

Spike and Leaf Development in Salt-Stressed Wheat

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ABSTRACT

Drought or salt stress while the shoot apex is in vegetative stage can markedly affect spike development and decrease yields of cereal grains. This study was conducted to determine the effects of salinity on shoot apex differentiation, particularly spike and spikelet development, and the number of tillers per plant on two wheat species (*Triticum aestivum* L. 'Probred' and *T. turgidum* L. 'Aldura'). Plants were grown in greenhouse sand cultures that were irrigated four times daily with modified Hoagland's solution. Two saline treatments with osmotic potentials (ψ_s) of -0.45 and -0.65 MPa were imposed beginning 4 d after planting by adding NaCl and CaCl₂ (5:1 molar ratio) to the base nutrient solution and were compared to a nonsaline control treatment at -0.05 MPa. Salt stress accelerated development of the shoot apex on the mainstem and decreased the number of spikelet primordia in both species. Terminal spikelet stage occurred 12 and 18 d (≈ 280 and 420 thermal units) sooner in Aldura and Probred plants, respectively, stressed at -0.65 than at -0.05 MPa. Anthesis also occurred earlier, but tillering was delayed 3 to 4 d. Compared with -0.05 MPa, ψ_s of -0.45 and -0.65 MPa decreased seed yield 38 and 54% in Aldura and 7 and 43% in Probred, respectively. These decreases resulted from fewer spikes per plant and fewer kernels per spike. Salt stress increased the phyllochron and reduced the final number of leaves initiated on the main stem. In sum, salt stress prior to and during spikelet development significantly decreased the yield potential of individual spikes of Aldura, but not of the more tolerant Probred. Salt stress decreased the yield potential of both species most by reducing the number of tiller spikes.

DROUGHT STRESS prior to shoot apex transition from the vegetative to the reproductive growth stage in wheat can affect spikelet development and reduce the number of kernels per spike, an important component of grain yield. Frank et al. (1987) demonstrated that drought stress imposed 12 d after seedling emergence (9 d before double ridge stage) shortened the spikelet development stage in hard red spring wheat and reduced the number of spikelets per spike. Their results indicate that yield potential is established at a very early plant-development stage and that drought stress prior to the double ridge stage can significantly decrease grain yield. Drought stress in their study was simulated by decreasing the osmotic potential of the root media with polyethylene glycol 6000.

Maas and Poss (1989) found that grain yields of wheat and durum were affected most by salinity when plants were stressed prior to boot stage. It would be informative to know whether salt and drought stress have similar effects on apex development. In the only known study of salt effects on spike development in cereals, Bastianpillai et al. (1982) reported that NaCl stress caused marked changes in the rate and extent of apex development in wheat. NaCl concentrations of 2.0 and 3.0 g/kg accelerated apex development and

reduced the final number of spikelets and seed per spike in 'Hatri', a summer wheat cultivar. However, salination with NaCl alone does not simulate a saline soil solution, and high NaCl concentrations may cause unique nutritional imbalances and plant injuries. Maas and Grieve (1987) observed that NaCl causes Ca deficiency and shoot damage in corn (*Zea mays* L.) and several small-grain species, including wheat.

This experiment was conducted to determine if salt stress affects shoot apex development of two different wheat species: Probred, a semidwarf winter wheat cultivar, and Aldura, a durum wheat cultivar. Probred is known to be more salt tolerant than Aldura under field conditions (Francois et al., 1986).

MATERIALS AND METHODS

Experiments were conducted in six sand tanks in the greenhouse at Riverside, CA. The tanks (1.2 by 0.6 by 0.5 m deep) contained washed sand having an average bulk density of 1.2 Mg/m³. At saturation, the sand had an average volumetric water content of 0.34 m³/m³. On 12 Feb. 1988, seeds of two wheat species (*T. aestivum* Probred and *T. turgidum* Aldura) were planted in two rows of each species per tank. Rows were spaced 15 cm apart with 51 seeds/row. The seedlings were later thinned to 40 plants/row. The plants were irrigated four times daily with a modified Hoagland's nutrient solution consisting of 2.5 mM Ca(NO₃)₂, 3.0 mM KNO₃, 0.17 mM KH₂PO₄, 1.5 mM MgSO₄, 50 μ M Fe as sodium ferric diethylenetriamine pentaacetate (NaFe-DTPA), 23 μ M H₃BO₃, 5 μ M MnSO₄, 0.4 μ M ZnSO₄, 0.2 μ M CuSO₄, and 0.1 μ M H₃MoO₄ added to local tap water. Phosphate concentration was reduced to avoid P toxicity (Nieman and Shannon, 1977). Each irrigation cycle continued ≈ 15 min until the sand was saturated, after which the nutrient solution drained into 565-L reservoirs for recycling in the next irrigation. Water lost by evapotranspiration was replenished each day to maintain constant osmotic potentials (ψ_s) in the solutions. The solution pH was maintained between 5.5 and 6.0 by adding H₂SO₄ as required. Two salinity treatments, with $\psi_s = -0.45$ and -0.65 MPa, were imposed by adding NaCl and CaCl₂ (5:1 molar ratio, to simulate saline soil solutions) to the nutrient solutions. The ψ_s was decreased at the rate of 0.20 MPa/d beginning on Day 4. The base nutrient solution served as the -0.05 MPa control. Treatments were replicated twice.

