Chromosomal location of a K/Na discrimination character in the D genome of wheat

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Summary. K/Na ratios have been determined in the leaves of salt-treated plants of 14 disomic substitution lines in which each of the D-genome chromosomes replaces the homoeologous A- or B-genome chromosome in the tetraploid wheat variety Langdon (AABB genome). Aneuploid lines of hexaploid bread wheat (cv Chinese Spring) having a reduced or an enhanced complement of chromosome 4D have also been examined. These investigations show that the gene(s) determining K/Na ratios in the leaves of wheat plants grown in the presence of salt is located on the long arm of chromosome 4D.

Key words: *Triticum aestivum* – *T. turgidum* – *Aegilops squarrosa* – Cation uptake – D genome

Introduction

Soil salinity, alkalinity (sodicity) and related problems such as waterlogging are major limitations to the productivity of much irrigated land and ones which are very expensive to correct by agricultural engineering projects. There is thus much interest in breeding crop plants with enhanced tolerance to such unfavourable edaphic conditions (Epstein et al. 1980; Kingsbury and Epstein 1984; Downton 1984; Rana 1985). While tolerance to salinity, alkalinity and associated problems in field conditions is certainly complex and influenced by a number of physiological, morphological and onto-genetic characters, salt tolerance in glycophytes, and especially in members of the Poaceae, is mainly associated with the ability to limit the accumulation of Na and Cl and with the maintenance of high K/Na ratios in the shoots (Greenway and Munns 1980; Gorham et al. 1985).

Hexaploid bread wheat (*Triticum aestivum* L.) contains three genomes, designated A, B and D, which originated from wild wheatgrasses of the genera *Triticum* and *Aegilops* (Feldman and Sears 1981). The D genome of wheat, derived from the diploid grass *Aegilops squarrosa* L. (syn. *Triticum tauschii* (Coss.) Schnal.), carries a gene (or genes) which determines the K/Na ratio in the shoots of wheat plants grown in saline hydroponic culture (Wyn Jones et al. 1984; Shah et al. 1987). When grown in hydroponic culture solutions containing 100 mol m^{-3} NaCl, *Aegilops squarrosa* (D genome) maintains high leaf K/Na ratios and has a lower total salt load compared with tetraploid wheats (*T. turgidum*, AABB genome). Many common bread wheats and synthetic, AABBDD-genome hexaploid wheats (in which the D genome of *Aegilops squarrosa* is combined with the A and B genomes of a tetraploid wheat) also display the high K/Na discrimination character. The A-genome species *Triticum monococcum* L. (sensu lato) also had a high K/Na ratio but the total monovalent cation content was considerably higher than in the other wheats and wheatgrasses (Wyn Jones et al. 1984). The poor K/Na discrimination shown by the tetraploid wheats was also exhibited by S genome *Aegilops* species (*A. speltoides*, *A. searsii*) which may be related to the ancestors of the B genome.

A high K/Na ratio combined with low leaf salt contents is characteristic of salt-tolerant members of the grass tribe Triticeae (Gorham et al. 1984a, 1985, 1986a, b). There is some evidence that a high K/Na ratio, particularly in the youngest leaf, might be associated with salt tolerance in bread wheat cultivars both in the field and in hydroponic studies (Joshi et al. 1979; Rashid 1986). A positive correlation of yield of bread wheats with leaf K contents under saline conditions, and a negative correlation with Na contents, has been

reported from field studies by Singh and Rana (1985). It has also been reported that durum wheats (AABB genome) having low leaf K/Na ratios are less tolerant of salt and alkalinity than hexaploid bread wheats with the AABBDD genome (Francois et al. 1986; Joshi et al. 1982; Rana 1985, 1986; Rana et al. 1980).

In order to exploit this character in breeding programmes to enhance the salt tolerance of tetraploid and hexaploid wheats it is desirable to identify the chromosome which carries the K/Na discrimination character. Several genes which affect characters such as plant height, resistance to hessian fly, the baking quality of the flour and cold resistance are also located on chromosomes of the D genome within hexaploid wheat. A number of such genes have been mapped, in some cases to the long or short arm of one chromosome (Ainsworth et al. 1984; Gale et al. 1975, 1983; Gill et al. 1987; Law and Jenkins 1970). We report here on experiments designed to determine which arm of which D-genome chromosome carries the gene(s) controlling the shoot K/Na selectivity character.

