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ORGANIC AND INORGANIC SOLUTE CONTENTS AS SELECTION CRITERIA FOR SALT TOLERANCE IN THE TRITICEAE.

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INTRODUCTION

This conference is itself a further indication of the growing international concern at the progressive salinization and alkalinization of many irrigated lands. While good agronomic practises and water management are essential to combat the problem, the urgent need to compensate, at least in part, for the degeneration in soil conditions and the paucity of good quality water by breeding crop plants of greater tolerance is also being appreciated (e.g. Epstein et al., 1980). Closely allied to this aspect of irrigation agriculture are the twin problems of drought and salt tolerance in arid zones where a combination of water and salt stress generally limit productivity.

In no group of plants is the need to understand and manipulate the characters conferring tolerance more apparent than in the graminaceous tribe, the Triticeae. Within this tribe are found several of the world's most important crop plants - various forms of wheat, barley, rye and the increasingly important hybrid, Triticale. Wheat alone accounts for approximately a quarter of the worlds food production, while barley, rye and triticale together account for a

further 15 - 18 %. Barley and rye are commonly regarded as robust crop species resistant to a number of environmental stresses including salt. Bread wheats are, in contrast, generally thought to be less resistant to salt stress (Maas and Hoffmann, 1977). Nevertheless, as wheats are the more important sources of human nutrition, the study and ultimately the improvement of salt tolerance in this crop deserves the highest priority.

There are cogent reasons to expect significant progress in the breeding of wheat for enhanced tolerance without recourse to the unproven, though exciting, techniques of genetic engineering. Within the existing 20,000 or so wheat cultivars there is a range of tolerance (e.g. Tornes and Bingham, 1973; Bernal *et al.*, 1974; Qureshi *et al.*, 1980) and, by selection and breeding from within this gene pool, it is possible that some improvement could be achieved. However, it might be more advantageous to cast the net wider as there are members of the Triticeae with relatively high salt and drought tolerances. Cytogeneticists are now able to hybridize many of these ´alien´ relatives with *T. aestivum* or *T. turgidum* (see Figure 1) and bring about the transfer of chromosome fragments (Sears, 1981). Thus there is an expectation that this genetic variability can in time be exploited to produce highly tolerant wheats. The problems of achieving such transfers should not be underestimated and it will undoubtedly take time to produce agronomically valuable cultivars in which characters from an alien grass are expressed in a genetic background giving other desirable agronomic traits. Unfortunately we know remarkably little about the nature, inheritance, segregation *etc.* of the character (almost certainly several different characters) which confer tolerance.

An essential first step in any attempt to exploit the variability in relation to salt tolerance in alien members of the Triticeae is a survey to establish the degree and mechanisms of salt tolerance in these species. Factors such as chromosome number must also be recorded as they will influence the ease with which subsequent cytogenetic manipulations can be carried out. Such data should then allow the selection of aliens for a wide crossing programme with wheat. It would also be advantageous to devise simple selection criteria in order to follow the fate of the salt tolerance characters through the extensive back crossing and commercial breeding programmes that will be required. A purely pragmatic approach could and perhaps ought to be followed in which the tolerance of progeny from a wide crossing programme are simply selected in field trials without any biochemical or physiological input. Such empirical methods have served breeders well over many decades (see Simmonds, 1983). Nevertheless, as we hope will become apparent in the course of this paper, there are good reasons to expect biochemical and physiological data to be of value in tackling this problem and that collaboration between biochemists and the cytogeneticists and breeders would be highly desirable.

In this paper we describe some experiments which contribute to laying the groundwork for a long term investigation of this problem. Two principal approaches have been used. Firstly, since the ancestry of the modern hexaploid bread wheats is now established with some confidence (see Feldman and Sears, 1981), we have compared the salt tolerance and patterns of ion accumulation found in these ancestors and in a selection of hexaploid cultivars. Any attempt at screening the formidable numbers of wheat cutivars now available

would be quite beyond our resources. Secondly, we have followed the earlier studies of Dewey (1960) and Shannon (1978) and examined accessions of both *Agropyrum elongatum*, which was shown by these authors to be a potential source of salt tolerance, and of other, previously unexamined, species of *Agropyrum*. Since *Elymus* (*Leymus*) species can now be hybridized with wheat (Mujeeb-Kazi and Rodriguez, 1981) and are often found in saline and arid environments, they have also been investigated.

