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Contribution of Individual Culms to Yield of Salt-Stressed Wheat

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ABSTRACT

Grain yield in wheat *(Triticum aestivum* L. emend. Thell.) is highly dependent upon the number of spike-hearing tillers produced by each plant. Soil salinity can greatly decrease their number and productivity. Knowing the contribution of specific tillers is essential for breeding salt-tolerant genotypes and for developing wheat growth simulation models. Our objective was to determine the effects of soil salinity on the contribution of individual cuhns to total grain and dry matter yields of two spring wheat cultivars, Anza and Yecora Rojo. Plants were grown in Pacbappa fine sandy loam soil (mixed, thermic, Mollic Haploxeralf) in outdoor lysimeters for 2 yr. Three salinity treatments were imposed by irrigating with waters containing equal weights of NaCl and $CaCl_2$ (electrical conductivities $\cong$ 1, 12, or 18 dS m^{-1}). Despite substantial losses in the number of tillers at moderate levels of salt stress, grain yields of the main stem (MS) and tillers Tl and T2 were as great or greater than those on nonstressed plants of both cultivars. The contribution of the MS to yield on a land area basis increased from about 25 to 35% in nonsaline treatments to over 80% with increasing salinity. The contribution of primary tillers ($\cong$58-65% in nonsaline conditions) decreased substantially only at the highest salinity levels. Salinity stress significantly decreased the number of spikelets per spike but the number of kernels per spike either increased or was unaffected except at the highest level of stress. Increasing salinity decreased total straw yields primarily because of fewer tillers, but dry weights of the MSs and remaining tillers were also smaller. Results show that loss of spike-bearing tillers accounts for most of the yield reduction in salt-stressed wheat.

IN WHEAT *(Triticum* spp.), grain yield per unit area is highly dependent upon the number of productive tiller spikes, particularly in multi-tillering cultivars (Power and Alessi, 1978; Nerson, 1980: McMaster et al. 1994). Maas and Grieve (1990) found that yield reductions of salt-stressed wheat and durum *(T. turgidum* L.) grown in a greenhouse were due primarily to the decrease in tiller spikes per plant. The detrimental impact of tiller losses on yield were also observed in the field (Francois et al., 1994). However, under conditions where control plants averaged less than one tiller per plant, soil salinity, i.e., mean rootzone electrical conductivity of a saturated-soil extract (κ_e) up to 14 dS m^{-1} (deciSiemens per meter = mmho cm-‘), did not reduce the number of tiller spikes per unit land area (Francois et al., 1986). Of course, since tillering is highly dependent upon plant population density (Puckridge and Donald, 1967; Darwinkel, 1978), the effects of salinity on tiller production could be expected to vary depending on the number of plants per unit area.

It is generally accepted that the MS and the primary true-leaf tillers produce most of the grain (Rawson, 197 1; Ishag and Taha, 1974; Fraser and Dougherty, 1978; Power and Alessi, 1978; Thorne and Wood, 1988). The coleoptilar, prophyll, and higher-order tillers are the most susceptible to environmental stresses. Knowing the contribution of specific tillers to total yield and their vulnerability to salt stress could greatly improve efforts to breed higher-yielding genotypes that are more tolerant of salinity. This information is also essential to the development of realistic wheat growth simulation models (Roy and Gallagher, 198.5).

The results reported here are part of a larger study designed to determine the effects of salt stress on the rate and extent of growth and development of all shoot organs of two semidwarf, hard red spring wheat *(T. aesti-*

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Abbreviations: κ_e, electrical conductivity of a saturated-soil extract; κ_{iw}, electrical conductivity of irrigation water; κ_{sw}, electrical conductivity of soil water; $\overline{\kappa}_{sw}$, depth-averaged electrical conductivity of soil water in the root zone; κ_{sw}, depth- and time-averaged electrical conductivity of soil water in the root zone during the growing season; MS, main stem; TO, T1, Tn. tillers; $LSD_{0.05}$, least significant difference at the 5% level of probability; HI, harvest index.

vum L. emend. Thell.) cultivars, Anza and Yecora Rojo. Some results have been reported (Grieve et al., 1992, 1993; Lesch et al., 1992). Tiller development and abortion were addressed earlier (Maas et al., 1994). Anza is a more vigorous tillering cultivar than Yecora Rojo and appears to be slightly more salt tolerant (Francois et al., 1994). Kelman and Qualset (1991) reported that Anza was more tolerant than Cajeme 71, a sib cultivar of Yecora Rojo. The specific objective of this paper was to determine the effect of soil salinity on the contribution of individual culms to total grain and dry matter yields.

