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Chromosome location of genes controlling tolerance to salt (NaCl) and vigour in *Hordeum vulgare* and *H. chilense*

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Wheat/*Hordeum vulgare* and wheat/*H. chilense* disomic chromosome addition lines have been used to locate genes influencing tolerance to salt to specific chromosomes of the H and H^{ch} genomes of *H. vulgare* and *H. chilense* respectively. The addition lines were grown in hydroculture containing either 0 mol m^{-3}, 175 mol m^{-3} or 200 mol m^{-3} sodium chloride. Various growth and yield parameters were measured and comparisons were made both between species and between chromosomes. Plat vigour was found to have a major effect on tolerance to salt in the wheat/*H. vulgare* addition lines. Vigorous genotypes, in control conditions generally performed well in saline conditions. However, significant interactions between genotype and salt concentration were found and this indicated specific chromosomes with positive and negative effects. Genes with positive effects for salt tolerance were located to chromosomes 4H and 5H of *H. vulgare* and $1H^{ch}$, $4H^{ch}$ and $5H^{ch}$ of *H. chilense*. The genetic control of salt tolerance is discussed.

INTRODUCTION

Salinity is a major factor limiting crop yields in many parts of the world. The problem is most acute in arid and semi-arid climates where low precipitation, high surface evaporation and weathering of native rocks combine to produce naturally saline soils. Irrigation with brackish water and poor drainage often produces secondary salinity. The area of land affected by salt continues to increase and it is likely that the effects of global warming will exacerbate the situation even further.

One approach to the problem is to develop cultivars with greater tolerance to salt. Consequently, an understanding of the genetic control of tolerance to salt is important in plant breeding efforts directed towards more tolerant cultivars. This paper describes the genetic control of salt tolerance in barley, the most salt tolerant of the major cereal crops (Maas and Hoffman, 1977; Gill and Dutt, 1982, 1987). Various tests and selections have been carried out on large populations of barley and significant and useful variation is available within the species (Storey and Wyn Jones, 1978; Epstein *et al.*, 1979; Jana *et al.*, 1980; Omara *et al.*, 1987; Ye *et al.*, 1987). The main aim here is to locate to specific barley chromosomes genes which influence tolerance to salt. The approach taken has been to test the response of wheat/barley chromosome addition lines to salt stress; these lines carry the complete wheat complement of 22 chromosome pairs plus an additional pair of chromosomes from barley, either from *Hordeum vulgare* or *H. chilense*. Thus the effect of individual barley chromosomes isolated in a wheat genetic background can be assessed and compared between species.

The chromosome nomenclature in this paper is based on homoeology, the genome symbol of *H. vulgare* is H and that of *H. chilense*, H^{ch}.

MATERIALS AND METHODS

Plants

The plant material consisted of 15 genotypes; bread wheat *Triticum aestivum* cv. Chinese Spring, (CS), ($2n = 6x = 42$, AABBDD), cultivated barley *Hordeum* vulgare cv. Betzes ($2n = 2x = 14$, HH), the CS/Betzes disomic addition lines ($2n = 42 + 2$) (Islam *et al.*, 1975) for chromosomes 2H, 3H, 4H,

5H, 6H and 7H (barley chromosomes 2, 3, 4, 7, 6 and 1 respectively) the CS/Betzes translocation line 2AS.1HS (a substitution for the intact 2A chromosome, $2n = 42$, chromosome 1H = barley chromosome 5), the CS/*H. chilense* telosomic addition lines $1H^{ch}S$ ($2n = 42 + 2/t$) and $2H^{ch}\alpha$ ($2n = 42 + 2t$), and the disomic addition lines for chromosome $4H^{ch}$, $5H^{ch}$, $6H^{ch}$ and $7H^{ch}$ ($2n = 42 + 2$) (Miller *et al.*, 1982).