Daytime air temperatures ranged from 20 to 33 °C (mean = 26 °C); nighttime from 17 to 23 °C (mean = 20 °C). Relative humidity ranged from 92 to 43%, with a mean of 60% during the day and 76% during the night. The phenological development of the plants from seedling emergence to maturity was rated with the Zadoks-Chang-Konzak (1974) growth-stage scale. Leaf development was rated by using the Haun (1973) scale in combination with the Zadoks-Chang-Konzak scale.

Three weeks after planting and for 8 wk thereafter, six seedlings from each treatment were randomly sampled at 2- to 3-d intervals. Main shoot apices and developing spikes were dissected and examined under a stereoscopic microscope and their development was documented by photographs.

Because salinity affected the rate of maturation, plants within each treatment were harvested as they matured. Main spikes were sampled to determine the length of spike, num-

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ber of spikelets, number of kernels per spike and per spikelet, dry weight of seed per spike, and kernel weight. Tiller spikes were sampled separately to determine the number of spikes, number of kernels per spike, dry weight of seed per spike, kernel weight, and total seed yield per plant.

Daily thermal units (Tu) were calculated from daily maximum (T_{max}) and minimum (T_{min}) air temperatures above a base temperature (T_b) following Baker et al. (1986): $Tu = [(T_{max} + T_{min})/2] - T_b$ where $T_b = 0^\circ\text{C}$. If $T_{max} > 30^\circ\text{C}$, then $T_{max} = 30^\circ\text{C}$.

The sum of Tu provided cumulative thermal units (ΣTu), expressed in degree Celsius days ($^\circ\text{C days}$). Yield data were analyzed statistically according to standard analysis of variance procedures (SAS, 1985). Logistic regression analysis (Weisberg, 1985) was used to test for differences in kernel distribution on the spike.

RESULTS

Shoot Development

Salt stress accelerated development of the mainstem spike of both Probred and Aldura; i.e., the time between double ridge and terminal spikelet stages was decreased (Table 1). The terminal spikelet stage occurred 7 and 18 d sooner in Probred plants stressed at -0.45 and -0.65 MPa, respectively, compared with the control, and 7 and 12 d sooner in Aldura. Representative spikes of 40-d-old Probred plants grown at -0.05 , -0.45 , and -0.65 MPa salinity are shown in Fig. 1. Spike development on salt-stressed plants was more advanced than that on control plants at this stage. Furthermore, salinity significantly decreased the number of spikelet primordia on the main spike (Fig. 1; Table 2).

Earlier development of the main stem spike continued to maturity. Anthesis in Aldura occurred ≈ 14 d earlier in plants stressed at -0.65 MPa than in control plants, and ≈ 9 d earlier in Probred.

Table 1. Effects of salinity on the growth and development of the mainstem of two wheat species.

Osmotic potential MPa	ΣTu † from planting to				Total leaves produced on mainstem no.
	Tillering	Terminal spikelet‡	Jointings§	Anthesis	
	°C d				
	<i>Triticum aestivum</i> 'Probred'				
-0.05	313	1269	1269	1675-1743	12-13
-0.45	336	1105	1105	1590-1675	11-12
-0.65	383	850	1038	1433-1590	10-11
	<i>Triticum turgidum</i> 'Aldura'				
-0.05	365	1083	1172	1652-1720	11-12
-0.45	437	919	1015	1500-1653	10-11
-0.65	457	804	919	1341-1412	8-9

† ΣTu = accumulated thermal units, 0°C base.

‡ Terminal spikelet differentiated in $\geq 50\%$ of individuals examined ($n = 6$).

