al., 1975; Kirby, 1988), environmental stresses affect their contribution to total grain yield differently depending on when they occur (Frank et al., 1987; Friend, 1965; Halse and Weir, 1974; Langer and Ampong, 1970). Maas and Grieve (1990) reported that salinity also affected yield components differently depending on when plants were stressed in the greenhouse. This study was initiated to determine whether these differences also occurred under field conditions and to quantify the differential crop responses caused by the timing of stress. It is expected that this information will provide new management options, such as establishing the feasibility of using saline irrigation waters to grow wheat during part of the growing season.

MATERIALS AND METHODS

This study was conducted at the Irrigated Desert Research Station, Brawley, CA, on a Holtville silty clay soil (Typic Torrifluvent). Each plot was 6.0 by 6.0 m and was enclosed by acrylic-fortified fiberglass borders that extended 0.75 m into the soil. The fiberglass borders protruded 0.15 m above the soil level and were covered with a berm, 0.18 m high and 0.6 m wide. Walkways, 1.2 m wide between plots, and good vertical drainage effectively isolated each plot.

Prior to sowing, triple superphosphate was mixed into the top 0.25 m of soil at the rate of 73 kg P ha^{-1}. To assure adequate N availability throughout the experiment, $Ca(NO_3)_2$ was added at the rate of 0.14 kg N ha^{-1} mm^{-1} of water applied at every irrigation for a total application of 71.4 and 72.6 kg N ha^{-1} for 1989 and 1990, respectively. Since the soil contained adequate levels of K, no additional K was added.

The two wheat cultivars used, Yecora Rojo and Anza, are semidwarf hard red spring wheats developed by the International Maize and Wheat Improvement Center (CIMMYT) in Mexico and released by the California Agricultural Experiment Station in 1970 and 1971, respectively. Both cultivars were sown in level plots on 12 Jan. 1989 and 18 Jan. 1990. Each plot contained 15 rows of each cultivar. The 6-m-long rows were sown 0.18 m apart, with the seed placed ≈25 mm apart within the row.

This factorial experiment consisted of three irrigation treat-

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Abbreviations: EC_e, electrical conductivity of saturated-soil extract; EC_{iw}, electrical conductivity of irrigation water; HI, harvest index; TSD, terminal spikelet differentiation.

Table 1. Average electrical conductivities (dS m^{-1}) of the irrigation water (EC_{iw}) and saturated-soil extracts (EC_e) before and after terminal spikelet differentiation (TSD) of wheat for three saline irrigation treatments.

Irrigation salinity treatment†	1989 EC_{iw} Pre-TSD	1989 EC_{iw} Post-TSD	1989 EC_e Pre-TSD	1989 EC_e Post-TSD	1990 EC_{iw} Pre-TSD	1990 EC_{iw} Post-TSD	1990 EC_e Pre-TSD	1990 EC_e Post-TSD
A	1.4	1.4	3.6	6.3	1.4	1.4	5.9	7.4
	10	10	6.5	11.3	8	8	13.1	14.1
	20	20	8.2	18.4	16	16	14.2	20.5
	30	30	8.5	23.4	24	24	21.1	25.1
B	1.4	1.4	3.2	4.9	1.4	1.4	5.5	6.9
	1.4	10	3.2	12.8	1.4	8	6.8	14.1
	1.4	20	3.2	18.9	1.4	16	7.6	18.5
	1.4	30	3.2	22.1	1.4	24	8.1	22.0
C	1.4	1.4	3.8	6.3	1.4	1.4	6.9	6.6
	10	1.4	4.9	9.2	8	1.4	13.1	10.5
	20	1.4	8.1	9.4	16	1.4	13.3	10.9
	30	1.4	9.0	9.8	24	1.4	18.2	10.8

† A, continuous salinity; B, salinity post-TSD; C, salinity pre-TSD.

ments and four salinity levels with all combinations replicated three times in a randomized complete block design. Prior to sowing in 1989, all plots were leached to remove excess salinity from the soil profile. At sowing, the EC_e (electrical conductivity of the saturated-soil extract) averaged to a depth of 0.9 m for all plots was <3.2 dS m^{-1}. In 1990, a minimum leaching irrigation with 100 mm of nonsaline water (1.4 dS m^{-1}) was applied to each plot prior to sowing to reduce the salt content in the top 0.15 m of soil. To assure good germination, 50 mm of nonsaline water was applied to each plot immediately after sowing.