There has been considerable interest in the possible role of proline and glycinebetaine in both drought and salt tolerance and in the possibility that the ability to accumulate these solutes might confer tolerance (*cf.* Valentine, 1983; Wyn Jones and Gorham, 1983). It was, therefore, of particular interest to examine the levels of these solutes in a variety of wheats and alien species which showed differences in tolerance and ion accumulation patterns.

ION ACCUMULATION PATTERNS AND SALT TOLERANCE IN HEXAPLOID WHEATS AND THEIR ANCESTORS.

The cytogenetic studies of Sears, Feldman and their colleagues, now supplemented by more biochemical data on DNA sequences, have established a probable evolutionary pathway for the hexaploid bread wheats (Feldman and Sears, 1981; Sears, 1981; but see also Peacock *et al.*, 1981 for reservations. see Figure 2). Paleobotanical studies have also partially illuminated the occurrence and distribution of the various primitive wheats (Harlan, 1981). By historic times the hexaploid wheats had become dominant although the tetraploid durum wheats derived from *T. turgidum* are still grown extensively in drier regions. Some primitive emmer and einkorn

wheats may still be found in remote areas.

A number of trials have been carried out to compare the salt tolerance and ion accumulation patterns of the wheat ancestors (Tables 1 and 2). The diploid *T. monococcum* was found to be very salt sensitive while *Aegilops searsii*, the putative source of the B genome, and the tetraploid *T. dicoccoides* were somewhat more tolerant. *A. squarrosa* exhibited marginally greater tolerance as did the hexaploid bread wheat used in this experiment, *T. aestivum* *cv.* Ciano 67. (Variations within the hexaploid wheats will be alluded to later). The ion accumulation patterns suggested interesting differences between the various species (Table 2,Figure 3). Both *A. searsii* and *T. dicoccoides* had very low K^+/Na^+ ratios even at modest salinities and appear to tolerate lower leaf K^+ levels than *T. monococcum*. In a direct comparison of *T. monococcum* and *T. dicoccoides* carried out under conditions of low transpirational demand (Figure 3), the differences between these species was illustrated dramatically. It should be noted that growth of *T. monococcum* was severely inhibited by 100 mol m^{-3} NaCl in this trial despite the low leaf levels of Na^+ and Cl^-. However, in experiments carried out in the summer, presumably with higher transpiration rates, high Na^+ and Cl^- levels were found even in *T. monococcum*. These data indicate tentatively that the B genome from *A. searsii* or a close relative contributed a modestly enhanced salt tolerance in comparison with *T. monococcum* and the ability to withstand a higher leaf salt load. In contrast, *A. squarrosa* is a more efficient salt excluder maintaining a higher K^+/Na^+ ratio. This same character is found in many of the hexaploid wheats (see also Figure 4) and may be associated with the D genome from *A.*

squarrosa. Since genotypic variation within these grasses is very great, and since we have examined the response to salinity of only a few individuals, any correlation of ion transport characters with evolutionary pathways must be regarded as extremely tentative.

Further data on four bread wheats, one *T. turgidum* cultivar and one *Triticale* are presented in Table 3 and Figure 4. Both with regard to the salt tolerance and ion accumulation patterns the cultivar Cheyenne is typical of a number of the hexaploid wheats. Data for Kogo II was presented since this was one of the most salt sensitive cultivars tested and appeared to be a less efficient excluder at salinities greater than 75 mol m^{-3} NaCl. By way of contrast Atou was the most tolerant cultivar tested. Few tetraploid wheats have yet been screened but the data from Cocorit 71 suggest that it has some characteristics similar to *T. dicoccoides*. The *Triticale* cultivar, on the other had, is an efficient salt excluder. Jeschke and his collaborators (Jeschke and Nassery, 1981; Jeschke and Moreth, 1979) have shown that there is an efficient K^+/Na^+ exchange system at the plasmalemma of cortical cells in *T. aestivum cv.* Carstacht, and in rye. It would be of great interest if differences in the efficiency of such exchange systems were to occur in the wheat ancestors and could be related to the ion accumulation patterns presented here. Certainly if particular ion transport characters can be associated with specific genomes, and ultimately with single chromosomes, it could open up a productive line of physiological and biochemical studies as well as being of potential practical importance.

