Theor Appl Genet (1991) 82:729–736

THEORETICAL AND APPLIED GENETICS

The presence of the enhanced K/Na discrimination trait in diploid *Triticum* species

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Received February 5, 1991; Accepted April 18, 1991
Communicated by J.W. Snape

Summary. A number of accessions of the three species of diploid wheat, *Triticum boeoticum*, *T. monococcum*, and *T. urartu*, were grown in 50 mol m^{-3} NaCl + 2.5 mol m^{-3} $CaCl_2$. Sodium accumulation in the leaves was low and potassium concentrations remained high. This was not the case in *T. durum* grown under the same conditions, and indicates the presence in diploid wheats of the enhanced K/Na discrimination character which has previously been found in *Aegilops squarrosa* and hexaploid wheat. None of the accessions of diploid wheat showed poor K/Na discrimination, which suggests that if the A genome of modern tetraploid wheats was derived from a diploid *Triticum* species, then the enhanced K/Na discrimination character became altered after the formation of the original allopolyploid. Another possibility is that a diploid wheat that did not have the enhanced K/Na discrimination character was involved in the hybridization event which produced tetraploid wheat, and that this diploid is now extinct or has not yet been discovered.

Key words: *Triticum* – K/Na discrimination – Salt tolerance

Introduction

The physiological responses of plants to salt are complex. There are many possible mechanisms of tolerance to salt, and only some of these may operate in a particular species. Furthermore, the effect of one mechanism may be either obscured or promoted by the effects of others. We are therefore pursuing an analytical approach to salt tolerance, with the aim of being able to identify physiological and biochemical mechanisms and, eventually, to integrate them into the design of wheat ideotypes that would be more tolerant of salt than existing genotypes.

One mechanism that has emerged from these studies is the enhanced K/Na discrimination character which was originally found in the D genome of hexaploid wheat (Wyn Jones et al. 1984; Shah et al. 1987). All plants discriminate to some extent in favor of K^+ and against Na^+ in ion uptake into the roots and in translocation of absorbed cations to the shoots. In *Triticum aestivum* and *Aegilops squarrosa*, this ability to discriminate between monovalent cations in transport from the roots to the shoots is much greater than in *T. durum*. The enhanced K/Na discrimination character does not have any large effect on anion concentrations in either roots or shoots, or on cation concentrations in the roots. It is most obvious in plants grown at salinities between 10 and 100 mol m^{-3} NaCl. Further details of the physiological effects of this character can be found in Gorham et al. (1990a).

The enhanced K/Na discrimination character was located on the long arm of chromosome 4D by examining leaf cation concentrations in disomic substitution lines of *T. durum* cv Langdon and aneuploid lines of *T. aestivum* cv Chinese Spring (Gorham et al. 1987). It also occurs in most, but not all, species of *Aegilops* in which either the D or U genomes are present (Gorham 1990b), in *Secale cereale* and in both hexaploid and octaploid triticales (Gorham 1990a). It does not occur in barley, which is one of the most salt tolerant of the annual Triticeae (Gorham et al. 1990b), and is thus only one of many mechanisms that may contribute to salt tolerance in the Triticeae. The beneficial effects of this character on tolerance to salinity or sodicity can only be assessed after it has been incorporated into a tetraploid wheat with a minimum of other genetic changes (Wyn Jones and Gorham 1990).

The original work on the putative ancestors of wheat grown in the presence of 100 mol m^{-3} NaCl suggested that, although diploid wheats maintained high K^+ con-