MATERIALS AND METHODS

The experiment was conducted in outdoor lysimeters at the U. S. Salinity Laboratory, Riverside, CA. Two cultivars, Anza and Yecora Rojo, were grown during two consecutive years, 1989 and 1990. Details of the experiment have been described (Maas et al., 1994). Briefly, seed were sown on 11 January in 1989 and 1990 in lysimeters (3.0 m by 3.0 m by 1.5 m deep) containing Pachappa fine sandy loam. A planting density of 167 plants m^{-2} was attained with seed placed 40 mm apart in 0.15-m rows. The experimental design consisted of three salinity treatments replicated three times in a randomized, split-plot design, with salinity as main plots and cultivars as subplots. Differential salination was initiated on 30 Jan. 1989 and 23 Jan. 1990 by irrigating with Riverside tap water (control) or one of two saline waters containing different amounts of a mixture of NaCl and $CaCl_2$ (1: 1 by wt.). The average electrical conductivities of the three irrigation waters (K,,) were 0.9, 11.3, and 17.5 dS m^{-1} in 1989 and 0.8, 12.2, and 17.7 dS m^{-1} in 1990. All lysimeters were irrigated every 7 to 10 d to keep the soil matric potential of the control treatment above -85 J kg^{-1} at the 0.25-m depth. The total amount of irrigation water applied to each lysimeter between sowing and harvest was 690 mm in 1989 and 580 mm in 1990. The electrical conductivity of the soil water (K,,) was determined on soil solutions extracted after most irrigations at 25-, 45-, 75-, and 105-cm soil depths. Since rooting depth increased throughout the season, κ_{sw} was averaged over progressively deeper depths in the root zone. The soil salinity data and the method of averaging were described previously (Maas et al., 1994). The mean rootzone $\bar{\bar{\kappa}}_{sw}$ values for the period between 20 Jan. and 9 May 1989 were 2.3, 13.0, and 15.9 dS m^{-1} for the control, medium, and high salinity treatments, respectively, and between 17 Jan. and 9 May 1990 they were 3.3, 18.7, and 25.8 dS m^{-1}.

Plants within each treatment were harvested as they matured (kernel hard)-Anza between 26 May and 8 June in 1989 and 30 May and 12 June in 1990; Yecora Rojo between 18 and 23 May in 1989 and 18 May and 4 June in 1990. Salt-stressed plants always matured first. Shoot dry matter and grain yields were determined on 10 randomly selected plants of each cultivar in each lysimeter. The plants were chosen from the third, fourth and fifth rows in from the edge of each lysimeter to minimize border effects. The MS and each tiller were identified and tagged as they emerged in accordance with the nomenclature of Klepper et al. (1982). Grain and straw yields of individual culms were measured after drying at 70°C.

Statistical Methods

The experimental design consisted of a split plot layout, with salinity as the whole plot treatment and cultivar as the subplot treatment. Three salinity levels were imposed on two cultivars within a block, and the layout was replicated three times. Additionally, the experiment was repeated over two years. Grain and straw yield data were analyzed with split plot analysis of variance (ANOVA) models. Separate ANOVA models were individually fit to the following measurements: total grain and straw yield, MS grain and straw yield, and T1, T2, and T3 primary tiller grain and straw yield. Because the observed lysimeter salinity levels significantly changed in 1990, it was necessary to analyze the 1989 and 1990 grain and straw yield data separately. In all the split plot models the data for each salinity-cultivar level consisted of the appropriate (grain or straw) mean response level, averaged across the 10 plants.

To test for statistical differences among tillers, a multivariate regression analysis was also performed on the MS, T1, T2, and T3 grain and straw tiller yield data. For this analysis, the individual tiller yield data from both years was combined together and averaged across replications within each salinity level. These data were then separated by cultivar and fit to the following regression model:

$$\ln(Y_{ij}) = b_{0j} + b_{1j}\kappa_i + b_{2j}\kappa_i^2 \qquad [1]$$

where the i subscript represents the six distinct salinity levels observed over 2 yr, j represents the specific tiller component (i.e., MS, T1, T2, or T3), Y_{ij} is the yield of the jth tiller at the ith salinity level, and b_{0j}, b_{1j}, and b_{2j} are the parameter estimates for the jth tiller. Note that in Eq. [1] the salinity level was treated as a continuous variable and was assumed to influence the natural log transformed yield data in a curvilinear manner. Furthermore, it was assumed that the year effect was negligible, and hence could be ignored. Multivariate F-tests were then used to test for equality of the parameter estimates across each pair of tiller equations. (In such a multivariate regression model, a significant difference between the estimated parameters of any two tiller equations indicates a systematic change in the yield/salinity response relationship between those two tillers.)

A limited analysis on some mean grain yield components, viz., number of spikelets and kernels per spike, kernels per spikelet, and mean weight per kernel, was also performed for the MS and individual primary tillers. Because the number of culms produced was extremely variable at the higher salinity levels, each cultivar was analysed separately with weighted one-way ANOVA models, where the weights were defined to be inversely proportional to the number of culms produced at each salinity level.