Procedure

Chromosome numbers of all the genotypes were checked using Feulgen-stained seedling root tip squashes (Darlington and La Cour, 1960). Seed were germinated of uniform size and weight within each genotype (seed size can influence plant vigour). Only seedlings with the correct chromosome constitution were used. An excess of seedlings for each genotype (about 25) were then vernalized in vermiculite-filled Japanese paper pots at 4°C with an 8 h photoperiod and an irradiance of 120 μmol m^{-2} s^{-1} for four weeks. Although CS carries the vernalization insensitivity gene *Vrn3* (Law *et al.*, 1976), it nevertheless has a small vernalization requirement and vernalization was carried out to reduce this effect and that of similar genes in the two sets of addition lines, thus improving the uniformity of flowering times between genotypes. After vernalization, 18 seedlings of approximately equal weight and size were selected from each genotype to reduce further variation in vigour. At this stage the seedlings weighed 0·2–0·3 g with shoots and roots both 8 cm in length; the 2H and $2H^{ch}\alpha$ lines were generally less vigorous and the 7H and $7H^{ch}$ lines were larger than average. Seedlings from each of the 15 genotypes were suspended, one genotype/tank, over 18 hydroculture tanks so that their roots were completely emersed in culture solution. The tanks were placed in a heated glasshouse (16–24°C) and irradiated with 300 μmol m^{-2} s^{-1} light. Both tank position and plant position within each tank were randomised. Half-strength culture solution (Hewitt, 1966) was used in all tanks for the initial week of hydroculture, after this salt (sodium chloride, NaCl, and calcium chloride, $CaCl_2$, in the ratio of 20:1 mol/mol) was added in daily increments (25 mol m^{-3} NaCl) to achieve final concentrations, in 6 replicate tanks, of 200 mol m^{-3}, 175 mol m^{-3} and 0 mol m^{-3} NaCl. These concentrations were chosen because they are close to the threshold tolerance of wheat. Culture solutions were replaced weekly. Plant fresh weight and survival were scored weekly. Flowering time was also scored as were mature plant characters: plant height, stem number, spikelet number, grain number and grain weight.

RESULTS

The mean scores for the various growth and yield parameters for the fifteen genotypes in the 3 environments are presented in table 1. In terms of overall performance the *H. chilense* (H^{ch}) addition lines performed better than the *H. vulgare* (H) addition lines (table 2). The effect of salt was to reduce the expression of all the characters measured. Prior to analyses, spikelet number, fresh weight and stem number were logarithmically transformed and the square root taken of grain number and grain weight in order to lessen interdependence of means and variances. The analyses of variance for these data are given in table 3 and show that there are significant differences between the salt treatments for all the characters measured. However, only in the case of plant height, grain number per plant and fresh weight were there significant differences between the 175 and 200 mol m^{-3} NaCl salt treatments. This indicates that the time period of vegetative growth was too short for the higher salt concentration to have an appreciable effect on plant performance, the main differences between the two salt treatments were detected relatively late in the life cycle after flowering.

Significant differences ($P < 0{\cdot}001$) were detected between the genotypes assessed for all the characters measured. The sums of squares for genotypes was partitioned in order to examine the contrast between the two sets of addition lines, H^{ch} and H. In all cases there were significant differences between the H^{ch} and the H groups with the H^{ch} lines performing better than the H lines (see table 2). The genetic variation accounted for by this contrast was small compared to the variation detected between individual lines. This indicates that each individual addition line must be considered when examining the effect of salt stress on plant performance.

With the exception of days to flowering there was a significant genotype X salt treatment interaction. This indicates that specific chromosomes other than those conferring vigour have significant effects on tolerance to salt. From the analysis of variance (table 3) the interaction between the two groups and between the two salt treatments are non-significant. Although formally significant for a number of characters, the interaction between

Table 1 Mean scores for Chinese Spring (CS), Betzes, the CS/*H. vulgare* (H) and CS/*H. chilense* (H^{ch}) addition lines in the three salt treatments, 0, 175 and 200 mol m^{-3} NaCl

