Proc. Natl. Acad. Sci. USA
Vol. 85, pp. 3805–3809, June 1988
Botany

On the evolution of the adaptation of *Lophopyrum elongatum* to growth in saline environments

(saline stress/salt tolerance/*Agropyron*/wheat)

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Communicated by Emanuel Epstein, January 7, 1988 (received for review October 8, 1987)

ABSTRACT **Most species of the genus *Lophopyrum* Löve (*Agropyron* Geartn.) grow in saline environments and are more tolerant of saline stress than the species of the related genus *Triticum* L. A 56-chromosome amphiploid from the cross *Triticum aestivum* cv. Chinese Spring × *Lophopyrum elongatum* exceeded Chinese Spring in salt tolerance, measured as plant dry-matter production and seed yield in solution cultures with 250 mM NaCl. Thus, the adaptation of *Lophopyrum* to saline environments is expressed in the wheat genetic background. None of the disomic additions or substitutions of *L. elongatum* chromosomes in Chinese Spring showed a similar level of saline stress tolerance, which indicates that the trait depends on the activity of genes on more than one chromosome. Comparisons of disomic additions, double monosomic additions from half-diallel crosses among disomic additions, and disomic substitutions of *L. elongatum* chromosomes in Chinese Spring with Chinese Spring indicated that the enhanced salt tolerance of the amphiploid is primarily controlled by genes with minor effects on three of the seven chromosomes, 3E, 4E, and 7E, interacting in a largely additive manner. The salt tolerance of *L. elongatum* additionally depends on several minor nonadditive gene interactions. It is concluded that the adaptation of *L. elongatum* to growth in saline environments evolved by accumulation of new alleles in a number of loci, each with a relatively small effect on salt tolerance. It is further inferred that most of these new alleles were codominant to the original alleles and were able to act independently in enhancing salt tolerance.**

Most species of the genus *Lophopyrum* Löve (syn. *Elytrigia* Desv. but originally classified as *Agropyron* Geartn.) occur naturally in saline environments, either in the littoral zone or in saline soils, and are tolerant of salinity (1, 2). *Lophopyrum* can be hybridized with the relatively salt-sensitive wheat *Triticum aestivum* L. ($2n = 6x = 42$, genomes AA BB DD). This provides an exciting possibility of cytogenetically partitioning the genome of a salt-tolerant species into individual chromosomes, chromosome arms, and chromosome segments in the background of the relatively salt-sensitive wheat and determining the genetic basis of the adaptation to growth under saline stress.

An octoploid amphiploid ($2n = 8x = 56$) from a cross, *T. aestivum* cv. Chinese Spring × *Lophopyrum elongatum* ($2n = 2x = 14$, genomes EE) was shown to have enhanced salt tolerance relative to the parental Chinese Spring (3), indicating that the gene system controlling the adaptation of *L. elongatum* to saline stress is expressed in the wheat genetic background. Each of the seven *L. elongatum* chromosome pairs has been added to and substituted for the *T. aestivum* homeologous chromosomes (4–7). This material was used in the present study to investigate the chromosomal control of the enhanced salt tolerance of the amphiploid with the objective of determining the genetic basis of the adaptation of *L. elongatum* to growth in saline environments.