Table 1. Sources of plant material

Bangor no.	Genus	Species	Subspecies or variety	Origin	Source
50024-26	*Aegilops*	*sharonensis*	A, B, C		IPSR
50041-43			AUS18890, 18802, 18803		AWC
50003	*Aegilops*	*squarrosa*	A		IPSR
50011			G		IPSR
50028			1454		IPP
50030			1456		IPP
50049			AUS18890		AWC
40046	*Hordeum*	*vulgare*	SUNBAR 400		KING CO.
40072			CM67		UCD
17043	*Triticum*		BBAAAA synthetic		JOPPA
10187	*Triticum*	*aestivum*	Tobari		UL
10310			Shorawaki		CIMMYT
10311			Kanchan		CIMMYT
10312			Sakha-8		CIMMYT
10313			CS (Sears)		CIMMYT
10314			CS doubled haploid		UCD
90066			*spelta*		IPSR
10003			Chinese Spring		IPSR
10118	*Triticum*	*boeoticum*	AUS90444		AWC
10217			*pseudoboeoticum*		UCR
10218			*thoudar v. fuscum*	(USSR)	UCR
10219-24				Turkey	UCR
10225			*boeoticum*	Azerbaijan	UCR
10226				Armenia	UCR
10227			*virido-boeoticum*	Crimea	UCR
10228-34				Iraq	UCR
10235			*paulotuberculatum*	Armenia	UCR
10236				Armenia	UCR
10237			*euboeoticum*	Azerbaijan	UCR
10238			*pseudoboeoticum*	Azerbaijan	UCR
10112			AUS90351		AWC
10304			TA182	Iran	KSU
10305			TA198	Lebanon	KSU
10306			TA213	Iraq	KSU
10307			TA571	USSR	KSU
10098			PGR6134		PGRC
10113			AUS90352		AWC
10099			PGR6136		PGRC
17044			G2520		JOPPA
17047					JOPPA
10126	*Triticum*	*dicoccoides*	AUS15825		AWC
10085-6			20454-55		IPP
10083,4			1473,3511		IPP
10189	*Triticum*	*durum*	Cappelli		UCD
10139,10146					ICARDA
17045			Langdon		JOPPA
17046			group 4 substitution		JOPPA
17048			56-1		JOPPA
10246,7	*Triticum*	*monococcum*			UCR
10248			*sinskajae*	USSR	UCR
10249,50					UCR
10251				Turkey	UCR
10252,3					UCR
10254				Armenia	UCR
10255				Georgia	UCR
10256				Ukraine	UCR
10257				Azerbaijan	UCR
10258				Georgia	UCR
10259				Azerbaijan	UCR
10245				Turkey	UCR
10239					UCR
10107			PGR6122		PGRC
10108			PGR6128		PGRC

Table 1. Continued

Bangor no.	Genus	Species	Subspecies or variety	Origin	Source
10122-25			AUS90423, 25, 32, 36, 56		AWC
10090			3522		IPP
10091			19733		IPP
10092, 3			20231, 20451		IPP
10240					UCR
10114			AUS0356		AWC
10119-21			AUS90416, 18, 19		AWC
10241				Turkey	UCR
10088, 89			3521, 1472		IPP
10242, 3					UCR
10116			AUS90457		AWC
10244				(USSR)	UCR
10002					IPSR
10106			PGR1933		PGRC
10293, 4	*Triticum*	*urartu*		Lebanon	UCR
10308				Turkey	KSU
10309				Lebanon	KSU
10295				Lebanon	UCR
10296			*spontaneorubrum*	USSR	UCR
10286-91				Turkey	UCR
10278				Turkey	UCR
10279				Iran	UCR
10115			AUS90459		AWC
10280				(Iran)	UCR
10281			*nigrum*	Armenia	UCR
10282, 3				Armenia	UCR
10284, 5				Turkey	UCR
10292				Lebanon	UCR

Source codes:

