Theor Appl Genet (1994) 87 : 872–877

Enhancement of the salt tolerance of *Triticum turgidum* L. by the *Knal* locus transferred from the *Triticum aestivum* L. chromosome 4D by homoeologous recombination

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Received: 4 January 1993 / Accepted: 28 June 1993

Abstract. Durum wheat, *Triticum turgidum* L. (2n = 4x = 28, genome formula AABB) is inferior to bread wheat, *T. aestivum* L. (2n = 6x = 42, genome formula AABBDD), in the ability to exclude Na^+ under salt strees, in the ratio of the accumulated K^+ to Na^+ in the leaves under salt stress, and in tolerance of salt stress. Previous work showed that chromosome 4D has a major effect on Na^+ and K^+ accumulation in the leaves of bread wheat. The 4D chromosome was recombined with chromosome 4B in the genetic background of durum wheat. The recombinants showed that Na^+ exclusion and enhanced K^+/Na^+ ratio in the shoots were controlled by a single locus, *Knal*, in the long arm of chromosome 4D. The recombinant families were grown in the field under non-saline conditions and two levels of salinity to determine whether *Knal* confers salt tolerance. Under salt stress, the *Knal* families had higher K^+/Na^+ ratios in the flag leaves and higher yields of grain and biomass than the *Knal*$^-$ families and the parental cultivars. *Knal* is, therefore, one of the factors responsible for the higher salt tolerance of bread wheat relative to durum wheat. The present work provides conceptual evidence that tolerance of salt stress can be transferred between species in the tribe Triticeae.

Key words: *Triticum* – Na^+ exclusion – K^+/Na^+ ratio – Salt tolerance

Communicated by G. E. Hart
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Introduction

Salt tolerance in the tribe Triticeae is associated with enhanced ability to discriminate between K^+ and Na^+ in the soil solution and to preferentially accumulate K^+ and exclude Na^+ (Storey et al. 1985; Gorham et al. 1985; Schachtman et al. 1989; Omielan et al. 1991). In the genus *Triticum*, durum wheat, *T. turgidum* L. (2n = 4x = 28), is generally less salt-tolerant than bread wheat, *T. aestivum* L. (2n = 6x = 42), and tends to accumulate more Na^+ and less K^+ than the latter when stressed with salt (Shah et al. 1987; Gorham et al. 1987). Since bread wheat differs from durum wheat by the presence of the D genome, it seemed reasonable to assume that the difference between the two species primarily resides in the D genome. Gorham et al. (1987) tested a set of disomic substitution lines in which each chromosome of the D genome of bread wheat was individually substituted for the homoeologous chromosomes of durum wheat (Joppa and Williams 1988) and showed that lines in which chromosomes 4A or 4B were replaced by bread wheat chromosome 4D discriminated better between Na^+ and K^+ under salt stress. Therefore, chromosome 4D plays a significant role in the superior K^+/Na^+ discrimination in bread wheat; its effect accounts for about 60% of the difference in this character between the two species of wheat (Dvořák and Gorham 1992).

Chromosome 4D of bread wheat was recombined with chromosome 4B in a durum background to investigate the effects of enhanced K^+/Na^+ discrimination by chromosome 4D on salt tolerance and to study the genetic and physiologic basis of K^+/Na^+ discrimination (Dvořák and Gorham 1992). Twenty-seven recombinant families were tested for their K^+/Na^+ discrimination under salt stress and 9 of them showed

the K^+/Na^+ discrimination typical of chromosome 4D. This enhanced K^+/Na^+ discrimination is controlled by a single codominant gene, *Knal* (Dvořák and Gorham 1992). Cytogenetic evidence indicated that the gene was incorporated into the long arm of chromosome 4B in all 9 lines (Dvořák and Gorham 1992). In this paper the parental lines and recombinant families with and without *Knal* are compared at different levels of salt stress to evaluate the effects of the recombinant chromosomes on agronomic characters.

Material and methods

Plants

The recombinant 4B/4D chromosomes were identified in F_1 plants that were a product of a backcross of disomic substitution line 4D(LDN4B) to the *ph1c* mutant (Dvořák and Gorham 1992). DS4D(LDN4B) has a pair of 4D chromosomes from *T. aestivum* cv 'Chinese Spring' (CS) substituted for chromosome 4B in *T. turgidum* cv 'Langdon' (LDN) (Joppa and Williams 1988). The homoeologous pairing mutant *ph1c* is in the background of the Italian cv 'Cappelli' (CP) (Giorgi and Cuozzo 1980). The F_1 plants were self-pollinated and from one to four F_2 plants homozygous for a specific recombinant chromosome were isolated and self-pollinated in the greenhouse. Each F_2-derived F_3 line was grown in two 3-m rows at Davis, California for seed increase. Lines derived from a common F_1 parent will be called a family. From one to four lines were grown per family. Because of the diversity of the parents segregation both within lines and within families was expected except for the recombinant 4B/4D chromosomes.