MATERIALS AND METHODS

Genetic Stocks. The 56-chromosome amphiploid ($2n = 8x = 56$) Chinese Spring × *L. elongatum* was supplied by A. Mochizuki and B. C. Jenkins (University of Manitoba, Winnipeg, Canada). The disomic addition lines of *L. elongatum* chromosomes 1E, 2E, 4E, and 6E were those described by Dvořák (5), and 7E was described by Dvořák *et al.* (8). Disomic addition lines 3E and 5E were produced by Hart and Tuleen (7). Ditelosomic addition lines 1Ep, 2Eq, 3ES, 4EL, 5Ep, 6Ep, 7Ep, and 7Eq were produced by Dvořák (9), and ditelosomic addition lines 1Eq, 2Ep, 3EL, 5Eq, and 6Eq, by Hart and Tuleen (7). Disomic substitution lines were produced by Dvořák (5) and Dvořák and Chen (6), except for the disomic substitutions of *L. elongatum* chromosome 3E for wheat chromosomes 3A, 3B, and 3D, and of 5E or 5Eq for chromosomes 5A, 5B, and 5D, which were produced and supplied by N. A. Tuleen (Texas A&M University, College Station). To identify the disomic substitution lines, the *Lophopyrum* chromosome present is listed first and the replaced wheat chromosome is given in parentheses. For example, 1E(1A) is the substitution of *L. elongatum* chromosome 1E for wheat chromosome 1A. All stocks are in the genetic background of Chinese Spring wheat. To investigate interactions between *L. elongatum* chromosomes, double monosomic additions were produced by intercrossing the seven disomic addition lines in a half-diallel manner.

Growth Conditions and Evaluation of Salt Tolerance. Salt tolerance was investigated at salinity levels of 100 mM and 250 mM NaCl in nutrient solution. For the 100 mM level of salinity, seeds were germinated in distilled H_2O and 120 seedlings were transferred at random into each of two solution-culture tanks containing 150 liters of modified 0.5× Hoagland nutrient solution (10) with a doubled concentration of $Ca(NO_3)_2$, 100 mg of Fe-EDTA per liter, and 50 mM NaCl. After 5 days the NaCl concentration was increased to 100 mM. The pH was maintained at 5.5. Electroconductivity was measured weekly and the salinity was adjusted as needed to maintain a constant level of 100 mM NaCl. To prevent depletion of nutrients, the solution was replaced once. When the plants had senesced, they were dried at 70°C for 48 hr and the total weight and seed yield per plant were determined.

For the experiment employing the 250 mM level of salinity, seeds were germinated in distilled water and a minimum of 12 plants per genotype, 12 plants of Chinese Spring, and 12 of the amphiploid were transferred into a tank with the nutrient solution described above but containing 100 mM NaCl. Salinity was increased to 200 mM after 5 days and to 250 mM

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Abbreviations: GCA, general combining ability; SCA, specific combining ability.

after another 5 days. The pH was maintained at 5.5 and the salinity at 250 mM NaCl throughout the experiments.

Experimental Design and Analysis of Data. A design with two blocks (tanks) and unequal sample sizes was employed at the 100 mM level of salinity. Survival of plants was determined after 30 days, and a few plants that were dying were recorded but not used in the final analysis of data because they probably were dying from causes other than saline stress. After senesence the plant dry weight and seed yield were determined. Data were analyzed with analysis of variance. The amphiploid and the disomic addition lines were compared to Chinese Spring by calculating least significant differences at the 5% probability level, taking into account the unequal sample sizes.

At the 250 mM level of salinity, survival of plants of the disomic and ditelosomic addition lines and the disomic substitution lines was determined after they had been in the solution containing 250 mM NaCl for 30 days. Plants that were dead or were dying produced essentially no new dry matter in the saline culture, and a weight of 0.0 g was assigned to them. The dry weight and seed yield were determined for the remaining plants after all plants senesced in the tank. Mean dry matter per plant and mean seed yield per plant were calculated by dividing the sum of the dry weights or seed yields of a specific genotype by the total number of plants that were originally transplanted into the tank. The resulting value, therefore, reflects both the productivity and the survival of a line in the saline environment. Because a large number of lines were tested at this level of salinity, it was necessary to grow plants in many solution-culture tanks over a period of several years. So that this practive would not unduly increase experimental error, the dry weights and seed yields of Chinese Spring plants in all tanks were averaged (Table 2). Then the differences between the mean plant dry weight and seed yield of Chinese Spring in a specific tank and the overall mean of Chinese Spring in all tanks were calculated. These differences in mean plant dry weight or seed yield were added to or subtracted from the corresponding values for each genotype in the specific tank. These mean plant dry weights and mean seed yields will be called adjusted means. Because of random variation some of the adjusted means are slightly less than zero.