Approximately 8 d after plant emergence, when the first leaf had emerged from the coleoptile, differential irrigation–salinity treatments were initiated. The electrical conductivity of the irrigation water (EC_{iw}) of the three saline treatments was increased in two steps over a 1-wk period until the desired salt concentrations were achieved. Equal weights of NaCl and $CaCl_2$ were added to Colorado River water (1.4 dS m^{-1}) to obtain

Table 2. Main stem yield components of two wheat cultivars grown for 2 yr under three saline irrigation treatments.

Irrigation salinity treatment†	EC_{iw}‡ Pre-TSD	EC_{iw}‡ Post-TSD	Yecora Rojo Spikelet number per spike	Yecora Rojo Total kernel number per spike	Yecora Rojo Total kernel wt. per spike	Yecora Rojo Mean kernel wt.	Anza Spikelet number per spike	Anza Total kernel number per spike	Anza Total kernel wt. per spike	Anza Mean kernel wt.
	dS m^{-1}		no.		mg		no.		mg	
					1989					
Control	1.4	1.4	19.8	36.5	1484	40.4	21.4	41.6	1396	33.5
A	10	10	19.4	36.4	1366	37.4	20.3	30.3	1080	35.9
	20	20	19.0	33.7	880	26.2	19.0	31.7	811	25.2
	30	30	16.7	32.9	837	25.6	18.7	36.0	869	24.2
B	1.4	10	19.8	38.2	1432	37.7	21.0	40.0	1352	33.7
	1.4	20	20.0	36.4	1134	32.2	20.3	28.0	828	29.4
	1.4	30	19.7	33.3	974	29.1	19.7	24.7	620	25.1
C	10	1.4	18.8	36.8	1498	40.7	21.3	39.7	1232	31.0
	20	1.4	18.7	34.1	1398	41.0	18.3	37.3	1314	35.2
	30	1.4	18.3	33.0	1323	40.1	17.3	39.7	1470	37.1
					1990					
Control	1.4	1.4	20.1	46.0	1515	33.1	20.3	44.1	1218	27.6
A	8	8	17.7	38.3	1236	32.0	18.3	39.0	1190	30.6
	16	16	15.0	28.3	652	23.0	16.3	20.7	614	30.3
	24	24	14.0	33.0	599	18.0	14.3	21.7	404	23.6
B	1.4	8	19.7	38.7	1546	40.1	21.0	44.7	1336	29.8
	1.4	16	19.9	38.6	1498	38.8	19.0	24.7	822	32.8
	1.4	24	19.8	34.4	974	28.1	18.7	23.0	777	33.6
C	8	1.4	18.2	36.6	1343	36.7	18.0	41.7	1227	29.3
	16	1.4	15.0	38.8	1404	36.4	15.7	40.0	1304	32.6
	24	1.4	13.4	35.8	1250	34.9	15.3	43.0	1407	32.7
					Combined 2-yr linear regression analysis§¶					
A			−0.16**	−0.34**	−33.3**	−0.65**	−0.17**	−0.66**	−27.3**	−0.24**
B			−0.01a	−0.22**	−18.1a**	−0.30a**	−0.07a**	−0.72**	−24.0**	−0.08a
C			−0.17**	−0.24**	−9.4a**	−0.03a	−0.19**	−0.14a	0.3a	0.10a

** Significantly different from the control at the 0.01 probability level.
† A, continuous salinity; B, salinity post-TSD; C, salinity pre-TSD.
‡ EC_{iw}, electrical conductivity of irrigation water.
§ Table values represent yield component change per unit increase in EC_{iw}.
¶ Values followed by the letter *a* are significantly different from continuous salinity (Treatment A) at the 0.01 probability level.

Table 3. Tiller yield components for 'Yecora Rojo' wheat grown for 2 yr under three saline irrigation treatments.

