Tiller Development in Salt-Stressed Wheat

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ABSTRACT

Wheat (Triticum aestivum **L. emend. Thell.) grain yields are highly dependent upon the number of spike-bearing tillers produced per plant. Salinity, drought, and other environmental stresses can greatly affect the development and viability of tillers. We determined the effects of soil salinity on the occurrence and rate of tiller development and the incidence of tiller abortion in spring wheat cultivars, Anza and Yecora Rojo. Plants were grown in Pachappa fine sandy loam soil (mixed, thermic, Mollic Haploxeralf) in outdoor lysimeters. Three salinity treatments were imposed by irrigating with waters containing equal weights of NaCl and $CaCl_2$ (electrical conductivities of $\simeq$ 1,12, or 18 dS m^{-1}). Salinity significantly decreased the number of primary and secondary tillers in both cukivars. Soil water salinities ≥ 7.5 dS m^{-1} (mean electrical conductivity of the soil water in the rootzone during tiller development, $\bar{\kappa}_{SW}$) eliminated most of the secondary tillers and greatly reduced the number of TO, T3, and T4 tillers. However, the percentage of tillers producing spikes actually increased at $\bar{\kappa}_{SW}$ up to 8 dS m^{-1}. Higher salinities reduced the percentage of tillers with spikes, but not as much as the reduction in tillers. Tiller and spike production per plant decreased about 0.13 to 0.15 organs for each unit increase in $\bar{\kappa}_{SW}$. Of all the potential tillers these cukivars can produce, the prhnary tillers on Leaves 1 and 2 (i.e., Tl and T2) were the least susceptible to salt stress, partly because they emerged before salinity builds up during the irrigation season. Adjusting planting densities to increase the number of anticipated spike-bearing culms per unit area could help to maintain yields on salt-affected soils.**

G RAIN YIELD in wheat is highly dependent upon the number of spike-bearing tillers produced by each plant (Power and Alessi, 1978; Nerson, 1980). The number of productive tillers depends on the environmental conditions present during tiller bud initiation and subsequent development stages. Environmental stress during tiller emergence can inhibit their formation and, at later stages, can cause their abortion. Numerous studies have shown that tiller appearance, abortion, or both are affected by limited soil water (Sionit et al., 1980; Schonfeld et al., 1989; Davidson and Chevalier, 1990), high temperature (Friend, 1965; Ishag and Taha, 1974; Rawson, 1971; Thome and Wood, 1987), low temperature (Huci and Baker, 1990), nutrient deficiencies (Black and Siddoway, 1977; Power and Alessi, 1978; Masle, 1985), shading (Fischer, 1975; McMaster et al., 1987), and salt stress (Maas and Grieve, 1990; Nicolas et al., 1993).

Soil salinity decreases grain yield of wheat more when plants are stressed prior to booting than when stressed later (Maas and Poss, 1989). The yield component affected most by salt stress is the number of spikes produced per plant (Maas and Grieve, 1990). Neither of these previous studies, however, provided information about the effects of salinity on individual tiller development and abortion. Knowledge of how salt stress affects

the production of spike-bearing tillers would be invaluable in increasing the salt tolerance of wheat and improving crop management practices. For example, breeding genotypes with fewer, but less vulnerable tillers, as suggested by Jones and Kirby (1977), and increasing planting density to offset the loss of tillers (Francois et al., 1994, unpublished data), could substantially increase yields on salt-affected soils. The potential for increasing wheat yields by restricting tillering was demonstrated in field trials by Islam and Sedgley (1981). Data that relate tiller productivity to soil salinity levels are also essential for development of growth simulation models that predict response to salt stress.

This experiment was conducted to determine the occurrence and rate of tiller development and the incidence of tiller abortion of two wheat cultivars grown at three levels of soil salinity. A logistic regression model was developed that estimates the number of spike-bearing tillers as a function of soil water salinity.

MATERIALS AND **METHODS**

Experimental Conditions

The experiment was conducted in outdoor lysimeters *(3.0 by 3.0 by 1.5 m deep)* at the U.S. Salinity Laboratory, Riverside, CA. The lysimeters contained Pachappa fine sandy loam. Triple superphosphate was mixed into the top *0.25* m of soil at *73* kg P ha-' prior to planting. All irrigation water contained *0.6* mol m^{-3} $Ca(NO_3)_2$ and 1.0 mol m^{-3} KNO_3 to ensure adequate N and K fertility throughout the experiment.

Two hard red spring wheat cultivars, Anza and Yecora Rojo, were planted in level beds in the center *2.4-* by 2.4-m area of each lysimeter on 11 Jan. *1989* and 1990. Each lysimeter contained eight rows of each cultivar. Rows were spaced 0.15 m apart, with the seeds placed 40 mm apart within the row. Plant population at this planting density was 167 plants m^{-2}. Sowing depth was approximately 1.5 cm. The planted area was surrounded by a wooden barrier extending 2.5 cm above and 12.7 cm below the soil surface to minimize runoff of ponded irrigation water.

The experiment consisted of three salinity treatments replicated three times in a split-plot arrangement of a randomized complete block design, with salinity as main plots and cultivars as subplots. To facilitate germination, 25 mm of low-salinity water (electrical conductivity = 0.9 dS m^{-1}) was applied to each lysimeter after sowing. Differential salination was initiated on 30 Jan. 1989 and 23 Jan. 1990 by applying irrigation water containing equal weights of NaCl and $CaCl_2$. Seedlings for 1989 and 1990 were at the two- and one-leaf stages, respectively. The average electrical conductivities of the three saline-irrigation waters (κ_{iw}) 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-'

Abbreviations: DAS, days after sowing; κ_{iw}, electrical conductivity of irrigation water expressed in deciSiemens per meter (dS m^{-1}); κ_{sw}, electrical conductivity of soil water; $\bar{\kappa}_{SW}$, depth-averaged electrical conductivity of soil water in the rootzone; $\bar{\kappa}_{SW}$, depth- and time-averaged electrical conductivity of soil water in the rootzone during tiller development.

at the 0.25-m depth. Between 25 and 50 mm of water was applied at each irrigation. The total amount of water applied to each lysimeter between sowing and harvest was 690 mm in 1989 and 580 mm in 1990. Lysimeters were protected from rainfall by covering them with clear plastic sheeting on rainy days. A neutron probe and tensiometers were wsed to monitor soil matric potential and to guide irrigation frequency. Soil water contents were measured before and after most irrigations at depths of 25, 45, 75, and 105 cm and at two locations within each lysimeter.