Data were analyzed with an analysis of variance for a completely random design with unequal sample size, using the adjusted means as observations. The number of such observations per genotype, thus, equals the number of replicated tanks. The data for each genotype were compared with those of Chinese Spring and the amphiploid by calculating least significant differences at the 5% probability level, taking into account the unequal sample sizes.

Table 1. Mean plant dry weight and seed yield of Chinese Spring, amphiploid Chinese Spring × *L. elongatum*, and disomic addition (DA) lines 1E through 7E in solution cultures containing 100 mM NaCl

Line	No. of plants	Mean plant dry weight, g	Mean seed yield, g
Chinese Spring	21	9.75	1.96
Amphiploid	22	19.48*	2.72*
DA 1E	16	5.44*	0.79*
DA 2E	18	3.31*	0.61*
DA 3E	20	6.35*	1.16*
DA 4E	19	5.20*	0.41*
DA 5E	16	1.90*	0.16*
DA 6E	18	6.97	1.34*
DA 7E	22	8.79	0.66*

*Significantly different from Chinese Spring at the 5% probability level.

A minimum of 12 F_1 double-monosomic addition progeny from the half-diallel crosses of disomic additions, along with 12 Chinese Spring and 12 amphiploid plants, were grown in solution culture tanks with 250 mM NaCl as described above.

Table 2. Mean plant dry weight and seed yield of Chinese Spring and adjusted mean plant dry weight and seed yield of the amphiploid Chinese Spring × *L. elongatum* and of the disomic addition (DA), ditelosomic addition (DTA), and disomic substitution (DS) lines in solution cultures containing 250 mM NaCl

Line	No. of replications	Mean plant dry weight, g	Mean seed yield, g
Chinese Spring	31	0.06	0.006
Amphiploid	25	1.70*	0.169*
DA 1E	2	−0.04	−0.006
DTA 1Ep	4	0.10	0.005
DTA 1Eq	2	−0.03	−0.006
DS 1E(1A)	2	−0.01	−0.004
DS 1E(1B)	2	−0.02	−0.006
DS 1E(1D)	2	−0.04	−0.006
Mean of DS	6	−0.02	−0.005
DA 2E	2	0.05	−0.004
DTA 2Ep	2	0.19	0.004
DTA 2Eq	2	0.08	−0.004
DS 2E(2A)	3	0.28	0.016
DS 2E(2B)	2	0.15	−0.003
DS 2E(2D)	5	0.37*	0.028
Mean of DS	10	0.27*	0.014
DA 3E	1	0.19	0.031
DTA 3ES	2	0.23	0.034
DTA 3EL	2	0.08	0.016
DS 3E(3A)	6	0.50*	0.072*
DS 3E(3B)	2	0.21	0.049
DS 3E(3D)	1	0.29	0.043
Mean of DS	9	0.33*	0.055*
DA 4E	2	0.34	0.045
DTA 4EL	2	0.13	0.034
DS 4E(4A)†	2	0.28	0.028
DS 4E(4D)	2	0.28	0.039
Mean of DS	4	0.28*	0.033
DA 5E	2	0.00	−0.006
DTA 5Ep	2	−0.03	−0.006
DTA 5Eq	2	−0.03	−0.006
DS 5EL(5A)	2	−0.03	−0.006
DS 5E(5B)	2	0.00	−0.006
DS 5E(5D)	2	0.10	−0.004
Mean of DS	6	0.02	0.005
DA 6E	2	0.10	0.006
DTA 6Ep	2	0.16	0.015
DTA 6Eq	2	−0.06	−0.006
DS 6E(6A)	2	0.04	0.000
DS 6E(6B)	2	0.41	0.053
DS 6E(6D)	2	0.01	0.000
Mean of DS	6	0.15	0.018
DA 7E	2	0.50*	0.019
DTA 7Eq	3	0.56*	0.043*
DTA 7Ep	2	0.25	0.015
DS 7E(7A)	2	0.68*	0.063*
DS 7E(7B)	2	0.83*	0.094*
DS 7E(7D)	2	0.48*	0.025
Mean of DS	6	0.66*	0.061*

*Significantly different from Chinese Spring at the 5% probability level.