Irrigation salinity treatment†	EC_{iw}‡ Pre-TSD	Post-TSD	Tillers per plant	Tiller spikes per plant	Spikelet number per spike	Total kernel number per spike	Total kernel wt. per spike	Mean kernel wt.
	dS m^{-1}		no.				mg	
				1989				
Control	1.4	1.4	—§	2.8	19.5	27.7	1036	37.4
A	10	10	—	2.6	19.0	27.4	898	32.6
	20	20	—	2.6	18.8	23.6	542	22.5
	30	30	—	1.6	16.7	20.7	440	21.0
B	1.4	10	—	3.3	19.1	27.0	922	34.1
	1.4	20	—	3.2	19.4	26.3	671	25.1
	1.4	30	—	2.0	19.4	22.4	568	25.1
C	10	1.4	—	2.8	19.4	26.4	940	35.2
	20	1.4	—	2.3	18.6	25.7	971	37.6
	30	1.4	—	1.6	18.3	27.4	1021	36.6
				1990				
Control	1.4	1.4	7.9	5.4	19.8	35.0	1000	28.5
A	8	8	5.2	3.5	17.7	28.2	753	26.5
	16	16	2.3	0.4	—	—	—	—
	24	24	0.9	0.2	—	—	—	—
B	1.4	8	7.3	4.3	19.3	30.2	1065	35.2
	1.4	16	7.3	4.1	19.2	29.3	939	31.8
	1.4	24	7.1	2.9	19.1	25.2	623	24.5
C	8	1.4	5.5	3.3	16.8	27.0	920	34.1
	16	1.4	3.5	2.4	14.7	32.3	984	30.3
	24	1.4	3.6	2.7	12.1	29.4	705	24.0
			Combined 2-yr linear regression analysis¶#					
A			−0.30**	−0.12**	−0.11**	−0.27**	−22.5**	−0.60**
B			−0.03a	−0.05a**	−0.02a	−0.23**	−15.2b**	−0.35a**
C			−0.21b**	−0.08**	−0.15**	−0.11b*	−5.9a*	−0.10a

*,** Significant from the control treatment at the 0.05 and 0.01 probability levels, respectively.
† A, continuous salinity; B, salinity post-TSD; C, salinity pre-TSD.
‡ EC_{iw}, electrical conductivity of irrigation water.
§ Data not collected.
¶ Table values represent yield component change per unit increase in EC_{iw}.
# Values followed by the letter *a* or *b* are significantly different from continuous salinity (Treatment A) at the 0.01 or 0.05 probability levels, respectively.

the desired irrigation water salinities. Control treatments were irrigated with Colorado River water only. The electrical conductivities of the four irrigation waters were 1.4, 10.0, 20.0, and 30.0 dS m^{-1} in 1989 and 1.4, 8.0, 16.0, and 24.0 dS m^{-1} in 1990. During both growing seasons, all plots were irrigated approximately every 10 to 12 d to keep the matric potential of the control treatments above −85 J kg^{-1} in the 0.15- to 0.3-m soil depth. A neutron probe and tensiometers were used to monitor soil water content and matric potential and to guide irrigation frequency.

Three irrigation treatments were imposed both years by applying saline water throughout the growing season (Treatment A), after the glumes of the terminal spikelet were clearly differentiated (referred to here as terminal spikelet differentiation, or TSD)] (Treatment B), or from the first leaf stage until TSD, after which nonsaline water was applied (Treatment C). To achieve a rapid change in soil salinity at TSD for Treatments B and C, the initial EC_{iw} was abruptly changed to the new EC_{iw} in one irrigation. In addition, the amount of water applied per irrigation after the change in EC_{iw} was doubled, to facilitate leaching. The total amounts of irrigation water applied before and after the change in EC_{iw} were 104 and 285 mm in 1989 and 75 and 324 mm in 1990.

Soil samples were collected from each plot just before the EC_{iw} change and again at harvest each year to determine soil salinity. Two soil cores per plot were taken in 0.3-m increments to a depth of 0.6 m for the pre-TSD sample and to 0.9 m for the post TSD (harvest) sample. These sampling depths were based on unpublished soil water extraction data for semidwarf spring wheat grown under similar saline conditions (E.V. Maas, unpublished data, 1992). The average EC_e for each sampling date for both years is presented in Table 1.