RESULTS AND DISCUSSION

Total Grain and Straw Yield

Treatment means and statistical results for total grain and straw yields of both cultivars and both years are given in Tables 1 and 2. The three $LSD_{0.05}$ values for each split plot model include an average salinity $LSD_{0.05\ salt}$, a $LSD_{0.05\ cv(salt)}$ for determining significant differences between cultivars across the same salinity level, and a $LSD_{0.05\ salt(cv)}$ for determining significant differences between salinity levels within the same cultivar. When no salinity x cultivar interaction occurred, the average $LSD_{0.05\ salt}$ was used to differentiate between the average yields across the three salinity levels (provided the overall salinity effect was found to be significant). If the salinity x cultivar interaction was statistically significant, then the $LSD_{0.05\ cv(salt)}$ and $LSD_{0.05\ salt(cv)}$ were used to differen-

Table 1. Mean grain yields of the whole plant and individual culms of Anza (A) and Yecora Rojo (YR) wheat grown at three salinity levels in lysimeters in 1989 and 1990.

Salinity treatment ($\overline{\overline{\kappa}}_{sw}$)†	Grain yield (g/culm)									
	Whole plant		MS		T1		T2		T3	
	A	YR	A	YR	A	YR	A	YR	A	YR
dS m^{-1}					1989					
2.3	4.12	6.52	1.24	1.57	0.80	1.24	0.76	1.09	0.59	0.95
13.0	4.51	5.14	1.59	2.11	1.00	1.64	1.03	1.35	0.38	0.34
15.9	4.11	4.05	1.50	1.68	0.88	1.21	0.77	0.92	0.36	0.18
					1990					
3.3	4.15	4.28	1.28	1.47	0.95	1.05	0.86	0.85	0.79	0.45
18.7	3.04	3.63	1.62	1.88	0.74	0.93	0.52	0.64	0.12	0.10
25.8	1.67	1.03	1.16	0.85	0.23	0.13	0.16	0.03	0.11	0.02
Analysis of Variance										
	1989	1990	1989	1990	1989	1990	1989	1990	1989	**1990**
F-test probability levels										
salt x cv.	0.031	0.187	0.273	0.103	0.247	0.113	0.346	0.222	0.184	0.120
cv.	0.005	0.520	0.004	0.622	0.001	0.244	0.002	0.841	0.677	0.041
salt	0.26	0.007	0.127	0.032	0.188	0.015	0.262	0.014	0.068	0.007
Standard errors (g culm^{-1})										
Salt x cv.	0.339	0.315	0.092	0.119	0.084	0.059	0.063	0.065	0.130	0.069
cv.	0.1%	0.182	0.053	0.069	0.049	0.034	0.036	0.038	0.075	0.040
Salt	0.481	0.348	0.118	0.123	0.104	0.115	0.130	0.100	0.113	0.067
$\text{LSD}_{0.05}$ (g culm^{-1})										
Salt	NS	1.37	**NS**	0.48	NS	0.45	**NS**	0.39	NS	0.26

† $\overline{\overline{\kappa}}_{sw}$ = Time- and depth-averaged electrical conductivity of the soil water for period from 20 Jan. to 9 May 1989 and 17 Jan. to 9 May 1990.

tiate between the individual salinity/cultivar treatment means (Petersen, 1994).

The salinity x cultivar interaction was significant ($P = 0.031$) for the 1989 grain yields (Table 1). Yecora Rojo grain yields exceeded Anza yields at the control and medium stress levels ($\text{LSD}_{0.05\ \text{cv(salt)}}$ = 1.17 g culm^{-1}), but not at the high level. Salinity had no significant effect on grain yield of Anza, but significantly decreased yield of Yecora Rojo in the high salinity treatment ($\text{LSD}_{0.05\ \text{salt(cv)}}$ = 1.86 g culm^{-1}). In 1990, the salinity effect on grain yield was highly significant ($P = 0.007$), but neither the salinity x cultivar interaction, nor the cultivar effect was statistically significant. Yield reduction at the high stress level was significantly different from both the control and medium levels ($\text{LSD}_{0.05\ \text{salt}}$ = 1.37 g /culm).