	Spikelets/plant			Grain no./plant			Plant height			Total grain weight (g)		
Genotype	0	175	200	0	175	200	0	175	200	0	175	200
CS	32·8	13·0	11·0	90·6	27·2	22·0	61·0	47·5	41·7	32·00	3·13	3·93
1H	28·5	13·6	9·8	62·8	25·4	16·8	51·5	42·0	36·4	19·85	3·42	2·28
2H	32·4	10·2	10·1	19·0	14·3	10·3	40·4	44·4	47·0	4·98	1·40	1·45
3H	27·8	10·8	13·6	28·3	18·0	7·5	50·3	42·0	43·0	8·50	2·65	1·44
4H	30·0	11·8	8·0	40·0	22·5	17·8	58·3	44·6	40·6	16·05	3·20	2·23
5H	20·7	9·2	8·3	28·8	10·5	9·8	44·2	40·0	33·5	10·12	2·28	1·66
6H	34·3	13·3	11·8	69·5	20·0	13·7	59·3	50·0	42·8	15·48	1·93	2·40
7H	43·7	16·8	12·7	25·2	11·4	7·7	57·7	43·2	39·8	9·80	2·68	1·62
$1H^{ch}S$	32·8	14·6	17·0	58·6	9·7	15·2	42·5	29·8	29·2	16·30	2·20	2·06
$2H^{ch}\alpha$	61·8	16·4	14·0	64·7	26·6	5·8	61·0	44·6	43·2	27·44	3·32	1·28
$4H^{ch}$	33·4	14·2	9·7	58·6	26·2	13·7	57·6	50·7	45·3	18·84	4·24	2·30
$5H^{ch}$	37·5	14·4	11·7	84·7	22·8	21·2	60·3	51·8	45·7	28·52	3·56	3·17
$6H^{ch}$	86·5	11·2	11·8	182·8	15·8	15·2	62·0	53·6	51·7	55·45	0·64	2·02
$7H^{ch}$	72·2	10·6	11·3	76·0	16·5	8·2	52·8	43·2	46·8	20·02	2·70	1·58
Betzes	332·3	44·8	35·7	181·0	33·4	11·0	78·6	43·0	32·4	74·25	12·14	3·54

	Days to flowering			Stem number			Max. fresh weight after flowering/plant		
Genotype	0	175	200	0	175	200	0	175	200
CS	54·6	46·5	46·6	2·8	1·0	1·2	17·5	5·8	4·1
1H	55·2	40·8	47·3	2·5	1·2	1·0	14·1	4·6	3·0
2H	58·2	48·5	51·0	2·8	1·0	1·0	8·6	4·2	2·1
3H	55·5	46·0	46·4	2·3	1·2	1·6	10·3	4·3	3·5
4H	56·0	48·0	54·2	2·8	1·0	1·0	13·4	4·5	2·8
5H	53·2	46·4	45·8	2·0	1·2	1·0	11·0	3·3	2·7
6H	57·2	47·8	48·8	2·8	1·0	1·2	16·7	5·2	3·7
7H	54·3	46·4	44·8	4·8	1·8	1·3	19·6	6·0	4·2
$1H^{ch}S$	58·8	52·8	49·2	3·2	1·2	1·4	12·6	3·1	3·5
$2H^{ch}\alpha$	60·2	50·0	49·8	5·4	1·4	1·5	20·3	5·5	3·4
$4H^{ch}$	58·6	50·0	55·2	2·8	1·0	1·0	14·9	6·3	3·1
$5H^{ch}$	53·8	47·2	49·0	3·3	1·2	1·2	17·6	6·2	4·6
$6H^{ch}$	60·5	53·6	52·2	6·8	1·0	1·0	28·9	4·2	3·8
$7H^{ch}$	59·0	52·3	52·7	7·0	1·4	1·3	23·7	4·3	3·6
Betzes	63·3	53·0	55·3	14·9	1·7	2·3	21·0	5·2	4·7

groups and the presence and absence of salt account for a small part of the interaction sums of squares. A large part of the variation is accounted for by differences between genotypes.

In order to examine and interpret the interaction effects, an analysis of variance was conducted on the H^{ch} and H groups separately (table 4). Considering the H group, only grain number exhibits a significant ($P<0·05$) interaction between salt concentration and genotype. For the other traits performance in the absence of salt provides a good indicator of performance in the presence of salt. In this situation tolerance to increasing salt concentration is confounded with overall plant vigour. Nevertheless, it is possible to rank the genotypes in terms of their overall performance (see table 5). The 6H and 7H addition lines generally have the highest ranking for the characters with non-significant interactions. The addition of these chromosomes tend to confer positive effects for all the characters measured. Secondly, addition lines 2H, 3H and 5H tend to rank the lowest for the traits measured. There is therefore consistency in the ranking of the addition lines over traits (coefficient of concordance = 0·5577*), suggesting that individual chromosomes carry genes which influence vigour.