In these experiments it might be objected that the Na^+/Ca^{2+} ratio is not kept constant (*cf.* Greenway and Munns, 1980). However, neither in *T. aestivum cv.* Flanders nor in *T. dicoccoides* (Table 4) were significant differences detected in the salt tolerance between plants subjected to NaCl or to NaCl with $CaCl_2$ added so as to maintain a constant Na:Ca ratio of 10:1. More detailed experimentation on the effects of different salt mixtures at different relative humidities *etc.* on the wheat ancestors is now in progress.

SALT TOLERANCE IN AGROPYRUM AND ELYMUS (LEYMUS) SPECIES.

With the possible exception of *Triticale* GLT 176 the degree of salt tolerance exhibited by the wheat cultivars and ancestors was modest. As already mentioned *Agropyrum* and *Elymus* species are possible sources of far greater tolerance. However, the earlier work also indicated great variation even within a single species. This was confirmed by a study of 5 different accessions of *Agropyrum elongatum* (Table 5). Great diversity was found even within this species and no simple correlation was observed with any of the ion uptake characteristics measured. The accession from China (20014) was considerably more tolerant than any of the hexaploid wheats tested so far and was apparently able to withstand a substantial leaf salt load. This accession could be regarded as a potential candidate for a crossing programme but unfortunately it has a high level of ploidy (Law. personal communication).

With the generous cooperation of Dr. Dewey we have been able to test a variety of other *Agropyrum* species, which again showed a wide range of tolerance from the relatively sensitive *A.*

intermedium (*cf.* Elzam and Epstein, 1969) to the highly tolerant *A. junceum* (Table 7). The latter also appears to exclude Na and Cl from its leaves very efficiently, thus exhibiting a character frequently associated with tolerance in glycophytic crop species (see Wyn Jones, 1981 and Greenway and Munns, 1980 for references). This species is also of particular interest since it has recently been reported to be very drought tolerant (Shimshi *et al.*, 1982). Furthermore its low chromosome number (2n=14) makes it a suitable subject for cytogentic work and Mujeeb-Kazi and Rodriguez (1981) have reported intergeneric hybrids between a hexaploid *A. junceum* (2n=6x=42) and *T. aestivum* and *T. turgidum*.

A similar trial to that on the *Agropyrum* species has been conducted on a number of *Elymus* species (Table 8). A considerable degree of salt tolerance was observed in all the species tested except for *E. triticoides*. However, very different ion accumulation patterns were observed, as may be seen from a comparison of *E. dahuricus* and *E. sabulosus*. The former grew quite well with a low leaf K^+/Na^+ ratio and high leaf Na and Cl load, whereas the latter maintained a high K^+/Na^+ ratio and efficiently excluded Na and Cl. This salt exclusion trait was even more pronounced in *E. sabulosus* than in *A. junceum*. It should also be noted that the two *Elymus* species differed radically in their morphology. *E. sabulosus* has tough, grey-green, waxy leaves while *E. dahuricus* has green, apparently less robust leaves. On the basis of these crude data it is not apparent how the former species is able to adjust osmotically to 200 mol m^{-3} NaCl and it must be assumed that some other (organic?) solutes are accumulated in quantity.

PROLINE AND GLYCINEBETAINE ACCUMULATION.

One aim of these experiments was to consider whether the cytosolutes, proline and glycinebetaine, might be correlated with tolerance in the Triticeae. Some typical data for glycinebetaine and proline for a range of species, cultivars and accessions are shown in Table 6. An inspection of this table and the salt tolerance data in Tables 1,3,5,7 and 8 immediately shows that no correlation was found. Similarly in the _Elymus_ species neither the constitutive nor salt induced levels of these solutes were related to salt tolerance (Table 9). Perhaps the only point to emerge is that in the two most efficient salt excluders found so far (_A. junceum_ and _E. sabulosus_) the leaf glycinebetaine content is completely unaffected by the stress. In _E. sabulosus_ there is no proline induction either, but this has yet to be tested in the _Agropyrum_ species.