The monthly mean maximum air temperatures for the months of January to April ranged from 22 °C to 34 °C in 1989 and from 21 °C to 31 °C in 1990; monthly mean minimum temperatures for the same period ranged from 2 to 12 °C in 1989 and from 1 to 12 °C in 1990.

At plant emergence, three plants of each cultivar in each plot were randomly selected to determine leaf and tiller appearance dates throughout the growing season. As leaves and tillers emerged on the main stem of these plants, they were tagged with small wire loops of a specific color. These colored wires provided rapid identification of leaves and tillers when the plants were completely senescent. Tillers were classified according to the system described by Klepper et al. (1982).

To determine the timing of TSD and the time to change the salinities in Treatments B and C, plant samples were taken about every 3 d to monitor apical meristem development. At each sampling, leaves of plants of both cultivars were removed and the apical meristem examined in the laboratory with a dissecting microscope. Sampling began when the plants were at the 3-leaf stage of growth and was discontinued at TSD. Because of constraints in the experimental design (i.e., every plot contained both cultivars), EC_{iw} was not changed until both cultivars had reached TSD. Yecora Rojo, the faster developing cultivar, was ≈5 d beyond TSD when EC_{iw} was changed for irrigation Treatments B and C.

Plants were harvested for seed yield from May 8 to 22 in

Table 4. Tiller yield components for 'Anza' wheat grown for 2 yr under three saline irrigation treatments.

Irrigation salinity treatment†	EC_{iw}‡ Pre-TSD	EC_{iw}‡ Post-TSD	Tillers per plant	Tiller spikes per plant	Spikelet number per spike	Total kernel number per spike	Total kernel wt. per spike	Mean kernel wt.
	dS m^{-1}		no.				mg	
				1989				
Control	1.4	1.4	–§	3.8	20.4	30.7	983	31.9
A	10	10	–	3.3	19.0	25.0	821	32.9
	20	20	–	3.0	16.9	19.2	429	22.3
	30	30	–	3.0	16.6	23.1	451	19.5
B	1.4	10	–	3.5	19.3	27.8	868	31.3
	1.4	20	–	3.7	19.0	20.5	551	26.5
	1.4	30	–	3.2	18.0	19.2	409	21.3
C	10	1.4	–	3.2	19.6	25.7	782	30.3
	20	1.4	–	3.0	16.3	27.0	888	32.8
	30	1.4	–	3.4	15.2	26.1	887	33.7
				1990				
Control	1.4	1.4	9.6	5.4	18.8	31.9	738	23.1
A	8	8	9.9	4.8	15.7	29.5	832	28.1
	16	16	5.5	2.6	14.8	19.3	465	24.1
	24	24	1.9	0.6	–	–	–	–
B	1.4	8	10.2	5.3	18.6	31.9	881	27.1
	1.4	16	9.5	4.5	17.5	22.0	666	30.3
	1.4	24	8.9	4.1	17.1	19.5	568	28.7
C	8	1.4	7.7	3.9	15.6	32.0	838	25.8
	16	1.4	4.7	3.5	14.1	28.6	810	28.1
	24	1.4	4.5	3.8	12.6	29.7	796	26.9
			Combined 2-yr linear regression analysis¶#					
A			−0.32**	−0.09**	−0.17**	−0.43**	−19.2**	−0.32**
B			−0.05a	−0.03a	−0.07a**	−0.45**	−15.1**	−0.13a*
C			−0.28**	−0.05b**	−0.21b**	−0.16a*	−3.0a	−0.04a

*,** Significant from the control treatment at the 0.05 and 0.01 probability levels, respectively.
† A, continuous salinity; B, salinity post-TSD; C, salinity pre-TSD.
‡ EC_{iw}, electrical conductivity of irrigation water.
§ Data not collected.
¶ Table values represent yield component change per unit increase in EC_{iw}.
# Values followed by the letter *a* or *b* are significantly different from continuous salinity (Treatment A) at the 0.01 or 0.05 probability levels, respectively.

1989 and from May 1 to 20 in 1990. Because salinity accelerated maturation, the high salinity plants were harvested first and the control plants last. To determine grain and straw yields of each cultivar, a 2.3-m^2 area was harvested from the center of each half of each plot. Spikes were harvested by hand, weighed, counted, and threshed. Grain was cleaned and weighed, and total straw yield from the harvested area was weighed and dried in a forced-air dryer at 70 °C for 21 d.