Table 5 also gives the rankings for the H^{ch} genotypes for the various yield data in control (0 mol m^{-3} NaCl) conditions. The H^{ch} set of genotypes are generally more vigorous than the equivalent H lines and three lines have overall rankings above euploid CS ($6H^{ch}$, $2H^{ch}\alpha$ and $7H^{ch}$). Group 6 and group 7 chromosome addition

Table 2 Mean performance data of Chinese Spring (CS), CS/*H. vulgare* (H) additions, CS/*H. chilense* (H^{ch}) additions and Betzes

	Spikelets			Grains/plant			Plant height			Total grain weight/plant		
Genotype	0	175	200	0	175	200	0	175	200	0	175	200
CS	32·8	13·0	11·0	90·6	27·2	22·0	61·0	47·5	41·7	32·0	3·13	3·93
H	31·1	12·2	10·6	39·1	17·4	11·9	52·1	43·5	39·7	12·34	2·58	1·91
H^{ch}	54·0	13·6	12·6	87·6	19·6	13·2	55·9	45·8	44·1	28·03	2·82	2·11
Betzes	332·3	44·8	35·7	181·0	33·4	11·0	78·7	43·0	32·3	74·26	12·50	3·53

	Days to flowering			Stem number			Max fresh weight/plant		
Genotype	0	175	200	0	175	200	0	275	200
CS	54·6	46·5	46·6	2·8	1·0	1·2	17·5	5·8	4·1
H	55·6	46·2	47·9	2·9	1·2	1·2	13·5	4·6	3·2
H^{ch}	58·4	50·9	51·5	4·8	1·2	1·2	20·0	4·9	3·7
Betzes	63·3	53·0	55·3	14·9	1·7	2·3	21·0	5·2	4·7

lines of both barley genomes rank highly for vigour. The 7H and $7H^{ch}$ addition lines rank particularly highly for vegetative characters such as stem number, fresh weight and spikelet number, but their rank position drops considerably for the fertility characters, grain number and grain weight. In contrast the vigour of the 6H and $6H^{ch}$ addition lines is maintained throughout the life cycle.

Considering the wheat/*H. chilense* addition lines, there are significant salt by genotype interactions for spikelet number, grain number, total grain weight and final fresh weight. In this situation performance in the absence of salt is not a good indicator of performance in the presence of salt. For these characters it is likely that there are specific genes influencing plant tolerance to salt. An examination of the interaction effects obtained from the analysis of variance offers an opportunity to rank genotypes in order of their tolerance to salt stress. Furthermore, the identification of tolerant and non-tolerant genotypes using this method is independent of the general vigour of the individual addition lines. The interaction effects for the six individual additions lines in the three environments is given graphically in fig. 1. Bar line shifts from negative to positive values with increasing salt concentration indicate chromosomes with positive effects, conversely shifts from positive to negative indicate chromosomes with negative effects on tolerance to salt. The relative magnitude of the performance data indicate that genes with major positive effects for response to saline environments are located on chromosomes $1H^{ch}S$, $4H^{ch}$ and $5H^{ch}$. Genes with negative effects are located on chromosomes $2H^{ch}\alpha$, $6H^{ch}$ and $7H^{ch}$. This approach may also be used for the H set of addition lines for the grain number data since this showed a significant interaction between salt concentration and genotype. For this character (fig. 1) addition lines 4H and 5H were found to have positive effects in the presence of salt, confirming the importance of these two chromosome groups in determining the response of barley genotypes to salt stress.

It is also important to note that the translocated substitution line 2AS.1HS (see Materials and Methods) performed relatively badly in salt stress conditions. This may be due to the loss of critical genes on 2AL rather than the addition of the 1HS genes in the genome.