No significant salinity x cultivar interaction occurred in the 1989 straw yield data (Table 2). The cultivar effect

Table 2. Mean straw yields of the whole plant and individual culms of Anza (A) and Yecora Rojo (YR) wheat grown at three salinity levels in lysimeters in **1989 and 1990.**

Salinity treatment ($\overline{\overline{\kappa}}_{sw}$)†	Straw yield (g /culm)									
	Whole plant		MS		T1		T2		T3	
	A	YR	A	YR	A	YR	A	YR	A	YR
dS m^{-1}					1989					
2.3	5.90	5.60	1.39	1.20	1.00	1 .00	**0.99**	0:91	0.85	0.80
13.0	4.41	3.11	1.38	1.01	1.02	0.87	1.00	0.74	0.49	0.26
15.9	3.80	2.24	1.11	0.82	0.81	0.63	0.72	0.54	0.44	0.16
					1990					
3.3	5.46	3.33	1.38	1.06	1.03	0.82	0.97	0.68	0.87	0.35
18.7	1.97	1.72	1.00	0.87	0.50	0.45	0.35	0.30	0.08	0.05
25.8	1.03	0.55	0.67	0.44	0.15	0.07	0.11	0.02	0.08	0.01
Analysis of Variance										
	1989	1990	1989	1990	1989	1990	1989	1990	1989	1990
F-test probability levels										
salt x cv.	0.363	**0.044**	0.258	0.426	0.280	0.294	**0.465**	0.103	0.695	0.011
cv.	0.023	0.009	0.001	0.005	0.042	0.003	0.018	0.010	0.142	0.006
salt	0.027	0.001	0.030	0.006	0.097	0.001	0.117	0.00:	0.028	0.001
Standard errors (g culm^{-1})										
Salt x cv.	0.426	0.307	0.048	0.065	0.050	0.049	0.067	0.049	0.127	0.059
cv.	0.246	0.177	0.028	0.038	0.031	0.028	0.039	0.028	0.073	0.034
Salt	0.441	0.221	0.055	0.067	0.071	0.056	0.085	0.060	0.097	0.029
$\text{LSD}_{0.05}$ (g culm^{-1})										
Salt	1.73	0.87	0.22	0.26	**NS**	0.22	**NS**	0.24	0.38	0.11

† $\overline{\overline{\kappa}}_{sw}$ = Time- and depth-averaged electrical conductivity of the soil water for period from 20 Jan. to 9 May 1989 and 17 Jan. to 9 May 1990.

Table 3. Harvest index of Anza and Yecora Rojo wheat grown 2 yr at three salinity levels in lysimeters.

Salinity† treatment	Harvest index	
	Anza	Yecora Rojo
dS m^{-1}	1989	
2.3	0.41	0.54
13.0	0.51	0.65
15.9	0.52	0.64
	1990	
3.3	0.46	0.56
18.7	0.61	0.68
25.8	0.62	0.65

† $\overline{\overline{\kappa}}_{sw}$ = Time- and depth-averaged electrical conductivity of the soil water for period from 20 Jan. to 9 May 1989 and 17 Jan. to 9 May 1990.

was significant ($P = 0.023$), indicating that, on the average, Yecora Rojo produced less dry matter than Anza. The salinity effect was also significant ($P = 0.027$). Straw yields at both the medium and high stress levels were significantly lower than the nonsaline control yield ($LSD_{0.05\ salt}$ = 1.73 g /culm). In 1990, straw yield was affected by a significant salinity x cultivar interaction ($P = 0.044$). Anza produced more dry matter than Yecora Rojo only in the control treatment [$LSD_{0.05\ cv(salt)}$ = 1.06 g culm^{-1}]. Salt stress significantly decreased dry matter yields of both cultivars [$LSD_{0.05\ salt(cv)}$ = 0.98 g culm-^{1}].

In general, cultivar differences in grain and straw yield occurred only at the control and/or moderate salinity stress levels. When significant cultivar differences did occur, Yecora Rojo always produced more total grain yield and less total straw yield than Anza. The salinity effects were much more pronounced in 1990 when medium and high soil salinity levels were significantly higher than in 1989. Overall, increasing salinity above 8 to 10 dS m^{-1} tended to decrease both total grain and straw yields of both cultivars.

Harvest Index

The harvest index (HI), the ratio of grain yield to total aboveground biomass yield, was 0.1 units or more higher for Yecora Rojo than for Anza except at the highest salinity levels in 1990 (Table 3); and it was 0.1 units or more higher in the saline treatments than in the controls for both cultivars in both years. A smaller and less consistent increase in HI with salt stress was found for these cultivars when grown at the same time in Brawley, CA (Francois et al., 1994). Kelman and Qualset (1991) also reported that salinity increased the HI and although the values were lower than those above, Anza had lower values than Cajeme 71, the sib cultivar of Yecora Rojo.

Grain and Straw Yields of Individual Culms

The statistical analysis of grain and straw yields of individual culms was restricted to the MS and tillers Tl, T2, and T3 because formation of most of the TO and all other true-leaf tillers was completely inhibited by the medium and/or high salt levels in 1990 (Tables 1 and 2). No significant salinity x cultivar interaction was observed for either yield component of any culm in either year with the exception of the 1990 straw yield of T3.