Soil water salinity (κ_{sw}) was determined by extracting soil solutions with porous ceramic suction tubes buried 25, 45, 75, and 105 cm below the soil surface at two locations within each lysimeter. Soil solutions were extracted from these soil depths after most irrigations and time- and depth-averaged κ_{sw} was calculated from measurements of electrical conductivity.

Standard meteorological measurements were made with a Class I agrometeorological station adjacent to the lysimeters. Air temperatures were measured about 2 m above the soil surface. Hourly temperatures were integrated over the 24-h period and the mean daily temperatures were summed to give cumulative thermal time, expressed as $\sum °C \cdot d$. The minimum air temperatures were always above 0°C except for 2 or 3 h on Days 46 and 47 in 1990.

Plant Growth Measurements

Tiller growth and development were monitored three times each week on 10 randomly selected plants of each cultivar in each lysimeter for a total of 30 plants per treatment. The plants were chosen from the third, fourth, and fifth rows in from edge of each lysimeter to minimize border effects. Main shoots, tillers, and all leaves were identified and tagged as they emerged. Tiller designations follow the numbering system of Klepper et al. (1982). Leaf and ligule appearance dates and blade length were determined on all culms. The plants were harvested at maturity and the culms with spikes were identified and counted.

Statistical Analyses

The relationships between average number of primary tillers, spikes, or both, and the κ_{sw}-stress levels were analyzed with linear regression models. All secondary tiller and spike-production data were analyzed with non-parametric analysis of variance tests (Kruskal-Wallis tests) for significant differences between control and saline treatments. The regression relating tillers to stress level was divided by the regression relating spikes to stress level to provide a predictor of the percentage
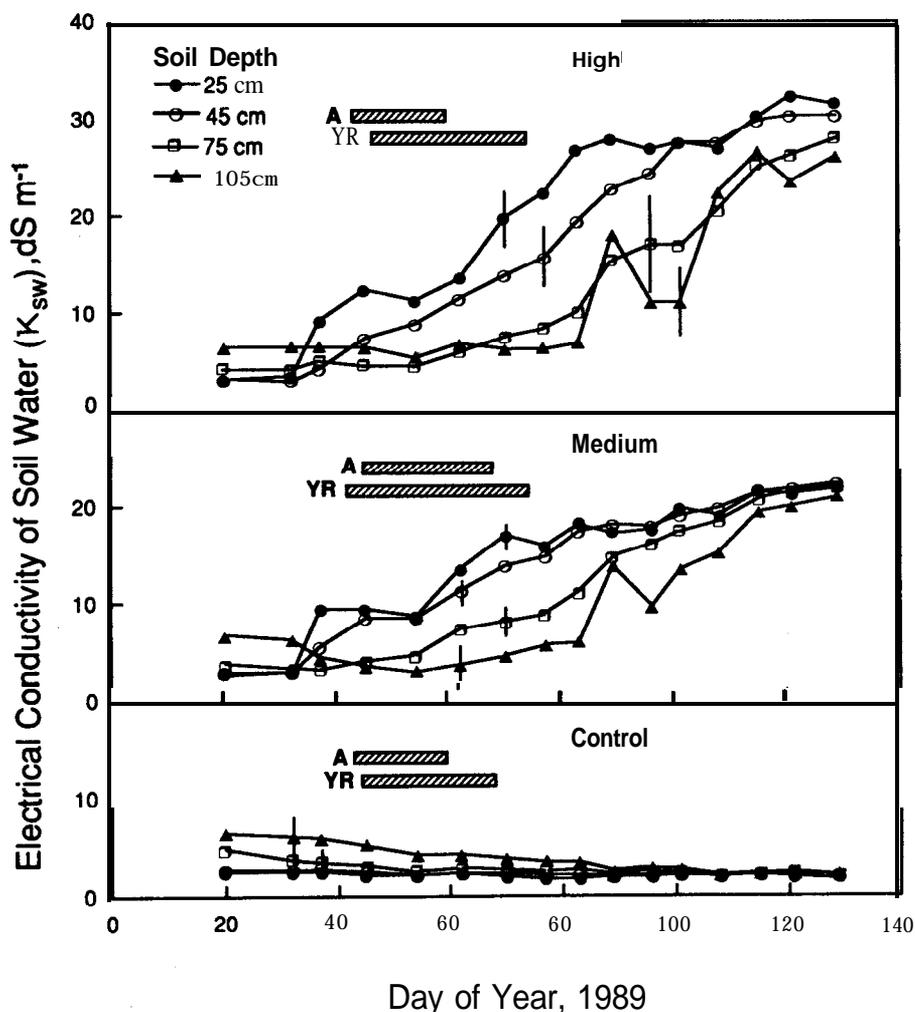

Fig. 1. Mean κ_{sw} during the 1989 growing season at 25-, 45-, 75-, and 105-cm depths for the three salinity treatments. Seeds were sown on Day 11. Horizontal bars indicate the period of tillering for Anza (A) and Yecora Rojo (YR). Each point is the mean of six separate measurements taken at two locations in each of three replicate lysimeters. Pooled standard deviation estimates, where larger than the symbols, are indicated by vertical bars at each depth.

of primary tillers that produced spikes as a function of salinity. Finally, the number of plants developing different numbers of spike-producing tillers was related to salinity stress with weighted logistic regression models. All statistical analyses were carried out with SAS (SAS, 1985). Details of the application of each of these procedures are given in the RESULTS AND DISCUSSION.

RESULTS AND DISCUSSION

Soil Salinity

Soil water salinities at **25-, 45-, 75-,** and 105-cm depths in the lysimeters during the two growing seasons are plotted for the three salinity treatments in Fig. 1 and 2. In the nonsaline control lysimeters, κ_{sw} was relatively constant at about 2.0 to 3.5 dS m^{-1} throughout the season except for initially higher conductivities at the 75- and 105-cm depths in 1989 and at the 25-cm depth in 1990. In the medium and high salinity lysimeters, κ_{sw} generally increased throughout the 1989 season and, consequently, soil salinities were higher initially in 1990 than in 1989, and they increased even more during the 1990 growing season.