The number of tiller spikes per plant was determined both years by examining each plant within the harvest area. In 1990, the total number of tillers per plant was also determined. At harvest, the main stem and tiller spikes from the 3 selected plants of each cultivar from each plot were dissected to determine the effect of the irrigation treatments on yield components (i.e., spikelet number, seed number, and seed weight).

All data from the study were analyzed with a linear regression model (Myers, 1986). With this model, it was assumed that, for a given irrigation treatment, yield decreased linearly with increasing EC_{iw}. Since the data were collected in two different years, it was also assumed that a year effect may be present. Additionally, it was assumed that yield losses would differ with different irrigation treatments. Note, however, that the control salinity (EC_{iw} = 1.4 dS m^{-1}) was the same for all irrigation treatments. The preceding assumptions suggest the following linear regression model:

$$E(\text{yield}) = B_0 + B_1(EC_{iw}) + B_2(EC_{iw} \times I_1) + B_3(EC_{iw} \times I_2) + B_4(\text{Year})$$

where E(yield) represents the expected yield value and I_1, I_2, and Year are indicator variables defined as follows: $I_1 = 1$ when the saline water was applied at the beginning (irrigation Treatment C); otherwise, $I_1 = 0$. $I_2 = 1$ when the saline water was applied at TSD (irrigation Treatment B); otherwise, $I_2 = 0$. B_0 through B_4 are parameter estimates: B_0 represents the intercept, B_1 represents the yield loss under continuous salinity (irrigation Treatment A), B_2 and B_3 represent the difference in yield loss between the continuous salinity and the irrigation Treatments C and B, respectively, and B_4 represents the year effect. Year = 0 for 1989 data and 1 for 1990.

To simultaneously test whether yield reductions in irrigation Treatments C and B differ from that of the continuous salinity Treatment A, an F-test was performed on the joint linear hypothesis $B_2 = B_3 = 0$. If this F-test was not significant at the 0.05 probability level, it was concluded that the EC_{iw} vs. yield relationship was the same for all three irrigation treatments. If significant at or below the 0.05 level, individual F-tests were then used to test the hypotheses $B_2 = 0$ and $B_3 = 0$. Note that rejection of either or both F-tests suggests that yield reduction was a function of the irrigation treatment. To test whether the continuous salinity treatment resulted in a yield reduction that was significantly different from 0, an individual F-test was performed on the hypothesis $B_1 = 0$. To test whether irrigation Treatments B and C resulted in yield reductions that were significantly different from 0, individual F-tests were conducted on the linear contrasts $B_1 + B_2 = 0$ and $B_1 + B_3 = 0$.