The yield responses of the MS and tillers Tl and T2 to soil salinity were similar within each cultivar. Yecora Rojo produced significantly more grain than Anza in 1989, but not in 1990 (Table 1); whereas, Anza consistenty produced more dry matter than Yecora Rojo both years (Table 2). Salinity, $\overline{\overline{\kappa}}_{sw}$, up to about 16 dS m^{-1} had no significant effect on the grain yield of these culms in 1989, but significantly decreased their grain yields when $\overline{\overline{\kappa}}_{sw}$ reached 25.8 dS m^{-1} in 1990. Salt stress significantly decreased the straw yield of only the MS at the highest level in 1989. Tillers Tl and T2 were unaffected. In 1990, straw yields of all three culms decreased significantly at both the medium and high salinity levels.

Tiller T3 responded somewhat differently. Although T3 produced more grain on Yecora Rojo than on Anza in the 1989 control treatment, the mean yields across salinity levels were not significantly different in 1989 (Table 1). And, in 1990, Anza produced more grain than Yecora Rojo ($P = 0.041$). The salinity effect was marginally significant in 1989 ($P = 0.068$), indicating that only the high salinity treatment reduced grain yield; whereas, it was highly significant in 1990, with grain yields at both the medium and high stress levels substantially below those of the control. The salinity effect on straw yield of T3 in 1989 was significant, with yields at both the medium and high stress levels being lower than those of the control (Table 2). In 1990, a significant interactive effect between salinity and cultivar on straw yield occurred ($P = 0.011$). The estimated $LSD_{0.05\ cv(salt)}$ of 0.20 g /culm indicates that Anza produced more dry matter than Yecora Rojo in the control treatment. The $LSD_{0.05\ salt(cv)}$ was 0.16 g /culm implying that dry matter yields of both cultivars decreased significantly at both the medium and high stress levels.

Generally, Yecora Rojo consistently produced more grain than Anza on the MS, Tl, and T2 tillers at the control and medium stress levels, yet produced less grain than Anza on the T3 tiller under high salt stress. However, Anza produced more dry matter than Yecora Rojo at all salinity levels on the MS, Tl, and T2 tillers, and at the control level on the T3 tiller. Additionally, salinity significantly reduced the grain and straw yields in both cultivars, particularly in 1990 when soil salinity levels were higher than in 1989.

Salinity Effects on Spike Yield Components

Despite a rather consistent and significant decrease in the total number of spikelets per spike with increasing salinity, the number of kernels per spike either increased or was unaffected except at the highest salinity level in 1990 (Table 4). Only data for the MS and primary tillers are shown because secondary tillers rarely appeared in the saline treatments (Maas et al., 1994). Tillers T4 on Anza and TO and T4 on Yecora Rojo were omitted for the same reason. The intermediate salinity level in 1989 ($\overline{\overline{\kappa}}_{sw}$ = 13 dS m^{-1}) increased the number of kernels in MS spikes of both cultivars, and while not statistically significant, mean number of kernels per spike for many tillers was also greater. Only at 25.8 dS m^{-1} in 1990,

Table 4. Mean grain yield components of main stem and tillers of Anza and Yecora Rojo wheat grown 2 yr at three salinity levels in lysimeters.