§ Culms of $\geq 50\%$ of samples ($n = 6$) were ≥ 25 mm, measured from soil surface to base of inflorescence.

Although salinity accelerated the reproductive development of both species, it delayed tillering (Table 1). Tillers on plants stressed at -0.65 MPa appeared 3 to 4 d later than they did on the nonsaline, control plants. First tillers were observed on both cultivars at a mainstem Haun stage of 3.0 to 4.0.

Salinity also decreased the number of leaves produced by the mainstem (Table 1). Under nonsaline conditions, Probred produced 12 or 13 leaves and Aldura produced 11 or 12. For plants treated at -0.45 MPa, the number of leaves was one less for both species. At -0.65 MPa, Probred produced 10 or 11 leaves, while Aldura had 8 or 9 leaves on the main stem.

Leaf production was not affected by salt stress for the first 5 d after imposition of full-strength saline

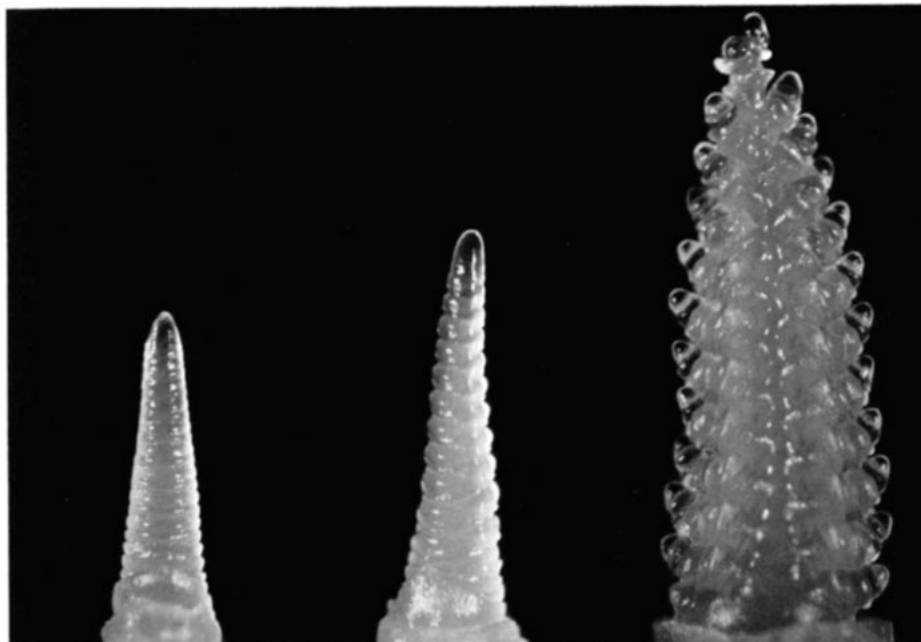


Fig. 1. Representative spikes of 40-d-old Probred plants grown at osmotic potentials of (left to right) -0.05 , -0.45 , and -0.65 MPa in the growth media. Spike lengths are 1.5, 2.0 and 3.0 mm, respectively.

Table 2. Effects of salinity on the development and yield parameters of the main spike of two wheat species.

Osmotic potential	Spike length	Spikelets per spike	Kernels per spike	Kernels per spikelet	Kernel dry wt.	Dry wt. of seed
MPa	mm	no.			mg	g/spike
<i>Triticum aestivum</i> 'Probred'						
-0.05	110	30.3	42.3	1.40	44.9	1.87
-0.45	104	27.2	40.0	1.49	46.7	1.85
-0.65	104	23.2	38.2	1.67	47.8	1.81
LSD (0.05)	1.4	0.4	1.4	0.06	0.1	NS
$P > F$ †	0.0001	0.0001	0.0049	0.0001	0.0121	0.435
<i>Triticum turgidum</i> 'Aldura'						
-0.05	71	20.5	47.7	2.32	47.0	2.24
-0.45	69	17.4	45.9	2.63	46.7	2.15
-0.65	62	14.3	39.8	2.80	45.2	1.80
LSD (0.05)	0.9	0.2	2.0	0.06	0.1	0.06
$P > F$ †	0.0001	0.0001	0.0001	0.0001	0.0004	0.0001

† Probability that a significant *F* value would occur by chance.

treatments. At this time, the seedlings were 9 d old. Subsequently, each salinity level reduced leaf production at a constant but different rate. Table 3 gives results of the linear regression for mainstem leaf number (Haun scale) vs. Tu. The slope is the leaf production rate in leaves per Tu; the reciprocal of this value is the phyllochron, or Tu required for production of successive mainstem leaves. Compared to control plants, leaf production rates of Probred and Aldura stressed at -0.65 MPa were reduced 12 and 9%, respectively.