†Chromosome designated 4A was originally placed into the B genome.

Table 3. Mean differences from Chinese Spring in adjusted mean plant dry weight and seed yield of disomic addition (DA) and disomic substitution (DS) lines and the amphiploid *L. elongatum* × Chinese Spring, grown in nutrient solution containing 250 mM NaCl

Lophopyrum chromosome	Plant dry weight, g		Seed yield, g	
	DA (rank)	DS (rank)	DA (rank)	DS (rank)
1E	−0.10 (7)	−0.08 (7)	−0.012 (7)	−0.011 (7)
2E	−0.01 (5)	0.21 (4)	−0.010 (5)	0.008 (5)
3E	0.13 (3)	0.27 (2)	0.025 (2)	0.049 (2)
4E	0.28 (2)	0.22 (3)	0.039 (1)	0.027 (3)
5E	−0.06 (6)	0.04 (6)	−0.012 (6)	−0.001 (6)
6E	0.04 (4)	0.09 (5)	0.000 (4)	0.012 (4)
7E	0.44 (1)	0.60 (1)	0.013 (3)	0.055 (1)
(Sum)	0.72	1.35	0.043	0.141
(Amphiploid)	1.64		0.163	

Each F_1 progeny was grown in a minimum of two tanks. Adjusted mean plant dry weights and seed yields were calculated following the procedure described above. The data were analyzed by analysis of variance for a completely random design, using the adjusted mean plant dry weights and adjusted mean seed yields of F_1 progenies per tank as observations. The significance of differences from Chinese Spring was determined by calculating least significant differences at the 5% probability level, taking into account the unequal sample sizes.

Estimates of the general and specific combining ability (GCA and SCA, respectively) effects of *L. elongatum* chromosomes were calculated from the half-diallel crosses of disomic addition lines according to Griffing (11). Standard deviations were calculated according to Griffing (11) by using the error mean square from the analysis of variance, from which data on Chinese Spring and the amphiploid were excluded.

RESULTS

The amphiploid produced more dry matter and yielded more seed than Chinese Spring at both levels of salinity (Tables 1 and 2), although in solution culture or pots devoid of NaCl the amphiploid was not superior to Chinese Spring (3, 12). The disomic addition lines were inferior to the amphiploid at both salinity levels. At 100 mM NaCl all were also inferior to Chinese Spring. At 100 mM NaCl the amphiploid yielded twice as much dry matter and seed as Chinese Spring, but at 250 mM NaCl it yielded about 30 times more (Tables 1 and 2). It was concluded that differences between tolerance and sensitivity are more apparent at 250 mM than at 100 mM NaCl, and 250 mM NaCl was therefore used in all of the later studies.

Disomic or ditelosomic substitution lines for 20 of the 21 wheat chromosomes were compared to Chinese Spring and the amphiploid at 250 mM NaCl. Disomic substitution line 4E(4B), originally designated 4E(4A), was not used because it naturally has a very low fertility. Like the disomic addition lines, all disomic or ditelosomic substitution lines had significantly lower adjusted plant dry weight and seed yield than the amphiploid. However, disomic substitution lines 2E(2D), 3E(3A), 7E(7A), 7E(7B), and 7E(7D) and disomic addition line 7E had significantly higher adjusted plant dry weight than Chinese Spring. Higher adjusted seed yields occurred in disomic substitution lines 3E(3A), 7E(7A), 7E(7B), and 7E(7D). Both disomic substitution lines involving chromosome 4E showed an increase in plant dry weight and seed yield relative to Chinese Spring, but the differences were not significant at the 5% probability level (Table 2).