IPSR	Dr. C.N. Law and Mr. T. Miller, Institute of Plant Science Research, Cambridge
IPP	Prof. M. Dambroth, Institut für Pflanzenbau und Pflanzenzüchtung, Braunschweig
UCD	Prof. J. Dvorak, University of California, Davis
UCR	Prof. J.G. Waines, University of California, Riverside
UL	Dr. T. McNeilly, University of Liverpool
CIMMYT	Dr. A. Mujeeb Kazi, Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico
ICARDA	International Centre for Agricultural Research in the Dry Areas, Aleppo
JOPPA	Dr. L.R. Joppa, USDA, ARS, Fargo
PGRC	Dr. R. Loiselle, Central Office for the Plant Gene Resources of Canada, Ottawa
AWC	Dr. K.J. Symes, Australian Wheat Collection, Tamworth
KSU	Dr. W.J. Raupp, Kansas State University
KING CO.	Northup King Co., California

centrations in their leaves, they also had high leaf Na^+ concentrations (Wyn Jones et al. 1984; Shah et al. 1987). The discovery of the much better K/Na discrimination in amphidiploids derived from hybrids between diploid and tetraploid wheats than in the tetraploid wheat parents (Gorham 1990c) has prompted a reexamination of this finding. We now report on the distribution of the enhanced K/Na discrimination character in a large number of diploid *Triticum* accessions and amphiploids, and discuss the implications of our findings in terms of current theories of wheat evolution.

For simplicity, we have adopted the classification used by Miller (1987) and the genome formulae proposed by Waines and Barnhart (1990). Genomes from different sources are distinguished by superscripts. The recommendations of the 7th International Wheat Genetics Symposium have been followed with respect to the group 4 chromosomes of wheat. Thus, the old chromosome 4B is now designated 4A, while the old chromosome 4A is designated 4B.

Materials and methods

Plant culture

The seeds used in these investigations were obtained from the sources listed in Table 1.

In the first experiment the seeds were sown on capillary matting attached to P180 plugtrays (Plantpak Ltd., Maldon, UK). Rock wool was subsequently found to provide a more uniform environment for germination, and in subsequent exper-

iments the seeds were sown on rock wool plugs in P180 plugtrays, with one or two seeds per cell, one or two accessions per row of ten cells and 18–36 accessions per tray, i.e., at least ten plants per accession. Accessions were assigned to particular rows in a random order. The seeds were germinated at 25 °C in the dark in a plugtray placed over vermiculite moistened with a solution containing 2 mol m^{-3} $Ca(NO_3)_2$ and 1 mol m^{-3} $MgSO_4$ (pH 5.5). After 4 days the plugtray was suspended over 25 dm^3 of aerated, 'Phostrogen'-based nutrient solution (pH 5.6) containing 6.8 mol m^{-3} K^+, 8.4 mol m^{-3} NO_3^-, 1.7 mol m^{-3} PO_4^{3-}, 0.73 mol m^{-3} Ca^{2+}, 0.92 mol m^{-3} Mg^{2+}, 0.3 mol m^{-3} Na^+ and the same micronutrients as one-half strength Hoagland's solution (Gorham et al. 1984). The plants were grown in a greenhouse at 15–25 °C with a photoperiod of 16 h, consisting of natural daylight supplemented, when necessary, with 400 W Son-T Na vapour lamps (GEC Ltd.). The nutrient solution was replaced every 10–14 days.

Experiments

Experiments 1, 2, 3 and 5 examined the K/Na ratios in leaves of plants grown at 50 mol m^{-3} NaCl for 14 days. Experiment 1 compared accessions of *T. monococcum*, *Ae. squarrosa*, and *Ae. sharonensis*. Experiment 2 examined a wider range of diploid accessions in comparison with barley and wheats at higher ploidy levels. Experiment 3 examined a synthetic hexaploid wheat incorporating the A^b genome from *T. boeoticum*, and experiment 5 included a number of amphiploids involving diploid wheats. The 4th experiment investigated the uptake of ^{22}Na into 'low-salt' shoots of *Ae. squarrosa*, *T. monococcum*, *T. durum* cv Langdon, the $4A^b$ ($4A^d$) substitution line in *T. durum*, the $BBA^dA^dA^bA^b$ synthetic hexaploid wheat and *T. aestivum* cv Chinese Spring.