Experimental designs

The field trials included 10 families with *Knal* and from 15 to 18 families without *Knal* (Dvořák and Gorham 1992). In addition, cvs LDN, CP, and the parental DS4D(LDN4B) were included. Field trials were planted at the University of California, Davis and at an experimental site at El Rico near Corcoran in the San Joaquin Valley. The Davis site is free from salinity. The El Rico site was developed for salt stress research by J. G. Boswell Co.

The field trial at Davis was a randomised complete block design with three replications. Each line was present once (a plot) within a block. Plots consisted of four rows 3 m in length. The plots were harvested with a combine and grain yield per plot was determined. The experiment was analyzed with analysis of variance for a randomized complete block design. Because of the heterogeneity of lines within a family, lines were used as variables in the analysis of variance.

Table 1. Electroconductivity in ds/cm of soil solutions at depths of 16 and 32 cm at the time of planting and harvest of the control plots and those with the intermediate and high salinities at the El Rico site

Salinity	Planting		Harvest	
	16 cm	32 cm	16 cm	32 cm
Control	1.6×10^3	1.4×10^3	1.0×10^3	0.9×10^3
Intermediate	4.8×10^3	5.6×10^3	2.8×10^3	5.0×10^3
High	5.8×10^3	6.8×10^3	7.9×10^3	10.6×10^3

The field trial at the El Rico site consisted of three juxtaposed but separately irrigated fields. Three replications (plots) of each line were planted in each field. The plots consisted of six rows 3 m in length. The experiment was planted on December 6, 1991. The fields were irrigated either three times with fresh water or once with fresh water and twice with drainge water of intermediate or high salinity. The electrical conductivities of the soil solutions at the depths of 16 and 32 cm are given in Table 1.

In each plot 1-m-long strips were harvested in the middle of rows three and four. The weight of the plant material (biomass) and grain were determined. The hypothesis was that the mean grain yield or biomass of the *Knal* families would not differ from those of *Knal*$^-$ families. Because of the heterogeneity of the background among the families the family means were used as variables in the analysis of variance for a randomized complete block disign (control field) and for nested design in which the genotypes (*Knal* and *Knal*$^{-1}$) were nested within the salt level (intermediate and high salt) utilizing the GLM procedure of the SAS package of statistical programs for personal computers (SAS 1985).

Accumulation of Na^+ and K^+

Flag leaves were harvested from ten plants per plot at anthesis at the El Rico site and dried at 60 °C. Samples were ground in a Udy Cyclone Mill using a 1 mm screen. Ground samples were extracted with water (1:1000, w/v) by shaking for 2 h on a horizontal shaker at room temperature, diluted five times with water, and filtered through a 0.45 µm Millipore filter (Fisher Scientific, Santa Clara, Calif.). The concentrations of Na^+ and K^+ were determined using ion chromatography (Hafez et al. 1992). The chromatography equipment consisted of a pump (model LC-6A Shimadzu Scientific, Columbia, Md.), injector (model 7126, Rheodyne, Cotati, Calif.), electrical conductivity detector (model 430, Waters, Milford, Mass.), and a column (model CM/D, 3.9 × 150 mm, Waters, Milford, Mass.). The eluent was 0.1 m*M*, EDTA plus 3 m*M* HNO_3 filtered through a 0.45 µm filter (Fisher Scientific, Santa Clara, Calif.) at a flow rate of 1.0 ml/min at room temperature. Aqueous solutions containing 1 and 3 ppm of Na^+ and K^+ were used as calibration standards. The computation of Na^+ and K^+ concentrations in samples was based on the peak areas that were collected using an electronic data-system (model CR-3A, Shimadzu Scientific, Columbia, Md.). Variation in the concentrations of Na^+, K^+, and in the K^+/Na^+ ratio was analyzed in the same way as grain yield and biomass at the El Rico site.

Results

K^+/Na^+ discrimination

In the low salt (control) field plants contained about 10 to 20 times more K^+ than Na^+ in the flag leaves at anthesis (Table 2). Little variation occurred among the recombinant families and the parental lines with respect to the accumulated Na^+ and K^+ and the K^+/Na^+ ratio. Statistical analysis indicated that the variation was random.