To scrutinize further the effect of each *Lophopyrum* chromosome on the expression of salt tolerance, the adjusted mean dry weights and adjusted mean seed yields per plant of disomic substitution lines involving the same *Lophopyrum* chromosome were averaged. Comparison of these means with Chinese Spring indicated that four chromosomes (2E,

Table 4. Adjusted mean plant dry weights of F_1 double-monosomic addition lines from crosses between disomic addition lines grown in solution culture with 250 mM NaCl

Added chromosome	Mean plant dry weight, g							Mean per chromosome	Rank
	1E	2E	3E	4E	5E	6E	7E		
1E	—	−0.063	0.088	0.269	−0.063	0.027	0.261	0.086	6
2E		—	0.177	−0.063	0.333	0.113	−0.020	0.079	7
3E			—	0.512*	0.167	0.230	0.210	0.230	3
4E				—	—	0.440*	0.380	0.308	1
5E					—	0.168	0.516*	0.224	4
6E						—	0.268	0.207	5
7E							—	0.269	2
				($S^{\dagger}$ = 0.096)				($S_{\bar{x}}$ = 0.067)	

*Significantly different from Chinese Spring mean plant dry weight (0.06 g) at the 5% probability level.
†Standard deviation.

Table 5. SCA and GCA effects from data of Table 4

Added chromosome	SCA effect							GCA effect	Rank
	1E	2E	3E	4E	5E	6E	7E		
1E	—	0.014	−0.016	0.095	−0.154	−0.049	0.111	−0.133	6
2E		—	0.083	−0.229	0.250	0.045	−0.162	−0.142	7
3E			—	0.164	−0.097	−0.200	−0.113	0.040	3
4E				—	−0.136	0.120	−0.014	0.110	1
5E					—	−0.069	0.206	0.027	4
6E						—	0.028	0.012	5
7E							—	0.086	2
				($S_{SCA(s_{ij}-s_{ik})}$* = 0.122)				($S_{(g_i-g_j)}$† = 0.060)	

*Standard deviation of difference between two SCA effects of F_1 progenies having one parental disomic addition line in common.
†Standard deviation of difference between two GCA effects.

3E, 4E, and 7E) resulted in a significant increase of adjusted mean plant dry weight, and two (3E and 7E) in a significant increase of adjusted mean plant dry weight, and two (3E and 7E) in a significant increase of adjusted mean seed yield, relative to Chinese Spring (Table 2).

The comparison of ditelosomic addition lines with Chinese Spring suggested that the enhancing effect on dry-matter production and seed yield of chromosome 7E is caused by the q arm (Table 2). An attempt to associate the enhancement of plant dry weight or seed yield with specific arms was unsuccessful for chromosomes 2E, 3E, and 4E (Table 2), although data for chromosome 3E suggested that the locus or loci may be in the short (S) arm rather than the long (L) arm (Table 2).

To determine whether the observed increases in dry-matter production and seed yield per plant of disomic substitution lines under saline stress were sufficient to account for the great difference between the amphiploid and Chinese Spring, the mean plant dry weight and seed yield of Chinese Spring were subtracted from the corresponding values for each disomic addition line and disomic substitution line. The data for disomic substitutions involving the same *Lophopyrum* chromosome were averaged. The resulting values, reflecting the effects of individual *Lophopyrum* chromosomes, were summed separately for the addition and substitution lines (Table 3). The sums of the *Lophopyrum* chromosome effects calculated from the disomic addition lines accounted for less than half of the difference between Chinese Spring and the amphiploid in plant dry weight and less than one-quarter of the difference in seed yield. However, the sums of the *Lophopyrum* chromosome effects calculated from the disomic substitution lines were close to the difference between the amphiploid and Chinese Spring (Table 3), suggesting that the increases in dry matter and seed yield observed in the substitution lines were realistic and that the *Lophopyrum* chromosomes may act largely independently of each other in enhancing salt tolerance.