Salinity treatment ($\bar{\bar{\kappa}}_{sw}$)†	Anza					Yecora Rojo			
	MS	T0	T1	T2	T3	MS	T1	T2	T3
dS m^{-1}									
YEAR 1989									
			Number of culms included in each mean						
2.3	26	14	24	24	25	27	27	26	26
13.0	30	16	29	30	13	30	30	28	10
15.9	28	18	27	24	14	30	29	27	6
			Spikelets per spike						
2.3	22.2	20.6	21.1	21.1	20.4	20.1	20.1	20.2	19.8
13.0	20.4	17.4	18.1	17.7	18.5	19.0	18.8	19.2	19.1
15.9	19.0	15.5	16.6	16.1	17.2	17.3	17.2	17.4	18.0
Prob.§	<0.00	<0.00	<0.00	<0.00	0.002	0.001	0.001	0.002	0.007
			Kernels per spike						
2.3	34.2	22.4	28.0	26.4	21.5	42.8	37.1	37.4	34.0
13.0	48.9	27.9	33.3	31.8	30.3	47.1	41.0	41.8	30.3
15.9	44.4	24.3	28.8	27.1	24.2	41.0	35.6	32.1	31.0
Prob.	0.050	0.458	0.378	0.362	0.261	0.037	0.213	0.056	0.380
			Kernels per spikelet						
2.3	1.55	1.06	1.32	1.24	1.05	2.13	1.87	1.85	1.71
13.0	2.40	1.60	1.83	1.79	1.63	2.41	2.17	2.17	1.58
15.9	2.34	1.55	1.72	1.66	1.39	2.36	2.06	1.81	1.71
Prob.	0.016	0.085	0.078	0.078	0.144	0.007	0.143	0.098	0.642
			Mean weight per kernel (mg)						
2.3	35.5	31.0	30.7	30.9	29.6	36.7	33.0	29.7	29.4
13.0	32.1	32.9	31.6	32.3	28.5	43.9	39.5	34.8	33.3
15.9	33.2	31.1	31.1	32.5	30.3	39.9	34.1	30.4	28.7
Prob.	0.416	0.807	0.942	0.848	0.899	0.221	0.322	0.292	0.635
YEAR 1990									
			Number of culms included in each mean						
3.3	27	14	26	23	23	28	27	25	13
18.7	30	‡	23	16	4	28	18	15	3
25.8	27		12	9	7	28	5		
			Spikelets per spike						
3.3	22.4	20.7	21.2	21.3	20.4	19.3	18.9	19.4	20.1
18.7	16.2		15.0	14.8	14.8	16.2	16.8	16.8	18.7
25.8	15.0		13.5	13.7	12.7	13.2	15.4		
Prob.	10.001	nsd¶	<0.001	<0.001	<0.001	<0.001	0.002	nsd	nsd
			Kernels per spike						
3.3	37.9	17.5	28.7	30.3	28.8	39.0	31.4	29.8	26.5
18.7	39.7		26.7	27.2	26.3	39.8	31.4	27.6	27.3
25.8	34.6		20.3	16.9	15.9	25.6	23.4		
Prob.	0.520	nsd	0.005	0.008	0.119	0.015	0.401	nsd	nsd
			Kernels per spikelet						
3.3	1.68	0.84	1.35	1.42	1.40	2.02	1.66	1.53	1.32
18.7	2.48		1.79	1.84	1.77	2.45	1.86	1.62	1.46
25.8	2.28		1.49	1.24	1.24	1.91	1.47		
Prob.	0.039	nsd	10.001	0.030	0.365	0.074	0.494	nsd	nsd
			Mean weight per kernel (mg)						
3.3	32.8	30.6	33.5	32.5	30.3	37.7	34.4	31.2	34.6
18.7	40.6		36.4	34.9	31.7	46.7	45.1	40.7	31.7
25.8	33.9		26.6	31.3	27.2	31.6	31.7		
Prob.	0.034		0.011	0.597	0.672	0.003	0.019	nsd	nsd

† $\bar{\bar{\kappa}}_{sw}$ = Time- and depth-averaged electrical conductivity of the soil water for period from 20 Jan. to 9 May 1989 and 17 Jan. to 9 May 1990.

‡ Missing data indicate that data were excluded from the analysis because fewer than 3 culms of that specific tiller were produced by the 30 plants sampled.

§ Prob. = Probability that a significant F ratio would occur by chance.

¶ nsd = Not sufficient data.

was there any decrease in the number of kernels per spike, and only the decrease for T1 and T2 on Anza and the MS on Yecora Rojo was significant.

Moderate salinity stress also increased the number of kernels per spikelet on the MS but the data were too variable to confirm a similar effect on most tiller spikes.

The mean weight per kernel was not significantly affected by salinity in 1989 but a quadratic effect was observed for the MS and T1 spikes in 1990. At $\bar{\bar{\kappa}}_{sw}$ = 18.7 dS m^{-1}, mean weight per kernel was greater than the nonsaline control values and at 25.8 dS m^{-1}, it was similar or less than the controls.

Table 5. Main stem, Tl, T2, and T3 grain and straw yield equations: regression model statistics, parameter estimates, and pairwise multivariate F-tests for Yecora Rojo.

Parameter	MS	Tl	T2	T3
		Grain yield		
Regression model statistics				
R':	0.914	0.984	0.982	0.963
MSE:	0.014	0.022	0.066	0.103
prob > F:	0.025	0.002	0.002	0.007
Parameter estimates ± standard errors				
b0:	0.190 ± 0.1246	-0.336 ± 0.1549	-0.736 ± 0.2667	-0.309 ± 0.3341
bl:	0.095 ± 0.0222	0.198 ± 0.0276	0.292 ± 0.0476	-0.015 ± 0.05%
b2:	-0.004 ± 0.0008	-0.010 ± 0.0010	-0.015 ± 0.0017	-0.004 ± 0.0022
		Straw yield		
Regression model statistics				
R^2:	0.950	0.990	0.988	0.951
MSE:	0.010	0.016	0.046	0.166
prob > F:	0.011	0.001	0.001	0.012
Parameter estimates ± standard errors				
b0:	0.070 ± 0.1066	-0.389 ± 0.1319	-0.750 ± 0.2230	-0.509 ± 0.4243
bl:	0.024 ± 0.0190	-0.128 ± 0.0235	0.221 ± 0.0398	-0.013 ± 0.0757
b2:	-0.002 ± 0.0007	-0.008 ± 0.0009	-0.014 ± 0.0015	-0.005 ± 0.0028
Pairwise multivariate F-test probability levels				
	Grain	Straw		
MS-Tl:	0.001	0.001		
MS-T2:	0.002	0.001		
MS-T3:	0.009	0.026		
Tl-T2:	0.005	0.003		
Tl-T3:	0.021	0.087		
T2-T3:	0.033	0.103		