Materials and methods

Disomic D-genome substitution lines in the tetraploid wheat variety Langdon were produced in Fargo, North Dakota by crossing Langdon with hexaploid wheat (cv Chinese Spring) lines developd by Sears (1966) which were nullisomic for particular A- or B-genome chromosomes and tetrasomic for the homoeologous D-genome chromosomes. Appropriate progeny were selfed and 28 chromosome plants selected. These were backcrossed with Langdon several times to remove the Chinese Spring A- and B-genome chromosomes and the progeny selfed and screened for the appropriate substitution lines. Details of the production, morphology and cytogenetics of these substitution lines have been reported elsewhere (Joppa 1973, 1987; Joppa and McNeal 1972; Joppa and Williams 1977, 1983; Joppa et al. 1979). Aneuploid Chinese Spring lines came from stocks held at the Plant Breeding Institute, Cambridge, UK. Synthetic hexaploid wheat was obtained by crossing Langdon with Aegilops squarrosa (Hollenhorst and Joppa 1983; Joppa and Williams 1982; Joppa et al. 1980).

In the first experiment seeds of the disomic D-genome substitution lines in Langdon, together with seeds of Langdon, A. squarrosa RL 5003 and the synthetic hexaploid derived from them, were soaked for 24 h in slowly flowing tap water. The seeds were germinated on capillary matting attached with 'Copydex'[1] adhesive to the underside of 25 mm thick expanded polystyrene sheets in which holes (12 mm in diameter) were made with a cork borer to allow the shoots to emerge. The top surface of the expanded polystyrene was covered with black polythene sheeting (with holes for the shoots) to prevent evaporation and contact between leaves and the salt solution. Each 25 dm³ container supported 24 seedlings in modified 'Phostrogen'[1] nutrient solution (Gorham et al. 1984b). Six

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[1] Mention of a proprietary product does not constitute a guarantee or warranty of the product by the US Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable

replicate plants of each substitution line were grown without salt and six in the presence of 150 mol m⁻³ NaCl plus 7.5 mol m⁻³ CaCl₂, the salt concentration being increased by 25 mol m⁻³ d⁻¹, starting when the plants were 2 weeks old. The plants were grown in a greenhouse at a minimum temperature of 15 °C with natural daylight supplemented by 400 W Son-T sodium vapour lamps to give a photoperiod of 16 h. The second experiment, using the Chinese Spring aneuploid lines, was conducted in a similar manner to the first.

Mature leaf samples were harvested after 3 weeks at the final salinity level, i.e. when the plants were about 6 weeks old, and placed in plastic syringe barrels with a 1.5 ml polypropylene centrifuge tube placed over the end. The plunger of the syringe and the microcentrifuge tube prevented changes in the water content of the sample during sap extraction. The samples were frozen and thawed before being centrifuged at 5,000 g for 5 min to extract the sap into the centrifuge tube, a small hole being made just below the rim of the microcentrifuge tube to allow air to escape. Extracted plant sap was treated with 9 parts of 25% propan-2-ol and centrifuged at 9,000 g for 1 min to remove the precipitated proteins. The supernatant was diluted prior to analysis with 10% propan-2-ol containing 20 mol m⁻³ RuBr (internal standards). Inorganic monovalent cations and inorganic anions were determined in the leaf saps using a Dionex[1] 2010i ion chromatograph coupled to a Pye 4700 autoinjector and a Pye DP 88 integrator. Samples of diluted sap (75 mm³) were introduced via the injection valve of the Dionex 2010i which was actuated by the pneumatic controls of the autoinjector. Anions were analyzed on an HPIC-AS4A column eluted with 2 mol m⁻³ Na₂CO₃ plus 0.7 mol m⁻³ NaHCO₃ in 2% propan-2-ol. Monovalent cations were separated on an HPIC-CS3 column eluted with a mixture of 30 mol m⁻³ HCl, 1 mol m⁻³ 2,3-diaminopropionic acid monohydrochloride and 0.5 mol m⁻³ ZnCl₂. The appropriate guard columns and suppressors were used, and detection was by conductivity.

Results

To locate the chromosome carrying the K/Na discrimination gene(s) we first examined the effect of growth in 150 mol m⁻³ NaCl + 7.5 mol m⁻³ CaCl₂ on the monovalent cation contents of leaves of plants from a series of disomic substitution lines in which each of the 7 pairs of D-genome chromosomes from the hexaploid wheat variety Chinese Spring was substituted for the homoeologous A- or B-genome chromosomes in the tetraploid wheat variety 'Langdon'. This experiment (Table 1) clearly indicated that the presence of chromosome 4D greatly enhanced the K/Na selectivity of both the 4D/4A and 4D/4B substitution lines. The higher K/Na ratios in these two lines were the result of both lower Na and higher K concentrations. Total monovalent cation (K + Na) and chloride contents of these leaves were similar to those in leaves of the other substitution lines and in the leaves of Langdon. Results for Aegilops squarrosa, Langdon and a synthetic hexaploid wheat grown in the same conditions as the substituion lines are also shown in Table 1 and confirm the previous observations on the effect of the whole D genome in hexaploid wheat (Wyn Jones et al. 1984;