Treatments

In experiments 1, 2, 3 and 5, salt was added to the nutrient solution starting on the 14th day after germination, when the seedlings were well established, increasing to 50 mol m^{-3} NaCl in two daily additions of 25 mol m^{-3} NaCl. $CaCl_2$ was added to maintain a nominal Na:Ca ratio of 20:1 (ignoring the small amount of Ca present in the nutrient solution). Control (no salt) treatments were not necessary to determine the presence or absence of the enhanced K/Na discrimination character. Since the character is easily detected, it was also not necessary to include a check accession in each experiment.

Chemical analyses

In the first three and the last experiment, three replicated samples of the youngest, fully emerged leaves of each accession (usually two to three leaves per replicate) were harvested after the plants had been growing at the specified salinity level for at least 14 days (i.e., after the initial osmotic adjustment had taken place). The youngest, fully emerged leaf was chosen as a standard leaf because of the steep gradient in ion concentrations from young to old leaves (data not shown). In all cases only fully turgid, green leaves that appeared to be healthy were used for solute analysis. Sap was extracted from frozen/thawed and crushed samples by centrifugation (Gorham et al. 1984). Inorganic ion analyses were performed on a Dionex ion chromatograph using the procedures described by Gorham (1987), except that the final dilution of the sample was made with eluant and the temperature of both the eluant and the column was maintained at 40 °C during the analyses. Values given in the tables for mean K/Na ratios are means of the K/Na ratios for individual replicates. These may differ slightly from the ratios of mean K and mean Na concentrations. As a general rule, at 50 mol m^{-3} NaCl external salinity, a K/Na ratio of <1.5 indicates the absence of the enhanced K/Na discrimination character, while a value greater than 2.5 is taken to indicate the presence of the character.

^{22}Na uptake, experiment 4

In this experiment, "low-salt"– seedlings were obtained by germinating the seed in the dark over 0.5 mol m^{-3} $CaSO_4$ (pH 5.5), and subsequently growing the seedlings in a growth cabinet maintained at 22 °C, with a 16-h photoperiod supplied by a mixture of warm white fluorescent tubes and tungsten light bulbs at 300 Ymol photons of photosynthetically active radiation (PAR) m^{-2} s^{-1}. Two days after germination the solution was replaced with a mixture containing 2 mol m^{-3} $Ca(NO_3)_2$ and 1 mol m^{-3} $MgSO_4$ (pH 5.4), and the seedlings were grown for a further 5 days before being used in ^{22}Na uptake experiments. The seedlings were incubated for 48 h in a solution (2 dm^3) of 1 mol m^{-3} NaCl and 100 mmol m^{-3} KNO_3 (pH 5.6) containing 148 kBq of ^{22}Na. At the end of the incubation the shoots were excised and weighed. ^{22}Na in shoot tissue was measured in a well-type gamma counter with a 76-mm diameter NaI crystal contained within a 49-mm thick lead shield.

Statistical analysis

All data were analysed by the STATPAK statistical package, using the *t*-test and ANOVA functions to assess significant differences ($P<0.05$) between means.

Results and discussion

K/Na discrimination in diploid wheats

When inorganic ion concentrations were measured in the leaves of plants of four accessions of *T. monococcum* grown for 14 days at 50 mol m^{-3} NaCl + 2.5 mol m^{-3} $CaCl_2$, and compared with values obtained from accessions of *Ae. squarrosa* and *Ae. sharonensis* (Table 2, Expt. 1), it was clear that *T. monococcum* displayed all the characteristics associated with the enhanced K/Na dis-

Table 2. *Experiment 1.* Inorganic ion concentration (mol m^{-3} expressed sap) in the youngest, fully expanded leaves of 30-day-old seedlings of *Triticum monococcum* (genome A^mA^m), *Aegilops squarrosa* (genome DD) and *Aegilops sharonensis* (genome S^lS^l), grown for 14 days in nutrient solution, plus 50 mol m^{-3} NaCl and 2.5 mol m^{-3} $CaCl_2$. Values are the means ± standard errors of all replicates (three replicate samples per accession)