Plants of all genotypes exposed to the intermediate level of salt stress had higher Na^+ and lower K^+ concentrations in the flag leaves than those grown under low salt, and had much lower K^+/Na^+ ratios (Table 2). Accumulated Na^+ levels were lower in the recombinant lines with *Knal* than in 'Cappelli' or

Table 2. Concentrations of Na^+ and K^+ and K^+/Na^+ ratios expressed as percentage of dry matter of flag leaves in 'Langdon' (LDN), 'Cappelli' (CP), disomic substitution (DS) line 4D(LDN4B), and recombinant families (Rec.) with *Kna1* (+) and without *Kna1* (−) grown under control conditions and two levels of salinity at the El Rico site

Genotype	Number of families	*Kna1*	Control			Intermediate salt			High salt		
			Na^+	K^+	K^+/Na^+	Na^+	K^+	K^+/Na^+	Na^+	K^+	K^+/Na^+
Rec.	8	+	0.17a*	2.47a	16.38a	0.60a	1.80a	3.34a	1.58a	3.23a	2.26a
			±0.05[a]	±0.32	±5.11	±0.16	±0.37	±1.37	±0.54	±0.65	±0.79
Rec.	18	−	0.26a	2.31a	11.75a	0.94b	1.39b	1.69b	2.06a	2.93a	1.47b
			±0.18	±0.82	±6.03	±0.26	±0.36	±1.27	±0.58	±0.76	±0.39
LDN	1	−	0.25a	2.35a	9.64a	0.94b	1.13b	1.20b	1.79a	3.49a	1.94b
CP	1	−	0.15a	1.58a	10.78a	0.83b	1.18b	1.42b	2.29a	3.65a	1.59a
DS4D(4B)	1	+	0.07a	1.99a	30.10a	0.48a	1.72a	3.61a	1.95a	4.56a	2.34a

* Means within columns followed by a common letter are not significantly different at the 5% probability level

[a] Standard deviation

'Langdon'. The Na^+ levels in the recombinant families with *Kna1* were lower than those in the recombinant families without *Kna1*. Families without *Kna1* did not differ from the cultivars with respect to Na^+ levels. The *Kna1* families accumulated more K^+ and had higher K^+/Na^+ ratios in the flag leaves than the cultivars or the *Kna1*$^-$ families (Table 2). The Na^+ and K^+ accumulation by DS4D(LDN4B) was similar to that of the *Kna1* families (Table 2).

At the high level of salinity the plants accumulated more of both Na^+ and K^+ in the flag leaves than the plants at the low (control) and intermediate levels of salinity (Table 2). The *Kna1* families accumulated slightly less Na^+ in the flag leaves than the *Kna1*$^-$ families and cultivars, but the differences were not statistically significant. The families with *Kna1* had, however, significantly higher K^+/Na^+ ratio than the *Kna1*$^-$ families. The flag leaf K^+ and Na^+ accumulation in the *Kna1* families was similar to those in DS4D(LDN4B).

Table 3. The grain yield in grams per plot of cvs 'Langdon' (LDN), 'Cappelli' (CP), disomic substitution (DS) of 4D for 4B, and recombinant families at a low salt environment at Davis

Family	Number of lines	Recombined arm	*Kna1*	Grain yield
3	1	L	+	903
46	1	L	+	795
56	1	L	+	831
65	2	L	+	631
83	1	L	+	816
112	2	L	+	641
133	4	L	+	889
146	2	L	+	822
173	2	L	+	779
Mean				789a*
17	2	L	−	567
23	1	L	−	698
91	2	L	−	699
109	2	L	−	1012
165	1	L	−	438
170	1	L	−	652
188	2	L	−	722
190	1	L	−	983
Mean				721a
18	1	S	−	886
21	1	S	−	853
52	1	S	−	981
68	1	S	−	829
124	1	S	−	641
151	3	S	−	826
152	2	S	−	828
Mean				835a
LDN	1	−	−	1146b
CP	1	−	−	765a
DS4D(4B)	1	−	+	665a

* Mean followed by a common letter are not statistically different from each other at the 5% probability level (LSD)

One recombinant family, no. 133, was, included in the trial although Dvořák and Gorham (1992) did not determine if it was *Kna1* or *Kna1*$^-$. The family appeared to have a high K^+/Na^+ ratio, and it was tentatively concluded that the recombinant chromosome had acquired *Kna1* from chromosome 4D.