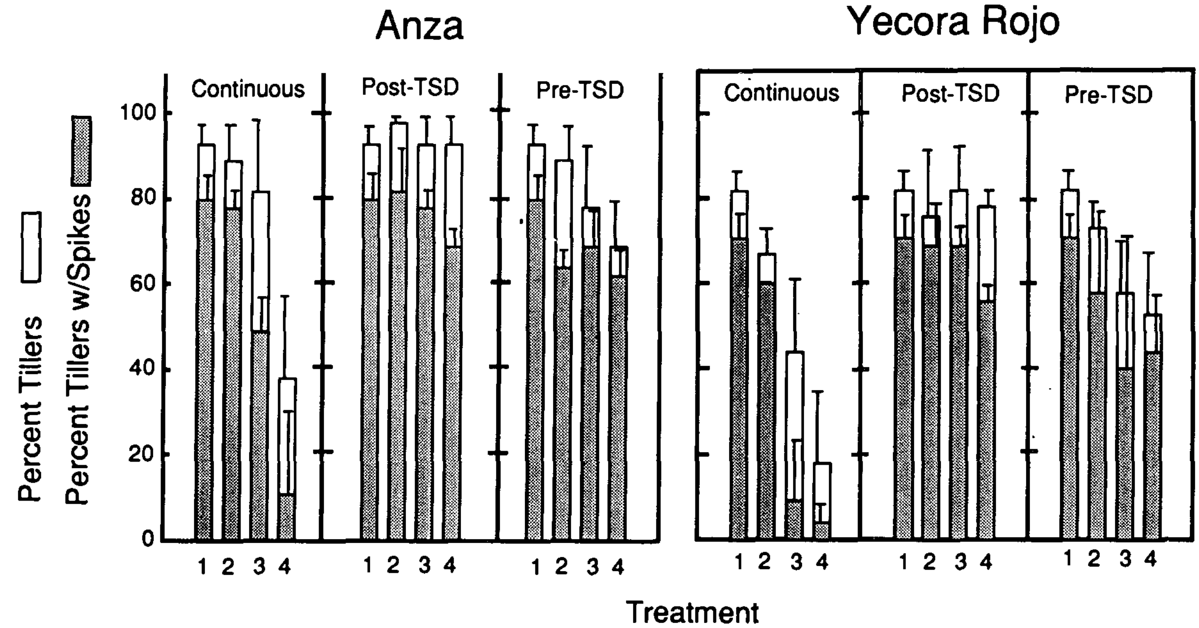

Fig. 1. Percent of plants with tillers and percent of tillers with spikes for two wheat cultivars grown in 1990 under three different saline irrigation treatments. Treatments 1, 2, 3, and 4 = electrical conductivity of irrigation water (EC_{iw}) of 1.4, 8.0, 16.0, and 24.0 dS m^{-1} associated with saline portion of growth cycle. Vertical bars on each column are standard deviation. TSD = Terminal spikelet differentiation.

RESULTS AND DISCUSSION

Main Stem Yield Components

In general, salinity significantly affected only those yield components on the main stem that were developing during the growth phase in which salt stress was imposed. With Treatment A, increasing salinity affected all yield components (Table 2). Spikelet number, which is determined prior to TSD (Kirby, 1988), was significantly reduced by irrigation Treatments A and C. The more saline the irrigation water, the fewer spikelets formed. Similar reductions in spikelet number are caused by moisture stress, temperature stress, and low light intensity prior to TSD (Frank et al., 1987; Friend, 1965; Halse and Weir, 1974; Langer and Ampong, 1970). Several studies have shown that these environmental stresses tend to shorten the duration of spikelet differentiation, resulting in fewer spikelets per spike (Frank et al., 1987; Friend, 1965; Oosterhuis and Cartwright, 1983). Salinity stress leads to a similar response (Grieve et al., 1993); however, when salinity stress was delayed until after TSD (Treatment B), spikelet number was relatively unaffected (Table 2).

Prior to TSD, environmental stresses can reduce the number of spikelets (Frank et al., 1987); thereafter, stress causes yield reduction by decreasing floret number, floret fertility, and the number and weight of kernels. Under saline conditions, the florets in the basal spikelets appear to be significantly less viable than those in the apical spikelets (Grieve et al., 1992). A reduction in floret viability seriously affects the total number of kernels per spike.

Discontinuing salinity stress after TSD (Treatment C) significantly increased kernel number in Anza but not in Yecora Rojo (Table 2). This difference is due, in part, to the greater ability of Anza to set kernels in floret Position 3 in each spikelet under highly saline conditions (Grieve et al., 1992). Furthermore, Yecora Rojo reached TSD before Anza; consequently, Yecora Rojo, unlike Anza, experienced stress 5 d after TSD under Treatment C because of the experimental design. For the same reason, salinity imposed after TSD (Treatment B) decreased kernel number significantly more with Anza than with Yecora Rojo.

Grain weight is largely determined by the duration and rate of grain filling (Kirby, 1974; Sofield et al., 1977; Wardlaw et al., 1980). Therefore, environmental stresses that tend to shorten the grain-filling period will significantly reduce final grain weight (Al-Khatib and Paulsen, 1990; Spiertz, 1974). Salt stress accelerates maturation and grain filling in some cereal crops (Francois et al., 1986, 1988). Therefore, the nearly consistent reduction in grain weight at the highest salinity levels in irrigation Treatments A and B could be the result of a shortened grain-filling period.