Additive and nonadditive interactions among the *Lophopyrum* chromosomes were investigated by determining dry-matter production and seed yield in F_1 progenies from half-diallel crosses among the seven disomic addition lines (Tables 4–7). Three progenies, 3E × 4E, 4E × 6E, and 5E × 7E had significantly higher plant dry weight and seed yield than Chinese Spring. Each of these three hybrids involved at least one chromosome that had been shown independently to increase growth and seed yield in the saline environment (Table 2). It was therefore possible that these effects were largely additive interactions among the *Lophopyrum* chromosomes. GCA and SCA effects of each chromosome were calculated to determine the importance of additive and nonadditive interactions among the *Lophopyrum* chromosomes. Since hybrid 4E × 5E was not available, the missing value was replaced with a mean of all hybrids involving disomic addition lines 4E and 5E. For plant dry weight GCA effects were highest for chromosomes 3E, 4E, and 7E; significantly lower ($P = 0.05$) for chromosomes 1E and 2E; and intermediate for chromosomes 5E and 6E. The same pattern was observed in seed yield, but the differences among the effects were not statistically significant (Tables 6 and 7). For plant dry weight, SCA effects were high for three progenies, 2E × 5E, 4E × 6E, and 5E × 7E. High plant dry weight of progeny 3E × 4E was not associated with a high SCA (Tables 4 and 5).

Because GCA reflects additive gene action, results from the diallel crosses and those obtained from disomic substitution lines are consistent in suggesting that chromosomes 3E, 4E, and 7E (further designated A) have largely additive effects on plant growth and seed yield at 250 mM NaCl. The data suggested that the other four chromosomes (further designated N) either have only minor additive effects or interact with other chromosomes in a nonadditive manner or have no effect at all. To test this, progenies 2E × 5E, 4E × 6E, and 5E × 7E, showing high SCA effects, were excluded from data in Tables 4 and 6 and the remaining progenies from N × N, N × A, and A × A crosses were averaged (Table 8). The means of

Table 6. Adjusted mean seed yields of F_1 double-monosomic addition lines from crosses between disomic addition lines grown in solution culture with 250 mM NaCl

Added chromosome	Mean seed yield, g							Mean per chromosome	Rank
	1E	2E	3E	4E	5E	6E	7E		
1E	—	−0.006	0.005	0.014	−0.006	0.009	0.019	−0.006	6
2E		—	0.016	−0.006	0.003	−0.004	−0.005	−0.000	7
3E			—	0.040*	0.013	0.019	0.018	0.019	3
4E				—	—	0.041*	0.032	0.024	1
5E					—	0.019	0.049*	−0.016	5
6E						—	0.023	0.018	4
7E							—	0.023	2
				($S^{\dagger}$ = 0.027)				($S_{\bar{x}}$ = 0.019)	

*Significantly different from Chinese Spring mean seed yield (0.0056 g) at the 5% probability level.
†Standard deviation.

Table 7. SCA and GCA effects from data of Table 6

Added chromosome	SCA effect							GCA effect	Rank
	1E	2E	3E	4E	5E	6E	7E		
1E	—	0.008	−0.004	0.000	−0.011	0.001	0.005	−0.010	6
2E		—	0.015	−0.012	0.005	−0.005	−0.012	−0.018	7
3E			—	0.011	−0.007	−0.005	−0.011	0.005	3
4E				—	−0.011	0.013	−0.002	0.010	1
5E					—	−0.000	0.023	0.001	5
6E						—	−0.005	0.004	4
7E							—	0.010	2
				($S_{SCA(s_{ij}-s_{ik})}$* = 0.035)				($S_{(g_i-g_j)}$† = 0.017)	

*Standard deviation of difference between two SCA effects in F_1 progenies having one parental addition line in common.
†Standard error of difference between two GCA effects.

Table 8. Means of adjusted mean plant dry weights and seed yields in progenies from crosses involving disomic addition lines 1E, 2E, 5E, and 6E (N) and 3E, 4E, and 7E (A)

Cross	No. of crosses	Plant weight, g	Seed yield, g
N × N	5	0.036	0.002
N × A	9	0.153	0.011*
A × A	3	0.367*	0.030*

*Significantly different from Chinese Spring mean plant dry weight (0.06 g) and mean seed yield (0.006 g) at the 5% probability level.

the N × N progenies were close to Chinese Spring in both plant dry weight and seed yield. The means of the A × A progenies were significantly higher than those of Chinese Spring and approximately twice the means of the N × A progenies, as expected if the effects of the A chromosomes were predominantly additive and the N chromosomes had little or no effect.