Despite the increased phyllochron with increasing salinity, the salt-stressed plants, with fewer leaves on the mainstem, required fewer Tu before initiating the flag leaf. Fully expanded flag leaves of Aldura occurred ≈3 phyllochrons (≈300 Tu, 14 calendar d) earlier on plants treated at -0.65 MPa than on control plants.

Yield Parameters of Main Spike

Salinity significantly decreased spike length, number of spikelets per spike, and number of kernels per spike in both species (Table 2). However, the decrease in kernels per spike was partially offset by an increase in the number of fertile florets per spikelet. The average numbers of kernels per spikelet in control plants of Probred and Aldura (1.40 and 2.32) increased ≈20% when stressed at -0.65 MPa. The distribution of kernels and florets along the spike is shown in Fig. 2 for Aldura. Results of a logistic regression analysis indicated that a significant change in the number of kernels per spikelet occurred in the -0.65 MPa treat-

Table 3. Effect of salinity on leaf development of two wheat species as a function of accumulated thermal units (ΣTu , 0 °C base).

Osmotic potential	Intercept	Slope	<i>r</i> ²	Phyllochron
MPa		leaves/°C d		°C d/leaf
<i>Triticum aestivum</i> 'Probred'				
-0.05	-0.054	0.00981	0.997	102
-0.45	-0.060	0.00943	0.996	106
-0.65	-0.014	0.00859	0.996	116
<i>Triticum turgidum</i> 'Aldura'				
-0.05	-0.337	0.00883	0.997	113
-0.45	-0.333	0.00831	0.992	120
-0.65	-0.325	0.00805	0.992	124

ment. Weights of individual kernels were affected differently in the two species (Table 2). In Aldura, weight per kernel decreased with increased salt stress, whereas in Probred, it increased. The net result of these compensating effects in Probred was that ψ_s as low as -0.65 MPa had no effect on seed weight of the main spike, while it significantly decreased seed weight of Aldura.

Yield Parameters of Tiller Spikes

Salt stress affected grain yield of tillers most by reducing the number of tiller spikes (Table 4). Probred, which produced 6.0 tiller spikes under nonsaline conditions, produced only 3.1 at -0.65 MPa. The percentage reduction was even greater for Aldura, where salinity reduced the average number of spikes from 4.1 in control plants to only 1.8 in plants stressed at -0.65 MPa. Tiller spikes produced ≈30% less seed per spike than main spikes. The number of kernels per spike and the weight per kernel were smaller for tillers than for mainstem spikes. The effect of salinity on yield parameters of individual tiller spikes was similar to that of main spikes. The number of kernels per spike decreased with increasing salinity in both species, while dry weight per kernel was decreased only in Aldura. A significant reduction in dry weight of seed per tiller spike was found only for Aldura.

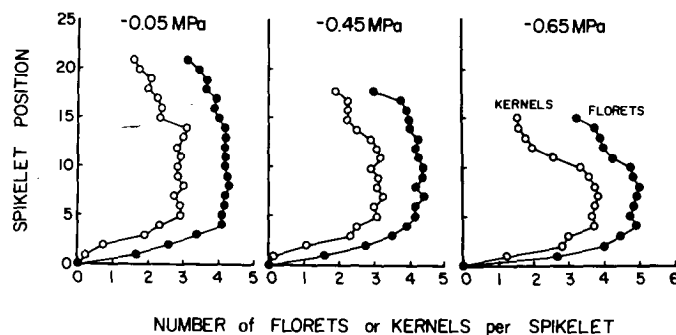


Fig. 2. Effect of salt stress on the average (*n* = 12) numbers of florets and kernels at each spikelet position on mainstem spikes of Aldura wheat grown at osmotic potentials of -0.05, -0.45, and -0.65 MPa in the growth media.

Table 4. Effects of salinity on the development and yield parameters of the tiller spikes of two wheat species.