DISCUSSION

The effects of plant vigour and earliness of flowering time are often confounding factors in stress tolerance research. These have been minimised in the present study so that a better understanding of the genetic controls could be obtained. Although vigour was uniform within a genotype there were considerable differences between the addition lines. For the H set of addition lines performance in the absence of salt was generally a good indicator of performance in salt stress, vigorous plants ranked well in both environments. However, in the H^{ch} set of additions vigorous genotypes in control conditions were not necessarily the most productive in saline conditions. Chromosomes carrying genes with positive and negative effects could be identified. In the one case where an

Table 3 Analyses of variance for the 15 genotypes grown in 0, 175 and 200 mol m^{-3} NaCl

Item	df	No. spikelets/ plant (log) M.S.	Grains/plant (square root) M.S.	Height M.S.	Total grain/ plant weight (log) M.S.	Days to flowering M.S.	Stem number (log) M.S.	Maximum fresh weight after flowering (log) M.S.
1. Differences between treatments	2	42·07***	456·86***	5,429·90***	147·95***	1943·80***	35·85***	56·14***
a. 0 vs. (175+200)	1	83·84***	880·92***	10,333·00***	292·23***	3813·44***	71·66***	108·33***
b. 175 vs. 200	1	0·30	32·80***	526·74***	3·65	74·15	0·04	3·96***
2. Differences between genotypes	14	3·11***	26·06***	549·75***	5·70***	153·64***	1·33***	0·91***
a. H^{ch} vs. H groups	1	3·67*	72·48***	508·18***	6·66***	717·75***	1·69***	2·12***
b. Lines within groups	13	3·06***	22·48***	552·95***	5·62***	110·25***	1·30***	0·82***
3. Genotypes × Treatments	28	0·60***	13·14***	186·73***	1·67*	18·49	0·47***	0·22*
a. (H^{ch} vs. H) × (0 vs. 175+200)	1	1·86***	93·67***	21·14	10·36***	13·13	2·68***	0·79*
b. (H^{ch} vs. H) × (175 × 200)	1	0·07	0·00	16·97	1·59	28·78	0·02	0·17
c. Between genotypes	13	0·93***	18·24***	350·36***	1·04	11·68	0·70***	0·22
d. Deviations	13	0·15	2·86	48·90	1·65	24·93	0·09	0·19
4. Replicate error	187	0·16 (38)†	2·98 (58)†	56·00 (35)†	1·06 (55)†	20·59 (42)†	0·12 (36)†	0·13 (28)†

† No. missing plants
*** $P < 0·001$.
* $P < 0·05$.

Table 4 Analyses of variance for the: (a) CS/*H. chilense* (H^{ch}) and (b) CS/*H. vulgare* (H) addition lines in the three salt treatments

Item	df	Spikelet No. M.S.	Grain No. M.S.	Height M.S.	Grain Weight M.S.	Stem No. M.S.	Fresh weight M.S.
(a)							
1. Differences between treatments	2	20·76***	261·21***	1598·89***	145·83***	19·38***	26·53***
2. Differences between H^{ch} genotypes	5	0·25	14·89*	1057·62***	2·08	0·55**	0·63**
3. Treatments × genotypes	10	0·64***	11·89***	40·86	3·45*	0·31*	0·33*
4. Replicate error	81 (9)†	0·16	4·79	59·24	1·46	0·13	0·15
(b)							
1. Difference between treatments	2	12·20***	55·10***	1555·09***	53·52***	9·32***	22·48***
2. Difference between H genotypes	6	0·76***	13·30***	237·18***	3·46***	0·57***	0·95***
3. Treatments × genotypes	12	0·13	5·16*	94·65	1·23	0·19	0·15
4. Replicate error	88 (17)†	0·16	2·56	57·01	0·83	0·11	0·13

† Number of missing values
*** $P < 0·001$.
** $P < 0·01$.
* $P < 0·05$.