Yield potential

The effects of the alien chromosome segments on the productivity of the recombinant families was investigated by growing the recombinant lines, the cultivars, and DS4D(LDN4B) under the condition of low salinity in a yield trial at Davis. The yield of LDN exceeded that of CP (Table 3). Since the same results were obtained in the control plots at El Rico (Table 4) we conclude that LDN is better adapted to the California environment than 'Cappelli'.

The replacement of LDN chromosome 4B by CS chromosome 4D in DS4D(LDN4B) reduced the yield potential of the disomic substitution line relative to 'Langdon' by almost 50%, indicating that this chromosome substitution has a detrimental effect on grain yield. Substitutions of only portions of chromosome 4B by homoeologous chromatin of 4D also had negative effects on yield, but on average these appeared to be less severe. The average yield of the recombinant families with *Kna1* was 789 g per plot at Davis (Table 3). The average yields of the *Kna1*$^-$ recombinant families were 721 g and 835 g for families with alien chromosome segments incorporated into the long and short arms, respectively. These mean yields were lower than the yield of LDN and were close to the yield of CP.

It was expected that the longer the alien chromosome segment the greater the likelihood that it

Table 4. The grain yields and biomass (grams per two 1-m rows) and relative grain yields and biomass expressed as percentage of the control in recombinant families, disomic substitution (DS) 4D for 4B, and cvs 'Langdon' (LDN) and 'Cappelli' (CP) under low salt conditions (control) and two levels of salinity at El Rico

Family	*Kna1*	Control		Intermediate salt (% control)		High salt (% control)	
		Yield	Biomass	Yield	Biomass	Yield	Biomass
3	+	569	2711	83	77	45	53
46	+	596	2689	85	95	34	59
56	+	533	2300	59	65	33	69
63	+	573	2422	44	77	33	70
65	+	350	2235	52	76	38	60
83	+	264	2111	91	84	63	61
112	+	514	2345	66	81	26	54
133	+	557	2592	64	75	41	63
146	+	432	2306	69	90	32	61
173	+	400	2084	80	78	30	62
Mean		479a*	2380a	69a	80a	38a	61a
17	–	432	2456	33	46	38	44
18	–	380	1856	79	88	55	70
21	–	396	2144	63	79	40	53
23	–	651	2911	64	73	23	52
52	–	678	2722	65	74	21	31
68	–	420	2267	97	90	36	71
91	–	486	2717	64	63	39	56
109	–	400	2073	62	76	36	64
124	–	564	2789	45	60	28	47
151	–	556	2775	40	64	24	36
152	–	566	2707	56	64	32	49
165[a]	–	253	1978	16	29	12	20
170	–	324	2600	90	81	45	57
188	–	588	2623	51	64	29	43
190	–	516	2300	35	52	39	59
Mean		496a	2495a	60a	71b	35a	52b
LDN	–	735b	3245b	57a	68b	15b	39c
CP	–	409a	2500a	38b	65b	7b	19d
DS4D(4B)	+	491a	2478a	34b	48c	29a	57ab

The numbers of F_4 lines per family are indicated in Table 3

* Means in columns followed by a common letter are not statistically different from each other at the 5% probability level (LSD)

[a] This line was excluded from the calculation of means and from statistical analyses because of its exceptionally poor performance

included a detrimental gene on it. Therefore, there should be a negative correlation between the lengths of the alien chromosome segments incorporated into the recombinant chromosomes (Dvořák and Gorham 1992) and the yield. The correlation was, however, poor. In the families in which homoeologous crossingovers occurred in the long arm $r = -0.29^{ns}$, and in those in which homoeologous crossingovers occurred in the short arm $r = -0.15^{ns}$. This suggests that a large portion of the variation in yield among the lines was caused by factors other than incorporation of the alien chromatin into chromosome 4B.

Salt tolerance

The effects of *Knal* on the salt tolerance of durum wheat was investigated at the El Rico site. Three levels of salinity were employed, low (control), intermediate, and high (Table 1). Grain yield and biomass at the intermediate and high salinity were expressed relative to the grain yield and biomass of the controls.

'Langdon' yielded more than CP and produced more biomass at all levels of salinity. In the field irrigated with fresh water the mean yields and biomass of the recombinant families were similar to those of CP and lower than those of LND (Table 4). Families with *Knal* did not significantly differ in yield and biomass from families without *Knal*.

In the fields irrigated with saline water, families with *Knal* produced significantly more biomass than families without *Knal* (Table 4). The grain yields of *Knal* families were also higher, but the differences were not satistically significant. At the high level of salinity both *Knal* and *Knal*$^-$ families had greater yields and produced more biomass than LDN and CP (Table 4).