Table 1. Monovalent cation concentrations (mol m^{-3}) in sap from leaves of *Aegilops squarrosa* RL 5003, *Triticum turgidum* cv Langdon, the synthetic hexaploid derived from them and the disomic D-genome substitution lines in Langdon grown in the presence or absence of 150 mol m^{-3} NaCl plus 7.5 mol m^{-3} CaCl$_2$. values for the first three are means of four replicates while values for the substitution lines are means of six replicates, in all cases ± standard errors

Species and variety	Sodium		Potassium		K/Na ratio	K + Na
	0 mol m^{-3} NaCl	150 mol m^{-3} NaCl	0 mol m^{-3} NaCl	150 mol m^{-3} NaCl	150 mol m^{-3} NaCl	150 mol m^{-3} NaCl
Aegilops squarrosa RL 5003	3 ± 1	195 ± 43	216 ± 10	220 ± 6	2.20 ± 0.46	349 ± 29
Triticum turgidum Langdon	3 ± 1	282 ± 28	228 ± 12	125 ± 9	0.45 ± 0.06	408 ± 22
Triticum aestivum L/RL 5003	1 ± 0	76 ± 43	250 ± 10	232 ± 41	6.95 ± 2.61	308 ± 18
Triticum turgidum Langdon disomic substitution lines						
1D/1A	2 ± 0	242 ± 23	259 ± 11	136 ± 10	0.60 ± 0.09	376 ± 20
2D/2A	3 ± 0	240 ± 22	227 ± 8	145 ± 28	0.58 ± 0.10	393 ± 36
3D/3A	3 ± 0	301 ± 29	217 ± 13	129 ± 8	0.47 ± 0.06	430 ± 28
4D/4A	3 ± 1	126 ± 42	210 ± 13	204 ± 20	2.77 ± 0.65	330 ± 25
5D/5A	3 ± 1	313 ± 35	237 ± 13	144 ± 7	0.47 ± 0.06	457 ± 37
6D/6A	2 ± 0	290 ± 37	231 ± 5	165 ± 16	0.62 ± 0.09	456 ± 44
7D/7A	2 ± 1	304 ± 21	226 ± 11	137 ± 20	0.48 ± 0.06	442 ± 33
1D/1B	2 ± 1	250 ± 14	241 ± 7	135 ± 32	0.47 ± 0.08	351 ± 14
2D/2B	3 ± 1	438 ± 57	227 ± 5	137 ± 7	0.38 ± 0.03	559 ± 77
3D/3B	3 ± 0	321 ± 18	209 ± 5	124 ± 7	0.40 ± 0.04	445 ± 19
4D/4B	4 ± 2	98 ± 17	241 ± 14	281 ± 13	3.43 ± 0.64	381 ± 22
5D/5B	2 ± 0	298 ± 14	238 ± 5	153 ± 12	0.53 ± 0.05	434 ± 13
6D/6B	3 ± 1	308 ± 38	215 ± 7	113 ± 6	0.41 ± 0.06	400 ± 32
7D/7B	2 ± 0	279 ± 3	209 ± 13	158 ± 26	0.57 ± 0.10	461 ± 30

Table 2. Monovalent cation concentrations (mol m^{-3}) in sap from leaves of *Triticum aestivum* cv Chinese Spring and various aneuploid lines derived from Chinese Spring grown in the presence of 125 mol m^{-3} NaCl plus 6.25 mol m^{-3} CaCl$_2$. Values are the means of at least five replicates ± standard errors

Chinese Spring line	Sodium	Potassium	K/Na ratio	K + Na
Euploid	85 ± 16	223 ± 6	3.6 ± 0.6	329 ± 25
Ditelosomic 4D short	261 ± 26	71 ± 3	0.6 ± 0.3	332 ± 26
Ditelosomic 4 D long	103 ± 25	232 ± 19	4.0 ± 1.3	335 ± 31
Tetrasomic 4D	78 ± 12	232 ± 16	3.5 ± 0.6	301 ± 12
Nullisomic 4B, tetrasomic 4A	95 ± 17	206 ± 12	3.4 ± 0.6	333 ± 35
Nullisomic 4B, tetrasomic 4D	61 ± 11	231 ± 12	5.5 ± 1.3	292 ± 90
Nullisomic 4D, tetrasomic 4A	274 ± 31	124 ± 38	0.5 ± 0.1	408 ± 54

Shah et al. 1987). These data also show that the enhanced K/Na discrimination character is not simply a ploidy effect (Joshi et al. 1982; Singh and Rana 1985). Further analysis revealed that the K/Na discrimination character was not apparent in root extracts (data not shown), i.e. it is the flux of Na and K between the roots and the shoots which is controlled.