No. of accessions	*T. monococcum* 4	*Ae. squarrosa* 7	*Ae. sharonensis* 6
Sodium	47 ± 7	41 ± 5	144 ± 5
Potassium	172 ± 13	205 ± 9	96 ± 5
Chloride	105 ± 14	101 ± 5	93 ± 4
Nitrate	50 ± 6	74 ± 5	67 ± 3
Orthophosphate	29 ± 3	30 ± 2	25 ± 1
Sulphate	8 ± 2	4 ± 1	2 ± 0
Potassium + sodium	219 ± 12	246 ± 9	240 ± 8
Potassium/sodium	6.4 ± 2.09	10.73 ± 2.53	0.67 ± 0.03
K/Na (range)	2.0–14.5	2.92–35.1	0.56–0.85

Table 3. *Experiment 2.* Monovalent cation concentrations (mol m^{-3} expressed sap) in the youngest, fully emerged leaves of barley and various *Triticum* species, grown for 14 days in nutrient solution, plus 50 mol m^{-3} NaCl and 2.5 mol m^{-3} $CaCl_2$. Values are means ± standard errors of all replicates (three replicates per accession)

Species	Genome	Accessions	Na	K	K+Na	K/Na (mean)	K/Na (range)
T. monococcum	A^mA^m	20	18±2	159± 5	176± 6	18.56±2.42	3.17–72.26
T. urartu	A^uA^u	19	13±1	185±12	198±12	19.39±2.14	4.45–49.83
T. boeoticum	A^bA^b	24	13±1	176± 2	189± 3	23.06±2.07	5.39–41.93
H. vulgare	II	2	92±3	126± 2	217± 2	1.39±0.06	1.34– 1.43
T. durum	BBA^dA^d	7	107±6	118± 5	225± 5	1.22±0.12	0.71– 2.27
T. dicoccoides	BBA^dA^d	5	100±5	122± 6	222± 8	1.25±0.08	1.0 – 1.73
T. aestivum	BBA^dA^dDD	15	11±1	155± 3	166± 3	15.70±0.79	10.98–23.50

crimination trait. Leaf Na concentrations in *T. monococcum* were similar to those in *Ae. squarrosa* (which also has the enhanced K/Na discrimination trait), and much lower than in *Ae. sharonensis* (which lacks the trait). Leaf K concentrations showed the opposite pattern, being considerably higher in *T. monococcum* and *Ae. squarrosa* than in *Ae. sharonensis*. The sum of leaf K and Na concentrations was similar in all species, but the ratio of K to Na was very much smaller in *Ae. sharonensis* than in *Ae. squarrosa* or *T. monococcum*. The mean K concentration and the sum of K and Na were, however, significantly ($P=0.05$) lower in *T. monococcum* than in *Ae. squarrosa*. Only minor differences in anion concentrations were recorded, and the Cl concentrations were not significantly different between the three species. There was no overlap in the K and Na concentrations of individual accessions or replicates of *T. monococcum* and *Ae. sharonensis*.

The 2nd experiment (Table 3) compared leaf Na and K concentrations in a large number of diploid wheat accessions (grown for 14 days at 50 mol m^{-3} NaCl + 2.5 mol m^{-3} $CaCl_2$) with those found in a range of other annual Triticeae. The species previously shown (Gorham 1990a, b; Gorham et al. 1990b) to lack the enhanced K/Na discrimination trait, viz. *T. durum*, *T. dicoccoides* and *Hordeum vulgare*, had mean leaf Na concentrations > 90 mol m^{-3}, mean leaf K concentrations < 130 mol m^{-3} and K/Na ratios < 1.5. The diploid wheats and *T. aestivum* had mean Na concentrations < 20 mol m^{-3}, mean K concentrations > 150 mol m^{-3} and K/Na ratios > 15. None of the diploid wheat or *T. aestivum* accessions had leaf Na concentrations as high as the lowest value found in *T. durum*, *T. dicoccoides* or *H. vulgare*. Although in this experiment K and K+Na concentrations were lower in *T. monococcum* than in *T. urartu* or *T. boeoticum*, they were also low in *T. aestivum*. Another, similar, experiment gave comparable results (data not shown).