The results indicate that as salt stress reduced the number of tillers and the number of spikelets per spike, the loss in grain yield was partially offset by the increasing number and weight of kernels on remaining culms. Possible explanations for the greater number and weight of kernels remains speculative (Grieve et al.. 1992). Islam and Sedgley (1981) found that in a water-deficient Mediterranean environment, plants surgically detillered to two culms not only produced more kernels per culm, but also outyielded freely tillering plants. This compensating effect may not always offset the loss of yield from other tillers (Jones and Kirby, 1977; Nerson, 1980; Marshall and Boyd, 1985), but it may explain why some salinity treatments appear to increase grain yields (Hassan et al., 1970; L.E. Francois et al., 1994, unpublished data).

Multivariate Regression Modeling

Regression modeling results for the grain and straw yield data of Yecora Rojo and Anza are presented in

Table 6. Main stem, Tl, T2, and T3 grain and straw yield equations: regression model statistics, parameter estimates, and pairwise multivariate F-test for Anza.

Parameter	MS	Tl	T2
		Grain yield	
Regression model statistics			
R^2:	0.925	0.992	0.993
MSE:	0.003	0.004	0.005
prob > F:	0.021	0.001	0.001
Parameter estimates ± standard errors			
b0:	0.084 ± 0.0528	-0.409 ± 0.0671	-0.49s ± 0.0749
bl:	0.057 ± 0.0094	0.113 ± 0.0120	0.122 ± 0.0134
b2:	-0.002 ± 0.0003	-0.006 ± 0.0004	-0.007 ± 0.0005
		Straw yield	
Regression model statistics			
R^2:	0.976	0.994	0.977
MSE:	0.003	0.005	0.030
prob > F:	0.004	0.001	0.004
Parameter estimates ± standard errors			
b0:	0.285 ± 0.0591	-0.192 ± 0.0749	-0.204 ± 0.1801
bl:	0.022 ± 0.0105	0.094 ± 0.0134	0.092 ± 0.0321
b2:	-0.002 ± 0.0004	-0.006 ± 0.0005	-0.007 ± 0.0012
Pairwise multivariate F-test probability levels			
	Grain	Straw	
MS-Tl:	0.001	0.002	
MS-Tt:	0.003	0.008	
Tl-T2:	0.219	0.148	

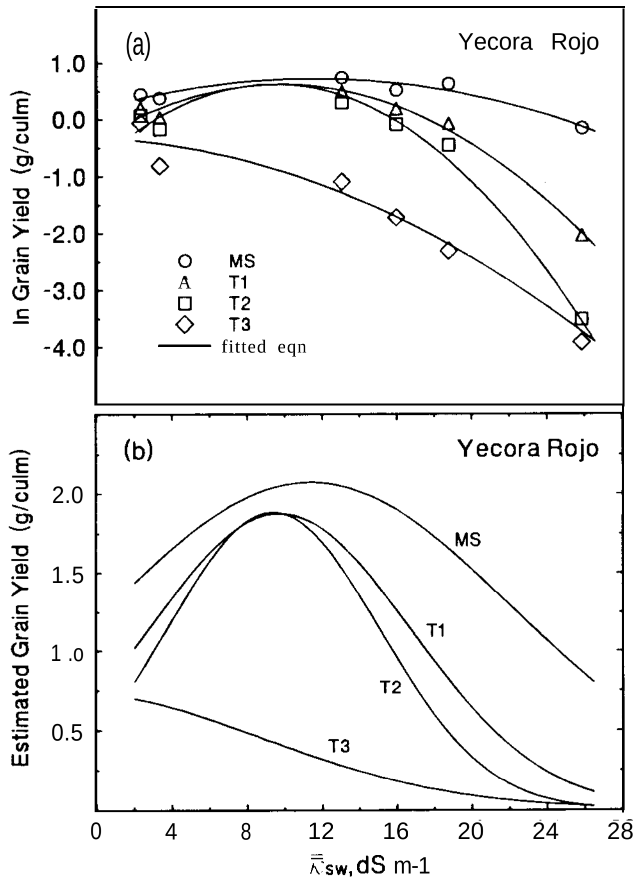

Fig. 1. Grain yields of the MS and tillers Tl, T2, and T3 of Yecora Rojo as a function of increasing soil water salinity. a) Regression curves fitted to the observed mean ln yield data. b) Estimated grain yields.