Tillering and Tiller Yield Components

The major determinant of grain yield per plant in wheat is the number of grain-bearing tillers per plant. Therefore, any loss of tillering can have a significant effect on final yield. Rickman et al. (1983) reported that each tiller appears at a predefined developmental stage, but stress may delay the appearance of a tiller or, if sufficiently severe, will cause the tiller to be skipped altogether. In the current study, tiller appearance of both cultivars generally followed the sequential order reported by Klepper et al. (1982). However, salinity stress imposed in irrigation Treatments A and C significantly delayed tiller appearance, with the highest salinity causing the longest delay. When salinity was not imposed until after TSD (Treatment B), tiller appearance was not delayed.

Increasing levels of salinity decreased the total number of tillers set per plant (Tables 3 and 4). Since tillering has been reported to occur only up to terminal spikelet

Table 5. Vegetative and grain yield of 'Yecora Rojo' and 'Anza' wheat grown for 2 yr under three saline irrigation treatments.

Irrigation salinity treatment†	EC_{iw}‡		Yecora Rojo				Anza			
	Pre-TSD	Post-TSD	Above ground biomass yield	Grain yield	Straw yield	Harvest index	Above ground biomass yield	Grain yield	Straw yield	Harvest index
	dS m^{-1}		g m^{-2}			%	g m^{-2}			%
					1989					
Control	1.4	1.4	855	563	292	66	1087	579	508	53
A	10	10	791	553	238	70	976	576	400	59
	20	20	357	250	107	70	496	300	196	60
	30	30	158	96	62	61	277	169	108	63
B	1.4	10	768	518	250	67	992	563	430	57
	1.4	20	603	400	203	66	830	457	373	55
	1.4	30	466	260	206	55	608	313	295	52
C	10	1.4	843	573	270	68	1117	615	502	55
	20	1.4	600	448	152	75	856	551	305	64
	30	1.4	408	329	79	81	749	510	239	69
					1990					
Control	1.4	1.4	1204	520	684	43	1356	450	906	33
A	8	8	992	430	562	44	1040	460	580	44
	16	16	345	140	205	41	499	207	292	42
	24	24	60	18	42	30	97	33	64	34
B	1.4	8	1249	596	652	48	1335	517	817	39
	1.4	16	1035	446	589	43	1088	454	634	42
	1.4	24	792	328	464	41	840	329	510	39
C	8	1.4	1059	474	585	47	1121	482	639	43
	16	1.4	727	383	344	53	886	414	472	47
	24	1.4	327	166	161	50	628	300	329	48
				Combined 2-yr linear regression analysis§¶						
A			−36.5**	−19.8**	−16.6**	−0.26**	−39.9**	−16.6**	−23.3**	0.24**
B			−16.9a**	−10.5a**	−6.5a**	−0.23**	−19.7a**	−8.3a**	−11.4a**	0.08
C			−25.1a**	−11.5a**	−13.6**	−0.35a**	−21.4a**	−5.4a**	−16.1a**	0.52a**

** Significantly different from the control at the 0.01 probability level.
† A, continuous salinity; B, salinity post-TSD; C, salinity pre-TSD.
‡ EC_{iw}, electrical conductivity of irrigation water.
§ Table values represent yield component change per unit increase in EC_{iw}.
¶ Values followed by the letter *a* are significantly different from continuous salinity (Treatment A) at the 0.01 probability level.

stage of growth (Kirby et al., 1985), salinity stress prior to TSD should reduce tiller number, while salinity stress imposed after TSD should have little effect on tiller number. Our data for irrigation Treatments A and B tend to confirm this effect; however, plants under Treatment C, where salinity stress was discontinued after TSD, set significantly more late tillers (i.e., T4 and T5) than those under Treatment A, where salinity stress was continued. This seems to indicate that the window of opportunity (as described by Klepper et al., 1982) for these late tillers was not completely closed at the time the stress was discontinued. These tillers appeared as late as 200 thermal units after TSD.

Gallagher and Biscoe (1978) stated that tiller abortion generally begins when tiller appearance stops, and that abortion stops just before anthesis. In our study, tiller abortion for both cultivars always occurred prior to spike emergence, with the last emerging tillers aborting first. Frequently, aborting tillers could be detected visually when the youngest emerged leaf became chlorotic. The number of aborted tillers was significantly greater under continuous salinity stress than when the stress was discontinued after TSD (Fig. 1). Salinity applied after TSD (Treatment B) did not significantly increase the number of aborted tillers, except in the highest salinity treatment.