The above results show that all three of the diploid wheat species showed an ability to discriminate between Na and K (when grown at 50 mol m^{-3} NaCl) similar to that which had previously been observed in *T. aestivum* and *Ae. squarrosa*. This contrasts with previous observations on diploid wheat grown at 100 mol m^{-3} NaCl (Wyn Jones et al. 1984; Shah et al. 1987), where the leaf Na concentrations were higher than in *T. aestivum* and *Ae. squarrosa*. In those experiments the leaf K concentrations were, however, higher than in *T. dicoccoides*, *Ae. speltoides* or *Ae. searsii* (all of which lack the enhanced K/Na discrimination character) and at least as high as in *T. aestivum* and *Ae. squarrosa*. The different results obtained at 50 and 100 mol m^{-3} NaCl may reflect differences in Na exclusion at higher salt concentrations. *T. monococcum* is reported to be much more sensitive to high alkalinity and salinity than *T. durum* or *T. aestivum* (Rana et al. 1980; Joshi et al. 1982).

The distribution ranges of the wild diploid wheats *T. boeoticum* and *T. urartu* overlap, but their hybrids are usually sterile (Johnson and Dhaliwal 1976) and they are clearly distinguishable on the basis of their isoenzymes and seed storage proteins (Caldwell and Kasarda 1978; Jaaska and Jaaska 1980; Waines and Payne 1987). Recent evidence suggests that *T. boeoticum* was the progenitor of the cultivated *T. monococcum*, whereas the A genomes of the polyploid wheats are derived from *T. urartu* (Kerby and Kuspira 1987; Dvorak et al. 1988).

Analysis of inorganic anions (data not shown) in the leaves of these plants showed no large differences in chloride concentrations (about 100 mol m^{-3}) between the diploid, tetraploid wheats and hexaploid species. There were no significant differences in nitrate concentrations (all ca. 100 mol m^{-3}) in these wheats, but *T. aestivum* had the lowest leaf phosphate and sulphate concentrations (38 and 0.5 mol m^{-3}, respectively). Phosphate concentrations were significantly higher in tetraploid wheats than in *T. aestivum*.

When the progenitors of modern bread wheat were examined for cation uptake in the presence of salt (Wyn Jones et al. 1984; Shah et al. 1987), it was found that the BBAA-genome tetraploid wheats (*T. durum* and *T. dicoccoides*) accumulated more Na and less K in their leaves than *T. aestivum*. A similar result was obtained by Weim-

Table 4. *Experiment 3.* Monovalent cation concentrations (mol m^{-3} expressed sap) in the youngest, fully emerged leaves of various aneuploids and their parents, grown for 14 days in nutrient solution, plus 50 mol m^{-3} NaCl and 2.5 mol m^{-3} $CaCl_2$. Values are means ± standard errors of three replicates

	Genome	Na	K	K+Na	K/Na
T. boeoticum G-2520	A^bA^b	10± 3	148±37	158±39	15.42±0.43
T. durum cv Langdon	BBA^dA^d	165±11	97± 4	261±11	0.59±0.05
Synthetic	$BBA^dA^dA^bA^b$	13± 2	193± 3	206± 3	15.10±2.11
T. durum cv Langdon 4D (4B) disomic substitution		12± 2	189± 6	200± 8	16.42±1.84
T. durum 56-1 (CI13423)	BBA^dA^d	159±11	129±15	288±26	0.81±0.04
56-1 nullisomic $4A^d$ disomic $4A^b$		8± 1	116±23	124±24	15.22±1.68
56-1 monosomic $4A^d$ disomic $4A^b$		6± 1	128± 7	134± 7	21.91±3.78

Table 5. *Experiment 4.* Accumulation of ^{22}Na in shoots of 'low-salt' seedlings after 48-h exposure to 1 mol m^{-3} NaCl plus 0.1 mol m^{-3} KCl labelled with 74 MBq m^{-3} ^{22}Na. Values are means ± standard errors