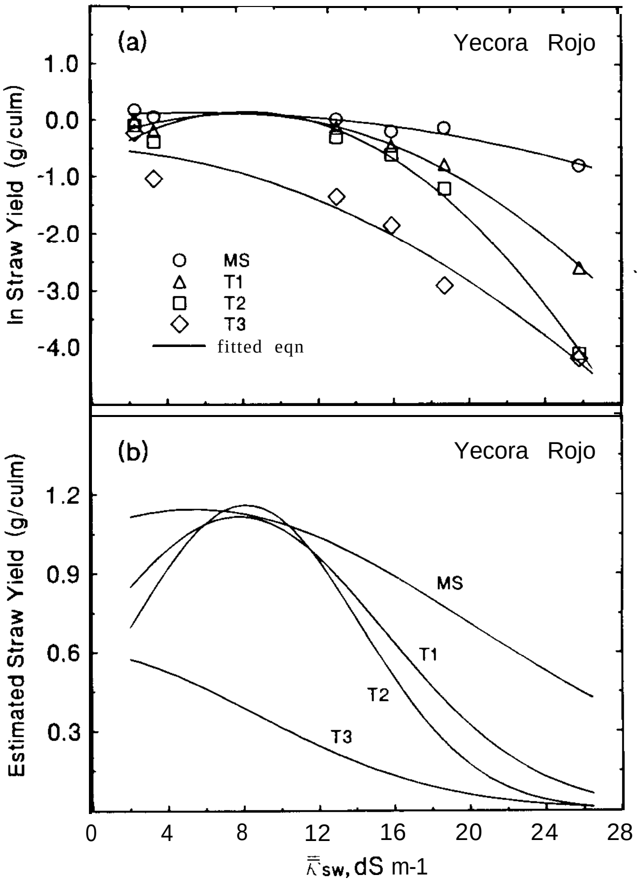

Fig. 2. Straw yields of the MS and tillers Tl, T2, and T3 of Yecora Rojo as a function of increasing soil water salinity. a) Regression curves fitted to the observed mean ln yield data. b) Estimated straw yields.

Tables 5 and 6. Univariate model statistics for the MS and each tiller, including the model R^2, MSE estimate, and overall model F-test significance level, along with the individual parameter and standard error estimates, and pairwise multivariate F-test significance levels are given. It was assumed a priori that the intercept estimates from each tiller equation would probably be different, since both grain and straw yields decrease in higher ordered tillers (Power and Alessi, 1978; Thorne and Wood, 1988). Therefore, the parameter equivalence test was defined as $(b_{1A} = b_{1B}, b_{2A} = b_{2B})$, to determine whether a systematic change in the yield/salinity response relationship occurred between Tillers A and B, independent of the change in the overall, average yield levels (Johnson and Wichern, 1988).

The results for Yecora Rojo (Table 5) confirm that ln grain and straw yields were closely related to the time- and depth-averaged salinity levels (R^2 values mostly exceeded 0.95 and all models were significant at or below $P = 0.025$). The pairwise multivariate F-test significance levels indicated that the grain yield/salinity response relationships were different for each tiller. Additionally, the MS, Tl, and T2 straw yield/salinity relationships in most cases also were unique. Figures la and 2a display the average observed ln grain and straw yield data, along with the fitted regression equations. Figures 2a and 2b display the estimated grain and straw yield as a function of salinity. These plots indicate that $\overline{K}_{sw}$ levels over about 10 dS m^{-1} caused a significant decrease in the MS, Tl, T2, and T3 grain and straw yield. These plots also indicate that grain and straw yield increased somewhat as $\overline{K}_{sw}$ increased from about 4 to 10 dS m^{-1}. However, no observed data fell within this salinity range, and hence this latter conclusion may not be entirely justified.

Natural log grain and straw yields for Anza (Table 6) were also closely related to the time- and depth-averaged salinity levels (R^2 values mostly exceeded 0.97 and all models were significant at or below $P = 0.021$). Furthermore, the pairwise multivariate F-test significance levels indicated that the grain yield/salinity response relationships for the MS were unique. However, the Tl and T2 tiller equations were indistinguishable from one another. Yields of T3 did not exhibit a curvilinear relationship with salinity; thus, it was not included in the analysis.

Summary

The loss of spike-bearing tillers accounted for most of the grain yield reduction in salt-stressed wheat. Under nonsaline conditions, the MS contributed between 25 to 35 % of the total grain yield on a land area basis, primary tillers contributed about 58 to 65 % , and secondary tillers from 4 to 18 % . As salinity increased above 8 to 10 dS m^{-1}, the contribution of the MS to total yield increased with both cultivars. The contribution of the primary tillers remained about the same at moderate increases in salinity but decreased substantially at the highest level. Secondary tillers produced little or no grain in the saline treatments. Salinity stress significantly decreased the number of spikelets per spike but the number of kernels per spike either increased or was unaffected except at the highest level of stress. Increasing salinity decreased total straw yields primarily because of fewer tillers, but dry weights of the MSs and remaining tillers were also smaller.

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