Salinity had a significantly greater effect on reducing the number of tillers that set a spike than on the total number of tillers formed. McMaster et al. (1987) reported a similar effect from light stress caused by shading. The yield components of the tillers, such as the number of spikelets, number of kernels, and individual kernel weight, tended to follow the same pattern as the main stem for both cultivars (Tables 3 and 4); however, the reduction per unit increase in salinity for each of the components was generally smaller.

Under nonsaline conditions in our study (control treatment), tillers contributed ≈70% to total plant seed yield (Tables 2, 3, and 4). Because of the reduction in tiller number and yield components of spikes when plants were continuously stressed with salinity, the contribution of tillers to total yield was significantly reduced with increasing salinity levels (data not shown). As expected, tiller yields were reduced least by salinity stress in irrigation Treatment B, while those in Treatment C were moderately affected.

Total Grain and Straw Yield

Both water stress (Oosterhuis and Cartwright, 1983) and salinity stress (Grieve and Francois, 1992; Maas and Grieve, 1990) during the early vegetative stage of growth have been shown to decrease leaf number in wheat. Since leaf number is determined prior to TSD (Kirby, 1974), stress imposed during this early growth stage is undoubtedly the cause of reduced leaf number. In contrast, stress applied after TSD will have no effect on the final number of leaves. In our study, main stem leaf observations in 1990 support this hypothesis. Final leaf number on control plants was 8 for Yecora Rojo and 11 for Anza. While plants growing at all salinity levels of Treatment B produced the same final number of leaves as control plants, those under Treatments A and C at an EC_{iw} of 16 and 24 dS m^{-1} consistently produced one leaf less. This reduction in leaf number was already apparent at TSD, as the number of emerged leaves in Treatments A and C was one lower than on the control plants.

For many cereal crops, straw yield has been shown to be more sensitive to salinity than grain yield (Francois et al., 1986, 1989; Pearson, 1959). Anza, in this study, showed such a response in all irrigation treatments. Yecora Rojo showed this response only under Treatment B, while under Treatments A and C grain yield was more sensitive to salinity than straw yield. Continuous salinity was the most detrimental and salinity imposed after TSD the least detrimental.

As previously pointed out for main stem and tiller yield components, grain yield was significantly higher when salinity was imposed for only part of the growing season than when it was imposed continuously. Grain yields, based on the combined data for 2 yr, were not significantly different for irrigation Treatments B and C, but were significantly higher than under Treatment A (Table 5). The grain yield losses under Treatments B and C were due to salinity effects on different yield components for the two treatments. While tiller loss under Treatment B was minimal in comparison with Treatment C, the reduction in kernel number per spike was significantly greater; therefore, the reduction in grain yield for each unit increase in salinity tended to be about equal for these two irrigation treatments.

Harvest index (HI), the ratio of grain yield to total biomass yield, provides an estimate of the conversion efficiency of dry matter to grain yield (Baker and Gebeyehou, 1982). Harvest index is quite sensitive to environmental stresses and stress differences from one year to another for a given cultivar on a given soil may result in significantly different HI values each year (Prihar and Stewart, 1990). Our data show similar trends, with the HI significantly higher in 1989 than in 1990 for all treatments. In general, HI increased as salinity increased in all irrigation treatments. Treatment C, where straw yield was reduced more than kernel yield, had the highest HI.

CONCLUSIONS

Grain yield in wheat can be described in terms of components that are determined sequentially in the course of phenological development. Salinity effects appear most pronounced on those components that are developing or growing at the time stress is imposed. If salinity stress is discontinued after TSD or is delayed until TSD, yield components that are developing during the nonstressed periods develop with little or no impairment, whereas continuous stress throughout the growing season reduces the contribution of all yield components.

This study clearly shows that good quality irrigation water does not have to be used during the entire growing season to maintain wheat yield. Full yields can be maintained by substituting moderately saline water for good quality water after TSD, when grain production is less susceptible to salt stress. Since there are generally more irrigations applied after TSD than before, this technique can conserve limited resources of good quality water.

This irrigation strategy offers a management option for use or reuse of saline waters in many agricultural areas; however, its feasibility will depend on the permeability and leachability of the soil, the salinity of the primary water supply, and the availability of a secondary water supply.

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