Discussion

Relative to the controls, K^+ accumulation in the flag leaves declined at the intermediate salinity level in all families, but at the high salinity level K^+ accumulation increased. A similar pattern is observed in data of Omielan et al. (1991) in which the genetic background was that of *T. aestivum* cv 'Chinese Spring'. This trend potentially indicates the existence of two K^+ uptake mechanisms: a low affinity one, which is constitutive and inhibited by Na^+, and a high affinity one, which is induced by high levels of Na^+. There is evidence for two K^+ uptake mechanisms with low and high affinity for K^+, but they are both constitutive (Epstein et al. 1963; Epstein 1973).

Screening for K^+/Na^+ discrimination in the greenhouse conditions clearly separated the recombinant families into two groups without an overlap (Dvořák and Gorham 1992). Screening of the recombinant families for the K^+/Na^+ discrimination in the field was less clear and without the prior knowledge of the presence or absence of *Knal* in the families it would have been difficult to assign them unequivocally into either the *Knal* class or the *Knal*$^-$ class.

In parallel to the relatively minor enhancements of the K^+/Na^+ ratio that occurred in the *Knal* families, the *Knal* families showed only a modest increase in salt tolerance over that of the *Knal*$^-$ families. The absence of *Knal* in a disomic substitution line in which *T. aestivum* chromosome 4D was replaced by chromosome 4E from *L. elongatum* also had only minor detrimental effect on salt tolerance, although the effect on K^+/Na^+ discrimination was large in that case (Omielan et al. 1991). *Knal* accounts for only a part of the difference between *T. turgidum* and *T. aestivum* in the K^+/Na^+ discrimination (Dvořák and Gorham 1992), and it is possible that its effectiveness is modified by interaction with other genes in the D genome. Many of the *Knal* lines acquired translocations (J. Dvořák, unpublished data) and potentially other structural chromosome changes as a result of homoeologous recombination. Additionally, the observation that the 3 highest yielding families under salt stress, 3, 46, and 133, were those with the shortest 4D segments accompanying a transfer of *Knal* into chromosome 4B (Dvořák and Gorham 1992) indicates that the 4D chromatin introgressed into *T. turgidum* has detrimental effects on yield. Elimination of structural changes and unnecessary 4D chromatin from the recombinant chromosomes by homologous recombination within the introgressed segments (Sears 1974) may increase the effectiveness of *Knal* in the genetic background of durum wheat.

At the high level of salinity both *Knal* and *Knal*$^-$ families had greater yields and produced more biomass than LDN and CP. For CP this may reflect poor adaptation to California environments, which was apparent at both experimental sites. However, LDN showed good adaptation, and it is not clear why it performed disproportionally worse at the high salinity level than the *Knal*$^-$ families.

The enhancement of salt tolerance of durum wheat by a gene transferred from the D genome of bread wheat by homoeologous recombination provides conceptual evidence that salt tolerance can be manipulated by interspecific transfer of single genes in wheat in a way analogous to that used for manipulation of disease resistance (for review see Knott and Dvořák 1976). The fundamental difference between the cytogenetic manipulation of salt tolerance and that of disease resistance is in the greater influence of the environment and the background genotype on the expression of salt tolerance, consequently requiring the use of associated markers for the detection of the genes.

The use of associated markers clearly is essential for the employment of *Knal*-based salt tolerance in durum wheat breeding programs. This gene should be introgressed into durum cultivars targeted for irrigated lands in semiarid areas. Selection for *Knal* in segregating populations must rely on linked markers. The only isozyme marker that has been mapped into the synteny group of arm 4L is acid phosphatase, *Acph* (Hart and Lagston 1977). Unfortunately, none of the recombinant chromosomes with *Knal* also have the *Acph* allele from chromosome 4D (G. Y. Zhong and J. Dvořák, unpublished). Apparently, the *Acph* locus is proximal to *Knal* in the long arm, and all homoeologous crossingovers were distal to it. Therefore, the identification of a distal marker that could be used for selecting *Knal* plants in segregating populations is critical to the use of *Knal* in breeding programs.

Acknowledgments. The authors express their gratitude to Drs. E. Epstein and D. W. Rains for valuable discussions and critical reading of the manuscript. They thank to L. R. Joppa for providing the seed of DS4D(4B) and 'Langdon' and B. Giorgi for the seed of 'Cappelli'. The authors express appreciation to USAID for financial support of M. M. N. and to J. B. Boswell Co. for providing field facilities for this research and for financial assistance for the trials. Appreciation is also expressed to the California Crop Improvement Agency and to Department of Energy, grant PR03-92ER14037, for providing operating funds for this research.

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