Table 5 Overall ranking (1 = highest, 8 = lowest) of the H and H^{ch} genotypes compared with CS for various mean yield data on a per plant basis in control (0 mol m^{-3} NaCl) conditions

Genotype	Stem No.	Height	Maximum fresh weight	Spikelet No.	Grain No.	Total grain weight	Overall ranking
CS	2	1	2	3	1	1	1
1H	6	5	4	7	2	2	5
2H	2	7	8	4	7	8	6
3H	7	6	7	6	6	7	=7
4H	2	4	6	5	3	4	4
5H	8	8	5	8	5	5	=7
6H	2	2	3	2	1	3	2
7H	1	3	1	1	4	6	3
CS	6	2	5	6	2	2	=4
$1H^{ch}S$	5	7	7	6	7	7	7
$2H^{ch}\alpha$	3	2	3	3	4	3	2
$4H^{ch}$	6	5	6	5	6	6	6
$5H^{ch}$	4	4	4	4	3	4	=4
$6H^{ch}$	1	1	1	1	1	1	1
$7H^{ch}$	2	6	2	2	5	5	3

interaction was found between the H genotypes and salt concentration (grain number fig. 1) chromosomes 4H and 5H were found to have positive effects. The data therefore provide evidence that homoeologous group 4 and 5 (and possibly group 1) chromosomes carry genes which have major effects on tolerance to salt.

Genetic control of vigour

Vigour is a difficult term to define. In this work we have assessed vigour by ranking genotypes for the accummulative effects of various plant growth and harvest yield parameters (table 5). This is the first report of vigour being quantified in this manner and being related to the genetic contribution of individual barley chromosomes. The rankings (table 5) show that most addition lines are less vigorous than euploid CS, with the exception of the disomic addition lines $6H^{ch}$ and $7H^{ch}$ and the ditelosmic addition line of $2H^{ch}\alpha$. Group 6 and 7 chromosomes of both *H. vulgare* and *H. chilense* confer positive effects on vigour for most of the characters studied, emphasising the importance of these two chromosomes in determining overall plant vigour. Much of the advantage of the 7H and $7H^{ch}$ addition lines is lost at maturity due to poor fertility. However, both group 6 addition lines maintain a high ranking for all the characters studied. The disadvantage of the group 6 or group 7 addition lines over euploid wheat is their lack of true breeding due to poor transmission of the extra chromosomes, particularly in the pollen. The positive effects of chromosome 6H on grain yield has also been noted in a barley doubled haploid population derived from the cross Dissa × Sabarlis (Powell *et al.*, 1990). Increased yields of doubled haploid lines were found to be associated with the α-amylase-1 phenotype of Sabarlis; the *α-Amy-1* gene is located on the long arm of 6H and this may provide a means of marking genes which influence vigour in barley (Powell *et al.*, 1990).

Genetic control of salt tolerance

The results indicate that there is a large genetic effect on tolerance to salt in barley and this can be located to the effects of genes on chromosomes 4H and 5H of *H. vulgare* and $1H^{ch}S$, $4H^{ch}$ and $5H^{ch}$ of *H. chilense*. Both the *H. chilense* group 1 and group 2 chromosomes are present as telosomics in the addition lines tested, the positive response of the $1H^{ch}S$ line therefore indicates that genes contributing to tolerance are located on the short arm of $1H^{ch}$ and the poor response of the $2H^{ch}\alpha$ line may indicate that genes conferring a negative effect are located on the α arm (not yet designated).

The effects of chromosomes $2E^{b}$ and $5E^{b}$ of *Thinopyrum bessarabicum* (synonymous with 2J and 5J of *Agropyron junceum*), and 2A, 2B, 2D, 5A, 5B and 5D of wheat, *Triticum aestivum*, on the salt tolerance of wheat have been reported earlier (Forster *et al.*, 1988). The effect of added group 2 chromosomes was to increase the susceptibility of wheat to salt, whereas the addition of $5E^{b}$ increased the tolerance. The poor performance of the $2H^{ch}\alpha$ addition line suggests that the telosomic chromo-