Since rooting depth increased throughout the season,

plant response was correlated with κ_{sw} averaged over progressively deeper depths in the rootzone. Depth-averaged κ_{sw} is denoted herein by $\overline{\kappa}_{SW}$. Evidence of rooting depth was indicated from decreases in soil water content between irrigations as determined with a neutron probe (data not shown), In 1990, these data indicated that roots in control lysimeters began to reduce water content approximately 20 d after sowing (DAS) at the 45-cm depth, 60 DAS at 75 cm, and 90 DAS at 105 cm. Similar results were obtained in the saline treatments. The same rooting pattern was assumed for 1989 despite lower salinities because less frequent measurements of soil water contents indicated similar rooting depths. Figures 3 and 4 show the relationship between depth-averaged salinities in the rootzone (right-hand scale) as a function of thermal time between 100 and $1000°C·d$ (left-hand scale) for both years.

Because soil salinity increased with time, $\overline{\kappa}_{SW}$ may be averaged over specific growth periods to give time- and depth-averaged salinities ($\overline{\overline{\kappa}}_{SW}$) during the development of any given plant structure. For example, $\overline{\overline{\kappa}}_{SW}$ for the period from sowing ($\overline{\kappa}_{SW}$ = 3.6 dS m^{-1}) until T3 appeared ($\overline{\kappa}_{SW}$ = 10.3 dS m^{-1}) on Yecora Rojo in the medium salt treatment in 1989 was approximately 7.0 dS m^{-1}.
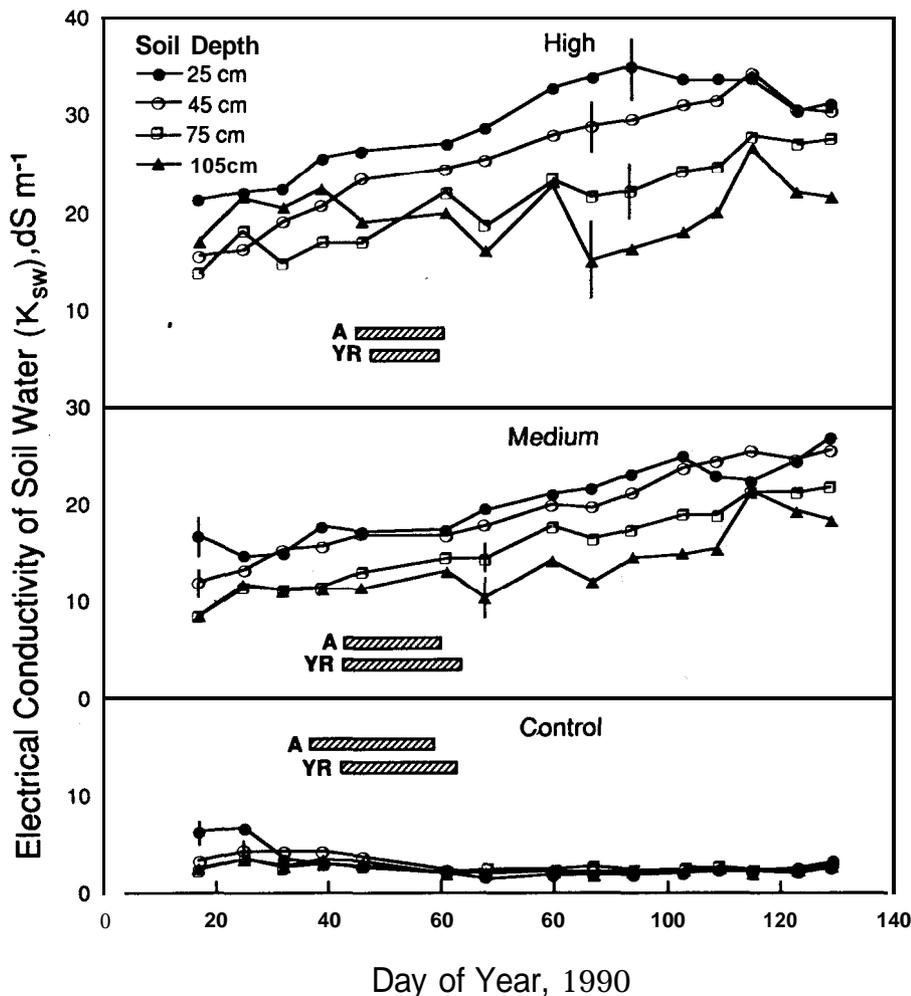

Fig. 2. Mean κ_{sw} during the 1990 growing season at 25-, 45, 75-, and 105-cm depths for the three salinity treatments. Measurements and notations same as in Fig. 1.