Expression of the K/Na discrimination character was further examined in a series of aneuploid lines derived from the hexaploid wheat variety Chinese Spring (Table 2). Low K/Na ratios were found in leaves from the line in which the long arm of the 4D chromosome was absent (ditelosomic 4D short) and in leaves from the line in which the 4D chromosome was totally absent (nullisomic 4D, tetrasomic 4A), thus confirming the conclusions of the first experiment. Since high K/Na discrimination was found in the line ditelosomic for the long arm of chromosome 4D, but not in the line ditelosomic for the short arm of 4D, it may be concluded that the gene(s) is located on the long arm of chromosome 4D. The lowest Na concentrations were found in leaves of the two lines containing an extra pair of 4D chromosomes (tetrasomic 4D and nullisomic 4B, tetrasomic 4D) suggesting that the effect may be enhanced by the presence of extra copies of the gene(s).

In both experiments there was, in comparison with the effects on K/Na ratios, little effect of chromosome 4D on total monovalent cation or anion concentrations in leaf saps. There was, however, some indication that the presence of chromosome 4D resulted in higher concentrations of free Ca and Mg in the leaves.

Discussion

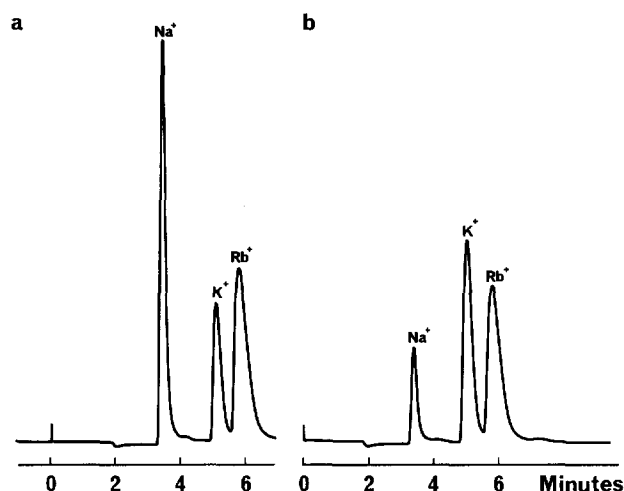In a previous paper we reported that a synthetic hexaploid wheat containing the A and B genomes of

Fig. 1a, b. Analysis of monovalent cations in sap from leaves of wheat grown at 150 mol m^{-3} NaCl (+7.5 mol m^{-3} CaCl$_2$). a The tetraploid wheat variety Langdon. b A 4D/4A disomic substitution line in Langdon. Rubidium bromide was added to the extracts to provide internal standards for cation and anion analysis

Langdon had better yield characteristics than Langdon itself when both were grown to maturity at 100 mol m^{-3} NaCl (Shah et al. 1987). Grain and leaf K/Na ratios were higher in the hexaploid. Francois et al. (1986) also reported a greater reduction in yield with high salinity in two durum wheat cultivars than in the hexaploid wheat variety Probred, and other workers have demonstrated that hexaploid wheat is more salt-tolerant than tetraploid wheat (Joshi et al. 1982; Rana 1985, 1986; Rana et al. 1980). The D genome also appears to be involved in the tolerance of hexaploid wheat to acid soils and frost (Barashkova 1981; Sloot-maker 1974). It is now necessary to establish that the gene(s) on the long arm of the 4D chromosome which determines the enhanced leaf K/Na discrimination in hexaploid wheat also contributes to enhanced salt tolerance in the absence of the other components of the D genome. Unfortunately the Langdon substitution lines are not particularly fertile, but by examining a wide range of 4D aneuploids in tetraploid and hexaploid wheat we hope to be able to determine the effect of this chromosome on yield under salt stress. The 4D aneuploids will also be useful in biochemical and physiological experiments on ion uptake mechanisms.

Despite the large amount of effort which has been devoted to studying the physiological and genetical basis of salt tolerance and sensitivity in higher plants, there are very few instances in which physiological characters have been shown to be under genetic control. The best examples are the genes for chloride transport in soybean (*Glycine max*) and Na accumulation in pepper (*Capsicum annuum*). Abel (1969) re-

ported the discovery of a gene (Ncl, ncl) which controlled chloride accumulation in the shoots of soybean. The recessive ncl gene allowed much more chloride to reach the shoot than the dominant, chloride excluding gene. The *Capsicum annum scabrous diminutive* mutant of pepper (Benzioni and Tal 1978; Tal 1984; Tal and Benzioni 1977) is rather similar in its effects to the K/Na discrimination character described here in that the mutant allows in much more Na than the wild-type and there is an accompanying loss of K. It is much easier in the case of such a mutant to demonstrate that a single gene is responsible for the effect than it is when only aneuploid lines are available. Inter- and intra-varietal differences in K/Na discrimination linked to the 4D chromosome of wheat are currently being investigated.

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588

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