Osmotic potential MPa	Tiller spikes per plant	Kernels per spike	Kernel dry wt. mg	Dry wt. of seed per spike g	Total dry wt. of seed of tillers per plant
<i>Triticum aestivum</i> 'Probred'					
-0.05	6.04	33.1	42.2	1.35	8.45
-0.45	5.47	32.4	44.3	1.37	7.79
-0.65	3.11	30.2	43.3	1.30	4.09
LSD (0.05)	0.28	1.2	0.1	NS	0.49
$P > F†$	0.0001	0.0228	0.0604	0.485	0.0001
<i>Triticum turgidum</i> 'Aldura'					
-0.05	4.06	34.3	45.8	1.57	6.41
-0.45	2.09	33.8	44.2	1.51	3.19
-0.65	1.81	29.6	40.4	1.22	2.20
LSD (0.05)	0.18	1.3	0.08	0.07	0.33
$P > F†$	0.0001	0.0001	0.0001	0.0001	0.0001

† Probability that a significant F value would occur by chance.

DISCUSSION

The results indicate that effects of a NaCl + CaCl₂ mixture on spikelet development of *T. aestivum* were comparable to those of NaCl alone (Bastianpillai et al., 1982). Terminal spikelet stage occurred earlier under salt stress, and the number of spikelet primordia was reduced. Treatments of apparently comparable stress in the two studies (0.2% w/w NaCl vs. NaCl + CaCl₂ at $\psi_s = -0.65$ MPa which reduced grain yield per plant by 39 and 43%, respectively) reduced the number of spikelets per spike by $\approx 24\%$. However, the effects of salt on grain yield components in the two studies did differ. Data of Bastianpillai et al. (1982) indicated that yield reductions were primarily the effect of fewer kernels per spike; whereas, we found that the greatest reduction was the result of fewer spikes per plant. It is not clear whether this difference is the result of differences in the cultivars, experimental conditions, or salts used.

The effect of salt stress on apex development also appears similar to that of water stress (drought) observed by Oosterhuis and Cartwright (1983), Frank and Bauer (1984), and Frank et al. (1987). They reported that spring wheat plants stressed during the apex vegetative stage had a shorter spikelet development stage, which resulted in fewer spikelets per spike.

Comparing yield components of Probred and Aldura plants grown in solution cultures in the greenhouse with those found when they were grown under field conditions (Francois et al., 1986) revealed an important difference in their response to salinity in the two environments. In the field, both Probred and Aldura produced less than one tiller spike per plant; whereas, in this greenhouse study, Probred and Aldura produced six and four tiller spikes per plant, respectively, under nonsaline conditions. Salt stress markedly reduced the number of spikes in the greenhouse, whereas it did not have any significant effect on the number of mature spikes produced per unit area in the field. The reason for the difference is unknown, although several environmental conditions differ including light intensity, CO₂ concentration, and border

effects. Plant population, which is known to affect tillering, was comparable in the two studies. The planting density in the greenhouse was 215 plants m⁻², while in the field, it was ≈ 267 plants m⁻²; however, the number of emerged plants in this field was similar to that in the greenhouse. Nevertheless, the number of spikes that matured was much different. This difference in plant response to salinity under the two different conditions demonstrates that effects of salt on yield parameters of plants grown in small containers in the greenhouse cannot be applied directly to field conditions.

Despite the difference in tillering, the effect of salt stress on individual spikes was similar in the two studies. Reductions in seed weight per spike for both main and tiller spikes at -0.45 and -0.65 MPa were close to those found in the field by Francois et al. (1986). The relationship $\psi_s = -0.725 \kappa_e^{1.06}$, used by Maas (1987), converts the electrical conductivity of saturated-soil extracts, κ_e , to osmotic potential in soil water at field capacity. Data of Francois et al. (1986) indicate that salt tolerance thresholds for Probred and Aldura, expressed in terms of ψ_s , are -0.71 and -0.48 MPa, respectively. In the greenhouse, grain yields per mainstem spike for Probred at -0.65 MPa and for Aldura at -0.45 MPa were 96% of the control treatment, indicating close agreement on a yield per spike basis.

CONCLUSIONS

Salt stress increased the phyllochron, reduced the final number of leaves on the mainstem, decreased the duration of the reproductive phase of apex development, and decreased the number of spikelet primordia on the main spike of both durum and bread wheats. However, seed yield on the main spike did not correlate with the number of spikelets, because salinity increased the number of kernels per spikelet. Except that salt stress decreased kernel size in Aldura but tended to increase it in Probred, the developmental characteristics of the two species responded similarly. The effects generally were greater in the more sensitive Aldura, however. The greatest effect of salinity on yield resulted from a significant reduction in spike-bearing tillers. Clearly, salt stress must be avoided prior to and during spikelet development on all tiller spikes if full yield potential is to be attained.

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