Fig. 3. Diagramatic representation of leaf and tiller appearances on Yecora Rojo and Anza wheat cultivars as a function of thermal time for three salinity treatments in 1989. The percentage of plants producing each tiller, and culms producing spikes, are indicated for each cultivar and treatment. Tillers that appeared on <10% of the plants are not shown. Values for the depth-averaged electrical conductivity of the soil water, $\bar{K}_{sw}$, are computed for the corresponding thermal times from depth-averaged salinities in the rootzone. (ms and T_n designate the mainstem and specific tillers).
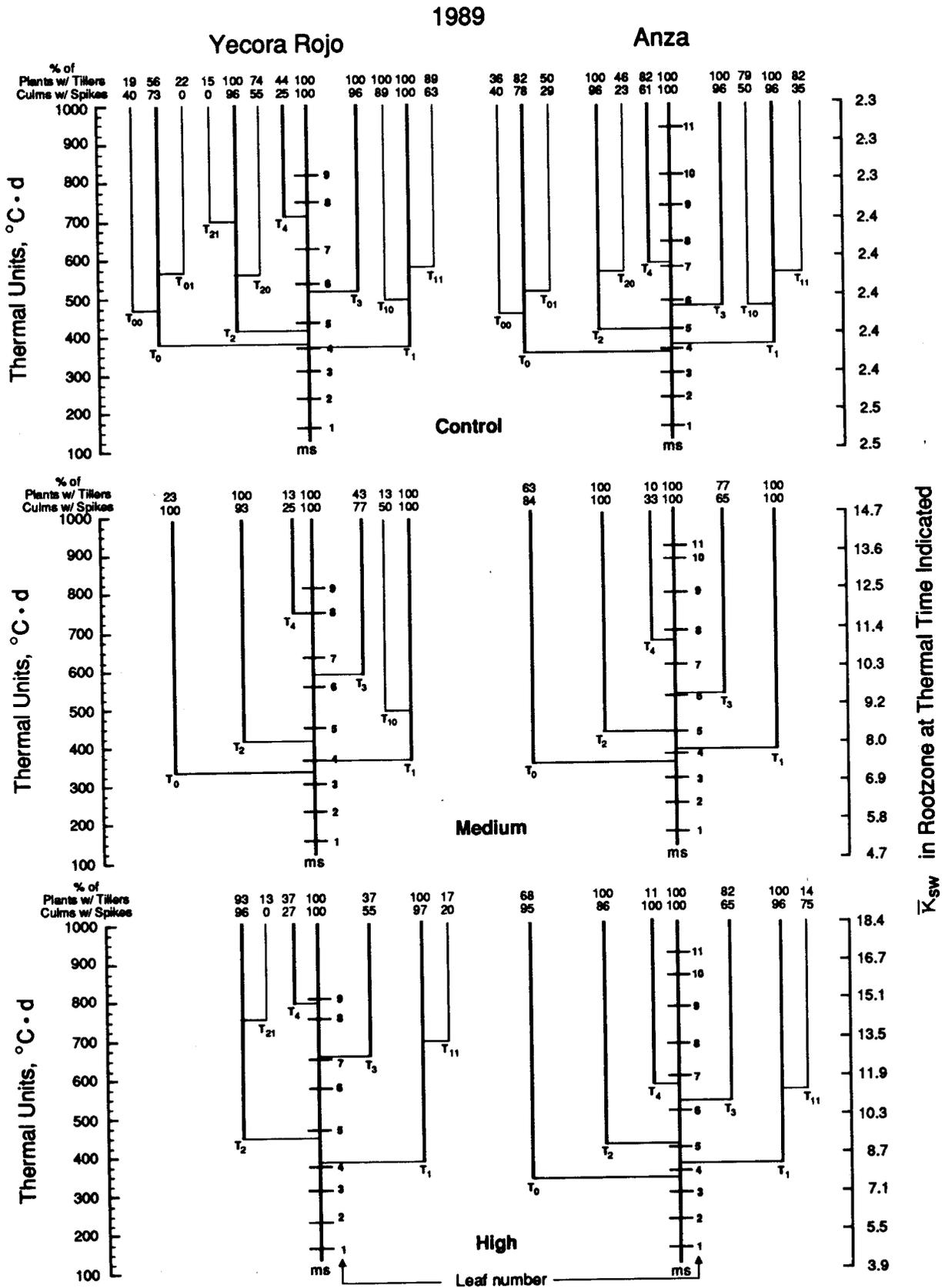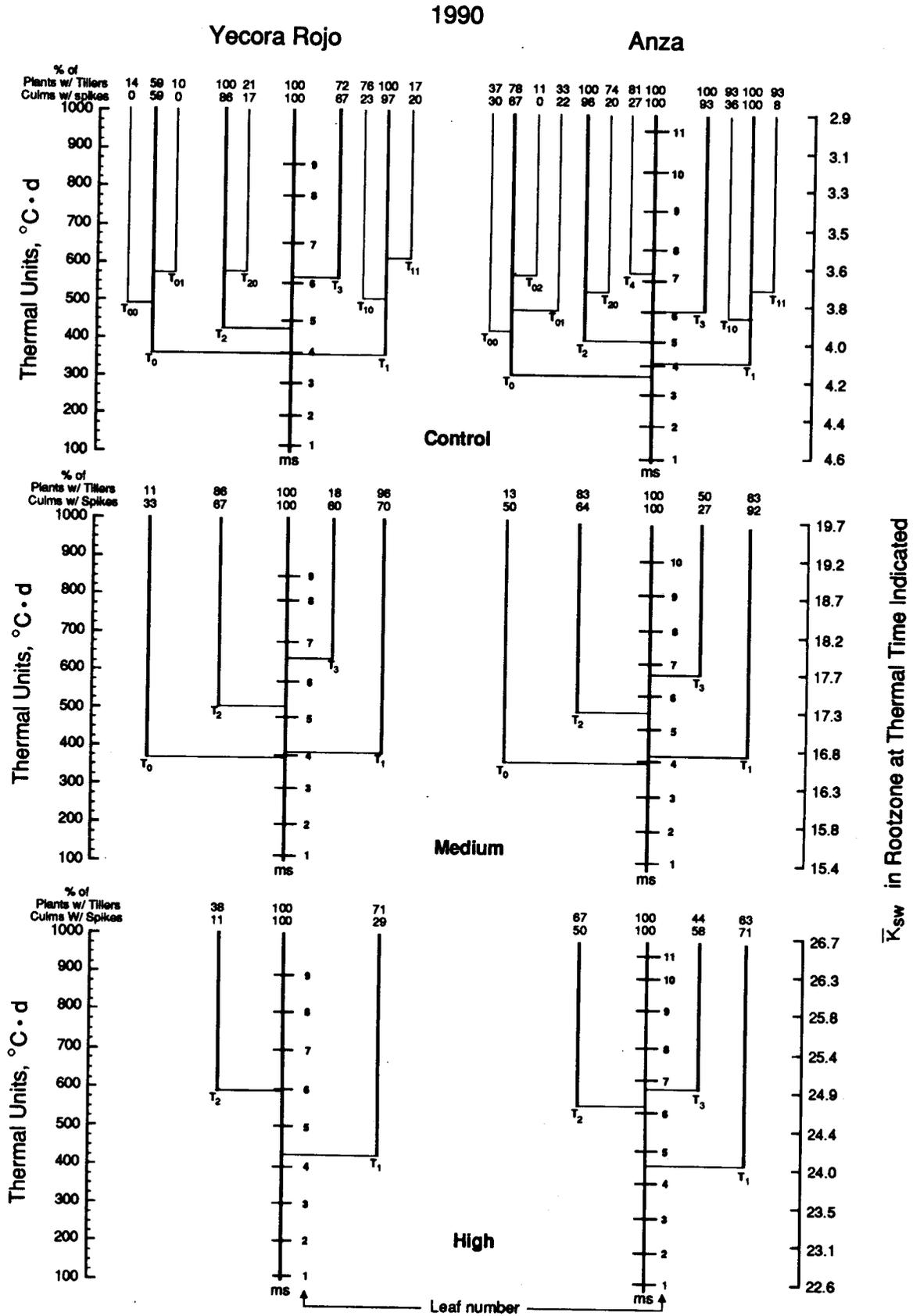
Fig. 4. Diagramatic representation of leaf and tiller appearances on Yecora Rojo and Anza wheat cultivars as a function of thermal time for three salinity treatments in 1990. Remarks same as in Fig. 3.