Plant material	Genome	Replicates	^{22}Na (Bq mg^{-1} fresh wt)
Aegilops squarrosa	DD	3	4.51±0.93
Triticum monococcum	A^mA^m	21	6.21±0.86
Triticum durum cv Langdon	BBA^dA^d	9	45.05±3.47
T. durum $4A^b(4A^d)$	$BBA^dA^d[4A^b(4A^d)]$	3	3.17±1.11
Synthetic	$BBA^dA^dA^bA^b$	5	8.61±0.90
T. aestivum cv Chinese Spring	BBA^dA^dDD	8	17.03±0.73

berg (1987). This difference could be ascribed to the presence of a trait for enhanced K/Na discrimination in the D genome (Shah et al. 1987; Gorham et al. 1987). The enhanced K/Na discrimination trait appears to be absent from the S-genome *Aegilops* species (Gorham 1990b), which are thought to form the basis of the B and G genomes of tetraploid wheats. The original results obtained with diploid wheat suggested that the trait was not present in the A genome, but subsequent work has indicated that it does occur in *T. monococcum*, *T. boeoticum* and *T. urartu* (Gorham 1990c; Tables 2–4 above). The lack of enhanced K/Na selectivity in BBAA-genome wheats may be the result of structural rearrangement of chromosome 4A preventing expression of the gene(s). The exact mechanism leading to the absence of enhanced K/Na discrimination in BBAA-genome tetraploid wheats is not known. A similar situation exists in a number of tetraploid *Aegilops* species. *Ae. ventricosa, Ae. biunicialis, Ae. kotschyi* and *Ae. variabilis* do not appear to exhibit the enhanced K/Na discrimination character, although it is present in other diploid and polyploid *Aegilops* species containing the D or U genomes (Gorham 1990b).

Chromosomal location of the enhanced K/Na discrimination trait in the A genome

In *T. aestivum* the enhanced K/Na discrimination trait has been located on the long arm of chromosome 4D (Gorham et al. 1987). In the 3rd experiment we have examined the leaf cation concentrations in a partial substitution line in which one $4A^d$ chromosome of *T. durum* 56-1 was replaced by the two $4A^b$ chromosomes from an accession of *T. boeoticum* (Joppa and Maan 1982). Two types of progeny were obtained from this line: plants with normal morphology that were monosomic for chromosome $4A^d$, and extremely dwarf plants that were nullisomic for chromosome $4A^d$. In both cases the leaf Na concentrations in plants grown for 14 days at 50 mol m^{-3} NaCl + 2.5 mol m^{-3} $CaCl_2$ were similar to those found in *T. boeoticum* and much lower than in the original *T. durum* parent (Table 4). K concentrations were, however, not significantly higher than in the euploid parent.

These findings appear to be confirmed by the results of Experiment 4, in which ^{22}Na accumulation in the shoots of 'low-salt' seedlings was measured in plants incubated for 48 h in labelled 1 mol m^{-3} NaCl + 0.1 mol m^{-3} KCl (Table 5). The $4A^b(4A^d)$ substitution line accumulated less than one-tenth the ^{22}Na accumulated by *T. durum* cv Langdon. Thus the enhanced K/Na discrimination character appears to be on chromosome 4 in both the A and D genomes.

Chromosome 4A of diploid wheats does not appear to occur intact in BBAA-genome tetraploid wheats (Wazuddin and Driscoll 1986; Gill and Chen 1987). The main reason for the previous misidentification of chromosomes 4A and 4B (Dvorak 1983; Rayburn and Gill

Table 6. *Experiment 5.* Monovalent cation concentrations (mol m^{-3} expressed sap) in the youngest, fully emerged leaves of various amphiploids, grown for 14 days in nutrient solution, plus 50 mol m^{-3} NaCl and 2.5 mol m^{-3} $CaCl_2$. Values are means ± standard errors of three replicates