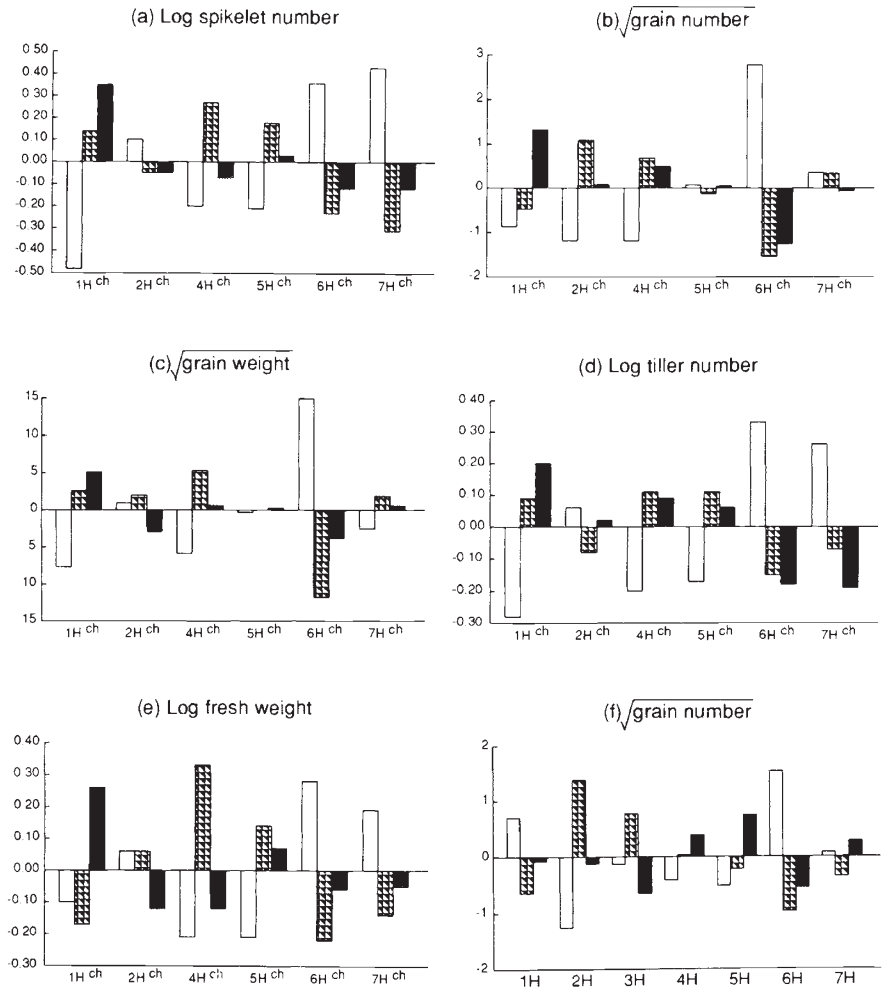

Figure 1 Estimated interaction effects of CS/*H. chilense* (H^{ch}) and wheat/*H. vulgare* (H) addition lines grown in 0, 175 and 200 mol m^{-3} NaCl.

some of *H. chilense* carried in this line carries a gene in the same homoeallelic series as other group 2 chromosomes having similar effects on tolerance to salt. Homoeologous group 5 chromosomes have been implicated in other genetic studies of stress tolerance. Work on aluminium stress indicated that genes for tolerance are located predominantly on chromosomes 5R of *Secale cereale* and $5R^{m}$ of *S. montanum*, but with genes on chromosomes 2R, 3R, 4R and 6R also having effects (Manyowa *et al.*, 1988; Aniol and Gustafson, 1984). Genes for aluminium tolerance were also located on chromosome 5D of the relatively tolerant wheat cultivar Atlas 66 (Prestes *et al.*, 1975). The 5H and $5H^{ch}$ disomic addition lines were not as tolerant to salt as the $5E^{b}$ addition line reported by Forster *et al.* (1988) and indicates that the barley species tested carry less potent alleles than those of the sand-dune grass *Th. bessarabicum*.

Genetic studies on the uptake of sodium have domonstrated that the transport of sodium to the shoots of hexaploid wheat is influenced by a gene or genes located on the long arm of chromosome 4D of *Aegilops squarrosa*, the progenitor of the D genome of hexaploid wheat (Gorham *et al.*, 1987). The positive effects of chromosomes 4H and $4H^{ch}$ in the present study may indicate the effect of similar genes in barley genomes and again this may form part of a homoeallelic series of genes in the *Triticeae*.