Tiller Development

Figures 3 and 4 provide a diagrammatic summary of all mainstem leaf and tiller appearances as a function of thermal time for both cultivars and both years for the three salinity treatments. Also shown for each tiller is the proportion of plants that produced a tiller and the proportion of culms that produced a spike. Some additional secondary and occasionally a few tertiary tillers appeared, but since they developed on fewer than 10% of the plants, they are not included on these tiller maps.

Tillering on non-stressed plants began at about the time the fourth leaf emerged on both cultivars. Tillers TO (coleoptilar) and Tl appeared nearly simultaneously each year at thermal times between 325 and 380°C·d. Yecora Rojo tillered more in 1989 than in 1990 (7.2 vs. 4.7 tillers/plant, Table 1). Anza developed about the same number of tillers both years, viz., 7.6 and 8.0 tillers/plant, respectively. Eleven different tillers were produced by the two cultivars each year with some variation among plants (Fig. 3 and 4). Except for Yecora Rojo in 1990, every plant produced tillers Tl, T2, and T3. Tillers TO and T4 appeared on 78 to 82 % of the Anza plants and on 44 to 59% of Yecora Rojo plants except that Yecora Rojo did not produce any T4 tillers in 1990. Both cultivars produced six different secondary tillers but T10 and Tll were the most consistent.

Salinity stress significantly decreased the number of primary and secondary tillers produced by both cultivars (Table 1). The decrease in tillering was related to $\bar{\kappa}_{SW}$ and since soil salinity concentrations in the medium and high salt treatments were higher in 1990 than in 1989, tillering was reduced more in 1990. In 1989, $\bar{\kappa}_{SW}$ was similar in the two salt treatments, about 8.5 dS m^{-1} during tiller development of Yecora Rojo and 7.5 dS m^{-1} for Anza. Consequently, plants produced about the same number of tillers in both treatments (half or less than that of the control plants). Salinity in this range eliminated most of the secondary tillers and greatly reduced the number of TO, T3, and T4 tillers. Tillers Tl and T2, however, appeared on nearly all of the plants. This may be due, in part, to the fact that these tillers emerged before soil salinity reached detrimental levels. It should be noted that TO, which appears at about the same time as T 1, was severely affected. Clearly, salinity, like other environmental factors, influences the development of the unpredictable coleoptilar tiller (Peterson et al., 1982).

In 1990, $\bar{\kappa}_{SW}$ increased substantially to about 17 dS m^{-1} in the medium and to 24 dS m^{-1} in the high salt treatments. At 17 dS m^{-1}, the number of tillers per plant decreased to 2.2 and 2.4 for Yecora Rojo and Anza, and at 24 dS m^{-1} the numbers decreased to 1.1 and 1.8, respectively. The increased stress eliminated T4, most TO tillers, and all secondary tillers of both cultivars (Fig. 4). The occurrence of T3 was affected less than that of TO by salt stress, but it was markedly reduced, particularly in Yecora Rojo. At the medium salinity level, tillers Tl and T2 appeared on most plants but their numbers were greatly reduced in the high salt treatment.

Tiller Abortion

Tiller abortion was also greater in 1990 than in 1989. Overall, 25% of Yecora Rojo and 33% of Anza tillers failed to produce spikes in the 1989 control treatments. Corresponding values for 1990 were 38 and 45 % . The most prolific tillers of both cultivars were Tl, T2, and T3. The 2-yr-average percentage of tillers that produced spikes was 98,9 1, and 82 % for the three primary tillers of Yecora Rojo, and 98,96, and 94% for Anza, respectively. Tiller TO aborted more often but produced spikes more often than TlO and Tl 1, the most productive secondary tillers. Tiller T4, when it appeared, was even less productive than TO. Interestingly, moderate salt stress, which greatly reduced the total number of tillers,

Table 1. Primary and secondary tiller and spike production on Yecora Rojo and Anza wheat cultivars grown at three levels of soil salinity during two growing seasons. Means and standard deviation of three replications of eight to 10 plants each.

Year	Salinity†	Yecora Rojo			Anza		
		Primary	Secondary	Total	Primary	Secondary	Total
		Mean number of tillers per plant					
89	Control	4.00 ± .28	3.19 ± .45	7.19	4.64 ± .04	3.00 ± .21	7.64
	Medium	2.80 ± .12	0.17 ± .12	2.97	3.50 ± .12	0.03 ± .03	3.53
	High	2.67 ± .41	0.37 ± .27	3.04	3.61 ± .21	0.29 ± .15	3.90
90	Control	3.38 ± .27	1.38 ± .08	4.76	4.56 ± .23	3.41 ± .37	7.97
	Medium	2.14 ± .12	0.04 ± .03	2.18	2.33 ± .23	0.03 ± .03	2.36
	High	1.04 ± .34	0.04 ± .04	1.08	1.81 ± .52	0.00 ± .00	1.81
		Mean number of spikes per plant					
89	Control	3.44 ± .19	1.93 ± .31	5.37	4.04 ± .09	1.11 ± .38	5.15
	Medium	2.53 ± .08	0.10 ± .06	2.63	3.07 ± .19	0.00 ± .00	3.07
	High	2.17 ± .30	0.03 ± .03	2.20	3.11 ± .29	0.14 ± .13	3.25
90	Control	2.69 ± .15	0.24 ± .09	2.93	3.63 ± .12	0.74 ± .28	4.37
	Medium	1.43 ± .01	0.04 ± .03	1.47	1.50 ± .15	0.00 ± .00	1.50
	High	0.26 ± .20	0.00 ± .00	0.26	1.07 ± .45	0.00 ± .00	1.07
		86.0 *Percent tillers with spikes*					
89	Control	**90.4**	60.5	74.7	87.1	37.0	67.4
	Medium		58.8	88.6	**87.7**		87.0
	High	81.3	8.1	72.4	86.1	48.3	83.3
90	Control	79.6	17.4	61.6	79.6	21.7	54.8
		66.8			64.4		63.6
	High	25.0	100.0	61.1	59.1		59.1

† Soil salinity levels during the 1989 and 1990 growing seasons are depicted in Fig. 1 and 2.

did not increase tiller abortion. The percentage of tillers that produced spikes increased in the medium salinity treatment (Table 1). In 1990 when the $\bar{\bar{\kappa}}_{SW}$ reached 24 dS m^{-1}, the percentage of tillers that produced spikes decreased sharply for Yecora Rojo but not for Anza. However, the percentage of primary tillers that produced spikes decreased in both cultivars.