	Genome	Na	K	K+Na	K/Na
T. boeoticum × *T. urartu*[a]	$A^bA^bA^uA^u$	32±16	275±33	307±48	12.57±3.81
T. boeoticum × *Ae. squarrosa*[b]	A^bA^bDD	25±13	240± 5	265±12	16.23±7.07
T. boeoticum × *T. araraticum*[a]	$A^bA^bGGA^aA^a$	39± 4	216± 2	255± 2	5.71±0.59
T. timopheevii × *Ae. squarrosa*[b]	GGA^tA^tDD	42± 5	225±16	268±20	5.37±0.40
Ae. speltoides × *T. monococcum*[a]	SSA^mA^m	75± 9	187± 8	262±12	2.57±0.36
T. durum × *Ae. caudata*[c]	BBA^dA^dCC	143± 5	146± 7	289± 8	1.02±0.06

Sources:
[a] Dr. D. Barnhart, University of California, Riverside, USA
[b] Prof. G. Kimber, University of Missouri, Columbia, USA
[c] Dr. R. Simeone, Plant Breeding Institute, Bari, Italy

1985) appears to be the extensive rearrangements of chromosomes 4A (Naranjo et al. 1987; Chao et al. 1989). One possiblity is that the enhanced K/Na discrimination trait may have been lost or may no longer be expressed, as a direct result of these rearrangements.

K/Na discrimination in amphiploids

The previous finding (Gorham 1990c) that the enhanced K/Na discrimination character was expressed in amphiploids derived from hybrids between tetraploid and diploid wheats (Gill et al. 1988) was confirmed in the present investigation (Table 4), using a $BBA^dA^dA^bA^b$-genome hexaploid obtained from Dr. L. R. Joppa. The diploid wheat parent, *T. boeoticum* G-2520, and the synthetic hexaploid both had low leaf Na concentrations and high leaf K concentrations, whereas the tetraploid parent (*T. durum* cv Langdon) had high leaf Na and low leaf K concentrations. The values for the synthetic hexaploid were similar to those obtained with the 4D(4B) disomic substitution line in cv Langdon (Gorham, et al. 1987). Accumulation of ^{22}Na in the shoots of 'low-salt' seedlings of the synthetic hexaploid was also lower than in the shoots of cv Langdon (Table 5). Thus, it is now well established that the enhanced K/Na discrimination trait on both the A and D genomes is dominant in hybrids with species lacking the trait.

K/Na discrimination in a number of synthetic amphiploids was measured in Experiment 5 (Table 6). In the *T. durum* × *Ae. caudata* amphiploid the enhanced K/Na discrimination trait was not expected to be expressed, since both parents lack the trait (Gorham 1990b). As expected, all of the amphiploids involving *T. boeoticum* showed enhanced K/Na discrimination, since in all cases the trait is present in both parents. The low leaf Na and high leaf K concentrations obtained with the *T. timopheevi* × *Ae. squarrosa* amphiploid confirm that the trait in the D genome is dominant in hybrids (Shah et al. 1987; Gorham 1990c). The hybrid between *T. monococcum* and *Ae. speltoides* also suggests that the enhanced K/Na discrimination trait on the A genome is dominant, although the Na concentrations are higher, and the K concentrations lower, than in the other amphiploids which are thought to possess this trait. Thus, if the progenitors of the tetraploid wheats resembled this AASS-genome hybrid, they would probably have had greater K/Na discrimination than modern tetraploid wheats. More examples of this type of amphiploid need to be examined.

Acknowledgements. The authors gratefully acknowledge the financial support of the Overseas Development Administration of the United Kingdom, and would like to thank Dr. L. R. Joppa, Dr. C. N. Law, Terry Miller, Prof. J. Dvorak, Prof. J. G. Waines, Dr. T. McNeilly, Dr. A. Mujeeb-Kazi, Dr. R. Loiselle, Dr. K. J. Symes and Dr. W. J. Raupp for supplying the seeds used in these experiments.

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