This study demonstrates that a major proportion of the genetic variation for salt tolerance may be accounted for by genetic loci on specific barley chromosomes. It is interesting to note that toler-

ance to several abiotic stresses are influenced by genes located on group 5 chromosomes and it is possible that genes controlling similar functions are clustered on specific chromosomes. Gene clusters for stress tolerance have been reported in bacterial plasmids, and in plants such as lettuce and maize (see Devine, 1982 for review) and this may indicate that gene clusters for stress tolerance are a universal phenomenon. Single genes for salt tolerance have not been identified in the *Triticeae*, however single gene mutants are known in the fern *Ceratopteris* (Warne and Hickok, 1987) and the single dominant gene *Nc1* restricts the influx of chloride to the shoots of *Glycine max* cv. Lee (Abel, 1969).

Morphological effects

The addition of both group 2 and group 5 chromosomes to wheat have major effects on plant morphology. These effects are contrasting; the addition of group 2 chromosomes produces a plant which is narrow leaved and with thin vitreous grains, group 5 addition lines are characteristically short, with broad leaves and coarse grains (Miller and Reader, 1987). Although the genes on these two chromosomes appear to have opposite effects they both carry genes targeted at plant growth and morphology. Group 2 and group 5 chromosomes also carry genes controlling time to flowering; the photoperiod insensitivity genes in the case of the group 2 chromosomes (Scarth and Law, 1984) and the vernalisation requirement genes in the case of group 5 chromosomes (Law *et al.*, 1975). The contrasting salt tolerance of group 2 and group 5 chromosome addition lines may be the result of altered plant morphology and growth. The establishment of a link between such characters and salt tolerance would be invaluable in both genetic, physiological and directed plant breeding efforts for more tolerant crops. Physiological mechanisms associated with salt stress such as ion exclusion, the build up of proline, glycine-betaine, abscisic acid, or sodium stomatal closure, osmotic adjustment or leaf rolling have not been linked to genes on group 2 or 5 chromosomes. However, sodium/potassium discrimination is influenced by genes on chromosome 4D of wheat (Gorham *et al.*, 1987).

Breeding for tolerance to salt

An important finding is that the *H. chilense* addition lines performed better than those of *H. vulgare*. The wild species therefore has more potent genes for tolerance to salt than the cultivated species. This is not surprising when one considers that barley cultivars have been selected for centuries on their performance in fertile soils, but it does emphasise the point that wild relatives of crop species are invaluable sources of genes for novel characters. Fertile hybrids between *H. chilense* and *H. vulgare* have not been produced and therefore introgression of genes between these two species is not possible by the normal processes of meiotic recombination. But the salt tolerance of wheat may be improved by transferring genes from *H. chilense* chromosomes to relevant wheat homoeologues.

Different strategies are possible in breeding for greater tolerance in barley. Genes for both tolerance to salt and genes for vigour are of importance in this context. These genes are located on different and potentially opposing chromosomes; group 6 and 7 chromosomes carry genes for vigour, but their respective addition lines have the worst response in salt stressed conditions relative to control conditions; homoeologous group 4 and 5 chromosomes carry genes for tolerance to salt, but can also confer poor vigour. There is therefore a dilemma in breeding for tolerance to salt, one option for the breeder is to select on the basis of vigour in which case vigorous lines would be expected to perform well in both fertile and saline field conditions (a strategy supported by Richards, 1983); the results presented here suggest that segments of chromosomes 6H and 7H would be of importance in such a breeding programme. Or a programme could be designed to transfer genes into the crop having direct positive effects. Homoeologous group 4 and 5 chromosomes of salt tolerant wild barleys such as *H. spontaneum* which can hybridise and recombine with *H. vulgare* would be potential sources for such genes. A collaborative programme between SCRI and the University of Haifa, Israel, has been initiated for this purpose.

Finally, selection for agronomic traits such as vigour and salt tolerance would proceed faster and with greater precision if marker based technology could be applied to the breeding process. Biochemical markers such as proteins (including isozymes) and DNA markers such as RFLPs (restriction fragment length polymorphisms) can be targeted at specific chromosomes, and linkage established with the character of interest. Such markers are actively being sought at SCRI.

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