Tiller and Spike Production Model

The following linear regression model was used to test for a significant relationship between the number of primary tillers, or spikes, (y) and salinity stress level ($\bar{\bar{\kappa}}_{SW}$):

$$\hat{y} = \beta_0 + \beta_1 \bar{\bar{\kappa}}_{SW} \qquad [1]$$

where $\hat{y}$ is the predicted number of primary tillers (or spikes), and β_0 and β_1 are empirically determined regression coefficients. Parameter values and regression statistics for both cultivars are shown in Table 2. The β_1 parameter values were significantly different from 0 ($t < 0.0001$) for both primary tiller and spike production within each cultivar. Tiller and spike production decreased at similar rates as salinity increased for both cultivars, ($\beta_1 \approx 0.13\text{-}0.15$ organs per unit increase in $\bar{\bar{\kappa}}_{SW}$). Since there were three replications at each treatment level it was possible to partition the sum of squares error into pure and lack of fit error estimates and test for model adequacy (Myers, 1986). In each of the four models, the F tests indicated no lack of fit, establishing that the regression equations adequately explained the primary tiller and spike production data. A plot of the fitted regression relationship for the observed Yecora Rojo data (averaged across replications) is shown in Fig. 5a.

Production of secondary tillers and spikes was nearly eliminated by the medium and high salinity levels in both growing seasons. Non-parametric Kruskal-Wallis tests were employed to confirm the statistical significance of these effects (Table 3). For these tests, the means of the medium and high salinity levels were grouped together and compared against the control means. The differences in mean secondary tiller and spike production between the control and saline treatments were found to
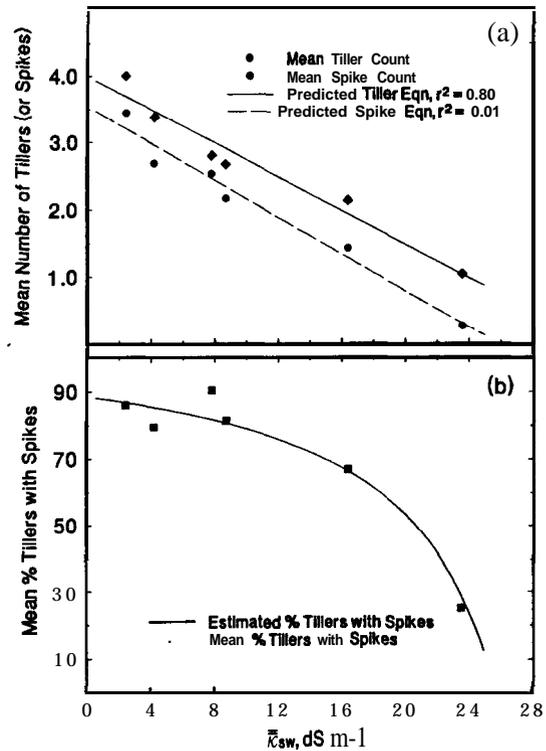

Fii. 5. Tiller and spike production as a function of $\bar{\kappa}_{SW}$ for Yecora Rojo in 1989 and 1990. (a) Mean number of primary tillers and spikes per plant. (b) Mean percent of tillers with spikes.

be significant at the 0.02 level within each cultivar over both years.

Estimates of the percentage of spike-bearing tillers at different $\bar{\kappa}_{SW}$ levels were obtained by using the values of parameters for tiller and spike number shown in Table 2. Note that if a tiller production function can be modeled as $g(t) = \alpha_0 - \alpha_1 \bar{\bar{\kappa}}_{SW}$ and a spike production function is modeled as $g(s) = \beta_0 - \beta_1 \bar{\bar{\kappa}}_{SW}$, then the percentage of spike-bearing tillers may be defined as:

$$\theta = 100[g(s)/g(t)]$$
$$= 100[\beta_0 - \beta_1 \bar{\kappa}_{SW})/(\alpha_0 - \alpha_1 \bar{\kappa}_{SW})] \qquad [2]$$

A plot of the spike-bearing tiller function for the Yecora Rojo data is shown in Fig. 5b, with the observed percentage of tillers with spikes over both years. The spike-bearing tiller functions for both Anza and Yecora

Table 2. Parameter estimates and regression model stat&tics for salinity-stress functions for primary tiller and spike production.

cultivar		β_0	β_1	R^2	MSE
		Tillers			
Anza	estimate	4.83	– 0.141	0.837	0.239
	SE	0.1%	0.016		
	t score	24.1	9.05		
Yecora Rojo	estimate	3.99	– 0.125	0.803	0.234
	SE	0.199	0.016		
	t score	20.0	8.06		
		Spikes			
Anza	estimate	4.22	– 0.147	0.878	0.185
	SE	0.172	0.014		
	t score	24.5	10.7		
Yecora Rojo	estimate	3.53	-0.137	0.909	0.113
	SE	0.139	0.011		
	t score	25.5	12.7		

Table 3. Kruskal-Wallis test on secondary tiller and spike production data; test of H_0: mean control tiller (spike) value = mean stress tiller (spike) values.

Cultivar	Year	Chi-square score	df	Prob > X^2
		Tillers		
Anza	89	5.59	1	0.018
	90	6.48	1	0.011
Yecora Rojo	89	5.44	1	0.019
	90	5.89	1	0.015
		Spikes		
Anza	89	6.40	1	0.011
	90	7.62	1	0.0%
Yecora Rojo	89	5.63	1	0.018
	90	5.84	1	0.016

Table 4. Number of plants producing exactly X spikes within each stress level in both the Anza and Yecora Rojo cultivars over both growing seasons and the corresponding Pearson and Freedman-Tukey W-Square scores.