DISCUSSION

Four of the seven *L. elongatum* chromosomes, 2E, 3E, 4E, and 7E, when substituted for homeologous wheat chromosomes of Chinese Spring, increased dry-matter production and seed yield over that of Chinese Spring in the saline environment. An attempt to compare the addition and substitution lines with Chinese Spring in a solution culture lacking salt yielded meaningless data (not shown) because the excess of nitrogen in the nutrient solution that is needed to sustain growth under saline stress caused the plants to grow excessively vegetatively, and many were sterile. However, plant weight, seed yield, and fertility of the disomic addition and substitution lines were previously compared with Chinese Spring in pot experiments. No disomic addition line was superior to Chinese Spring (5, 6, 12). It is, therefore, reasonable to conclude that superior dry-matter production or seed yield of some substitution lines to Chinese Spring in saline cultures was caused by their superior salt tolerance.

The same chromosomes that increased salt tolerance in disomic substitution lines did not necessarily increase salt tolerance in disomic addition lines. It is very likely that this was caused not by the lack of gene expression in addition lines but by the negative effects of the aneuploidy of the disomic addition lines, which negated the effects of superior salt tolerance. As a result of an increase in the level of salt stress, some disomic addition lines that were inferior to Chinese Spring at 100 mM NaCl became superior at 250 mM NaCl. Presumably, at high salt stress the advantage of salt tolerance outweighs the reduction in general plant vigor and fertility due to aneuploidy. Additionally, some double monosomic additions from diallel crosses among disomic addition lines did show increased salt tolerance at 250 mM NaCl despite the aneuploidy. Because of the confounding effects of aneuploidy on the determination of stress tolerance, disomic substitution lines are a more valuable tool than disomic addition lines. If only disomic addition lines are available, present results suggest that a diallel cross may provide more meaningful data than comparisons of disomic addition lines with the recipient wheat line.

In agreement with results obtained from the disomic substitution lines, double monosomic additions from diallel crosses revealed additive effects by chromosomes 3E, 4E, and 7E on salt tolerance and failed to detect any by chromosomes 1E, 5E, and 6E. Chromosome 2E was an exception because it appeared to have no effect in double monosomic additions but appeared to have positive effect in disomic substitution lines. It is concluded that this chromosome may have only a minor effect or that its effect on salt tolerance may depend on specific interactions with wheat homeologous chromosomes.

Lophopyrum and *Triticum* are closely related genera and likely are results of a divergence from a common lineage in the tribe Triticeae (13). Only a small minority of species of Triticeae occupy saline environments. With the assumption that saline environments are a specialized ecological niche, it is likely that the facultative halophytism of *Lophopyrum* is derived from the nonhalophytic habit prevailing in the tribe. Data presented here show that the high salt tolerance of *Lophopyrum* relative to wheat is primarily controlled by genes on three *Lophopyrum* chromosomes that interact in a largely additive manner. The data further show that minor nonadditive interactions may occur among all chromosomes except chromosome 1E. In light of the close genetic relationship between *Lophopyrum* and *Triticum* (5, 13), it is very likely that loci controlling the high salt tolerance of *Lophopyrum* are present also in wheat but at different allelic states. While the amphiploid Chinese Spring × *L. elongatum* is more salt tolerant than Chinese Spring it is less salt tolerant than *L. elongatum* and most other *Lophopyrum* species, which tolerate the salinity of sea water or even higher levels of salinity (2). This indicates that the *Lophopyrum* alleles are incompletely dominant to the wheat alleles. These observations and the observation that some *Lophopyrum* chromosomes individually increase salt tolerance suggest that the adaptation to growth under saline stress evolved by mutations in a dominant direction in a number of loci and that the resulting alleles had the potential for increased tolerance of saline stress independently of other alleles.

We thank D. R. Knott for critical reading of the manuscript and valuable comments. This project was supported by U.S. Department of Agriculture Grant 84-CRCR-1-1367 to J.D.

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