Cultivar	Year	$\bar{\kappa}_{sw}$†	Number of spike-producing tillers, X						Total # of plants
			0	**1**	**2**	**3**	**4**	**5**	
Anza	89	dS 2.4⁻¹	0						
		7.5	0	0	0	7	13	8	28
									30
		7.1	0	0	7	15 12	8	4	28
	90	4.2	0	0	2	10	11	0	27
		16.3	3	14	8	5	0		30
		23.6	8	12	4	3	0	1	27
Yecora Rojo	89	2.4	0	0	2	12	12	0	21
		7.8	0	1	15	11	3		30
		8.1	1	3	7	3	5	1	30
	90	4.2	6	7	13	12	1	0	29
		16.4				1			28
		23.6	22	4	0	1	0	0	27

Chi-square tests

Cultivar	Year	df	Pearson score	Prob $> \chi^2$	Freedman Tukey score	Prob $> \chi^2$
Anza	89	10	22.0	0.001	26.6	0.001
	90		61.4	0.001	80.6	0.001
Yecora Rojo	89	8	36.4	0.001	40.3	0.001
	90	10	65.4	0.091	74.1	0.001

†$\bar{\kappa}_{SW}$, = depth- and time-averaged electrical conductivity of soil water in the rootzone during tiller development.

Table 5. Methodology used for changing observed plant count data (Anza data, Table 4) into logit transformed frequency scores.?

$\bar{\kappa}_{sw}$	X	n_i	z_x	C_x	δ_x	γ_x§	$n_i[\delta_x(1-\delta_x)]$ weight
dS m⁻¹							
		28			**YEAR 1989**		
2.4	1	28	0 0	28 28	1.000 1.000	n/a‡	0
2.4	2					n/a	0
2.4	3	28	7	28	1.000	n/a	0
2.4	4	28	13	21	0.750	1.099	5.250
2.4	5	28	8	8	0.2%	− 0.916	5.714
7.5	1	30	0	30	1.000	n/a	0
7.5	2	30	7	30	1.000	nla	0
7.5	3	30	15	23	0.767	1.1%	5.361
7.5	4	30	1	8	0.267	− 1.012	5.867
7.5	5	28	0	28 1	0.000 033	− 3.361	0.967
7.1	1					n/a	0
7.1	2	28	7	28	1.000	n/a	0
7.1	3	28	12	21	0.750	1.099	5.250
7.1	4	28	8	9	0.321	− 0.747	6.197
7.1	5	28	1	1	0.036	− 3.296	0.964
					YEAR 1990		
4.2	1	27				nla	0
4.2	2	27	2 0	27 27	1.000 1.000	n/a	0
4.2	3	27	10	25	0.926	2.526	1.852
4.2	4	27	11	15	0.556	0.223	6.667
4.2	5	21	4	4	0.148	− 1.749	3.407
16.3	1	30	14	27	0.900	2.197	2.700
16.3	2	30				− 0.268	7.367
16.3	3	30	5	13 5	0.430 0.167	− 1.609	4.167
16.3	4	30	0	0	0.000	n/a	0
16.3	5	30	0	0	0.000	nla	0
23.6	1	27	12	19	0.704	0.865	5.630
23.6	2	27	3	1	0.259	− 1.050	5.185
23.6	3	47	0	0 3	0.000 0.111	-2.079	2.661
23.6	4					n/a	0
23.6	5	21	0	0	0.000	nla	0

† X represents the number of spike-bearing tillers and the index value of all x-subscripted variables; z_x, the exact plant counts; C_x, transformed cumulative counts; and δ_x, frequency score and $\bar{\kappa}_{sw}$, depth- and time-averaged electrical conductivity of soil water in the rootzone during tiller development.

‡ n/a: undefined (observation not used In regression model).

§ $\gamma_x = \ln[\delta_x/(1 - \delta_x)]$.

Rojo appeared similar and illustrates that an increase in $\bar{\kappa}_{SW}$ decreased the chances of primary tillers producing spikes.

Table 4 displays the total number of Anza and Yecora Rojo plants with exactly X ($0 \leq X \leq 5$) primary spike-bearing tillers for each salinity level in both growing seasons. The variable X has only integer values. The Pearson and Freedman-Tukey Chi-Square scores (Bishop et al., 1975) shown in Table 4 confirm a dependency between z_x, the number of plants producing X spikes (see Table 5), and the $\bar{\kappa}_{SW}$ stress levels. Weighted logistic regression models (Myers, 1986) were used to model this relationship. The exact plant counts (z_x) were first transformed into cumulative counts (CX), by summing the number of plants in each salinity level that produced at least X tillers. These cumulative counts were then divided by the total number of plants within that salinity level (n_i) to produce a frequency score δ_x (6, $= C_x/n_i$, $0 \leq \delta_x \leq 1$). A logit transformation $\{\gamma_x = \ln[\delta/(1 - \delta)]\}$ was then applied to all frequency scores that were not equal to 0 or 1, and the following weighted logistic regression model was fit to the data from each cultivar:

$$\hat{\gamma}_x = \beta_0 + \beta_1 X + \beta_2 \bar{\kappa}_{SW} \qquad [3]$$

where $\hat{\gamma}_x$ represents the predicted logit transformed frequency scores, X represents the number of spike-bearing tillers and is simultaneously the index value of all x-subscripted variables and $\beta_0, \beta_1, \beta_2$ are again empirically determined regression coefficients. The remaining variables are defined as before. The weights used in the regression analysis were $n_i[\delta_x(1-\delta_x)]$. Table 5 shows how the original Anza plant count data were transformed into the dependent response variable used in Eq. [3].

Note that Eq. [3] provides the probability of observing at least X spike-bearing tillers within a specific cultivar,

Table 6. Parameter estimates and regression model statistics for primary tiller count logistic functions.

	β_0	β_1	β_2	R^2	MSE	N
Anza						
estimate	8.12	−1.74	−0.251	0.881	1.04	17
std. error	0.827	0.172	0.028			
t score	9.82	10.1	9.04			
Yecora Rojo						
estimate	7.05	−1.75	−0.253	0.849	1.50	21
std. error	0.741	0.182	0.030			
t score	9.51	9.64	8.47			

given X and $\bar{\kappa}_{SW}$. To estimate the probability of observing exactly X tillers (ζ_x), the following relationship was used:

$$\zeta_x = L^{-1}(\hat{\gamma}_x) - L^{-1}(\hat{\gamma}_{x+1}),\qquad [4]$$

where L^{-1} represents the inverse of the logistic transformation; i.e., $L^{-1}(\hat{\gamma}_x) = \exp(\hat{\gamma}_x)/(1 + \exp(\hat{\gamma}_x))$, with $L^{-1}(\gamma_0) = 1$ and $L^{-1}(\gamma_6) = 0$, respectively. The number of plants in a population of n_i plants, estimated to have exactly X tillers was then simply $n_i\zeta_x$.

Table 6 displays the parameter estimates and logistic regression model statistics for both cultivars. In both cases the t-tests for β_2 were highly significant ($t <$ O.OOOl), confirming the correlation of $\bar{\kappa}_{SW}$ and the distribution of spike-bearing tillers within both cultivars. The final predicted number of plants having exactly X tillers for the different combinations of salinity levels and years are shown in Table 7 for both cultivars. The agreement between the observed and predicted cell counts was generally good. Overall model adequacy for Anza was confirmed by the new Chi-square test statistics (which were recomputed to measure the discrepancy between the observed and predicted counts). These test statistics detected a mild amount of model inadequacy for Yecora Rojo. Nonetheless, the improvement over the simple independence model was still considerable. Figure 6 shows the predicted count distribution of spike-bearing
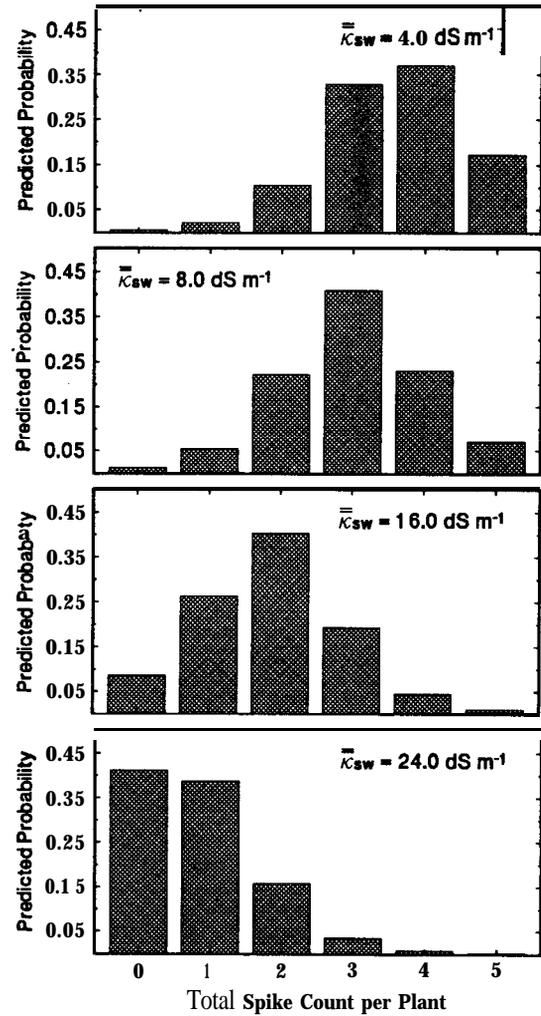

Fig. 6. Predicted frequencies of the total number of primary Anza spikes for selected $\bar{\kappa}_{SW}$ levels.

Table 7. Predicted number of plants producing exactly X spikes within each stress level in both the Anza and Yecora Rojo cultivars across both growing seasons.

Cultivar	Year	$\bar{\kappa}_{sw}$†	X: Predicted number of spike producing tillers						Total no. of plants
			0	1	2	3	4	5	
		dS m⁻¹							
Anza	89	2.4	0.09	0.40	2.05	7.58	11.2	6.65	28
		7.5	0.33	1.45	6.14	12.2	7.49	2.39	30
		7.1	0.28	1.23	5.34	11.3	7.41	2.44	28
	90	4.2	0.13	0.59	2.93	9.05	9.83	4.46	27
		16.3	2.76	8.20	12:o	5.49	1.25	0.28	30
		23.6	10.5	10.6	4.61	1.03	0.19	0.04	27
Yecora Rojo	89	2.4	0.25	1.12	4.98	10.9	7.34	2.40	27
		7.8	1.05	4.13	11.2	9.84	3.04	0.73	30
		8.7	1.30	4.93	11.8	8.86	2.50	0.58	30
	90	4.2	0.41	1.83	7.22	11.9	5.95	1.69	29
		16.4	6.77	11.4	7.45	1.96	0.37	0 .08	28
		23.6	17.9	6.90	1.77	0.33	0.06	0 .01	27

		Chi-square (goodness of fit) tests				
Cultivar	df	Pearson score	Prob > χ^2	Freedman-Tukey score	Prob > χ^2	
Anza (89-90)	27	22.7	0.702	24.7	0.591	
Yecora Rojo (89-90)	27	39.1	0.062	41.4	0.038	

† $\bar{\kappa}_{sw}$ is the depth- and time-averaged electrical conductivity of soil water in the rootzone during tiller devebpment.

tillers on Anza for various hypothetical $\bar{\bar{\kappa}}_{SW}$ levels. These results imply that the distribution of spike-bearing tillers tended to shift in a highly predictable manner as $\bar{\bar{\kappa}}_{SW}$ increased.

Similar relationships might also be expected to hold for the count distribution of secondary spike-bearing tillers. However, an insufficient number of secondary tillers were produced to verify this hypothesis.

CONCLUSION

Salinity stress significantly decreased the number of primary and secondary tillers produced by both wheat cultivars, Anza and Yecora Rojo. Mean rootzone salinity ($\bar{\bar{\kappa}}_{SW}$) equal to or greater than 7.5 dS m^{-1} eliminated most of the secondary tillers and greatly reduced the number of TO, T3, and T4 tillers. Tillers Tl and T2, however, appeared on nearly all of the plants until $\bar{\bar{\kappa}}_{SW}$ exceeded 17 dS m^{-1}. Moderate salt stress had little effect on the ability of tillers to produce spikes. At $\bar{\bar{\kappa}}_{SW}$ of 7 to 8 dS m^{-1}, the percentage of tillers with spikes actually increased. At higher salinities, where surviving tillers were mostly primary tillers, the percentage of tillers with spikes was reduced, but not as much as the reduction in tillers.

A regression analysis indicated that tiller and spike production per plant decreased about 0.13 to 0.15 organs with each unit increase in $\bar{\bar{\kappa}}_{SW}$ for both cultivars. Furthermore, salinity stress strongly influenced the distribution of spike-bearing tillers of both cultivars.

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