DISCUSSION.

The data presented here are derived from a preliminary survey of some members of the Triticeae and must be supplemented by further screening of other alien accessions, and by more detailed work on the aliens which appear to be of physiological or biochemical interest and of agronomic potential. Even these initial results show clearly that some accessions could provide sources of salt tolerance characters for the bread wheats. However, they have also raised other difficult issues. The characters which confer such tolerance and their possible agronomic consequences are remarkably badly defined. In a number of instances there are indications that tolerance is associated with more efficient Na^+ or Cl^- exclusion,

e.g. in *Aegilops squarrosa*, and certainly this is a major character in *Agropyrum junceum* and *E. sabulosus*. However, other species (*E. dahuricus*, possibly *Agropyrum scirpeum* and, to a limited extent, even *Aegilops searsii*) seem to exhibit tolerance (certainly a considerable tolerance in the case of *E. dahuricus*) with a relatively high leaf salt load.

One major issue which must now be faced is whether these differences are of importance agronomically. For example, the difficulty of understanding, on the basis of this very limited evidence, how osmotic adjustment is achieved in *E. sabulosus* introduces the question of the cost of turgor regulation to the plant. As we have argued previously (*e.g.* Wyn Jones, 1981), naive calculations indicate that tolerance by salt accumulation requires less diversion of metabolic energy than the alternative of ion exclusion from the leaves and the accumulation of organic solutes. Nonetheless, there is no firm basis for such speculations and in this context a detailed examination of the relative growth rates and patterns of osmotic and turgor regulation and solute accumulation of the two pairings, *E. sabulosus vs. E. dahuricus* and *Agropyrum curvifolium vs. A. scirpeum*, could be of great value. Certainly this question is crucial to any programme of genetic manipulation. If tolerance by exclusion is compatible with rapid growth and high yields then its introduction from the aliens described in this paper is a distinct possibility. Furthermore, characters such as a high leaf K^+/Na^+ ratio and low Cl^- content offer the prospect of simple screening procedures which could be automated to meet the requirements of plant breeders. If, on the other hand, this is not the case then we are faced with the much more difficult

physiological and biochemical problem of identifying the characters which are associated with an ability to tolerate a high leaf salt load, and the problem of clearly distinguishing this type of tolerance from the sudden increase in leaf NaCl so often associated with severe growth inhibition (see Figure 4, Cheyenne). Furthermore, if we compare the data presented in Figure 4 for the 3 bread wheats, Cheyenne, Atou and Kogo II, we have no objective way of explaining the differences between salt uptake into the leaves of Kogo II, which is associated with inhibition of leaf growth, and that in Atou in which it appears to be tolerated. Differences in solute compartmentation may be involved, but there is insufficient hard evidence to support such speculations. Clearly there is also an urgent need for more fundamental studies if we are to be able to give meaningful advice to plant breeders.

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TABLE 1. INFLUENCE OF SALT STRESS ON THE GROWTH (FRESH WEIGHT) OF A REPRESENTATIVE BREAD WHEAT AND SOME ANCESTORS OF MODERN BREAD WHEATS.

Species[2]	Shoot fresh weight yield as % of low salt control Plants grown with additions of NaCl (mol m^{-3})[1] 0	75	150
T. monococcum	100	22	12
A. searsii	100	40	30
T. dicoccoides	100	52	33
A. squarrosa	100	52	42
T. aestivum cv. Ciano 79	100	62	40

[1] Plants grown in hydroponic culture in 1/2 strength Hoagland's medium in a glasshouse with supplementary light. Salt was added in 25 mol m^{-3} increments per day until the final concentration in the medium had been reached. The plants were harvested after 2 weeks at the final salinity.

[2] Ancestral species kindly supplied by Dr.C.N. Law, Plant Breeding Institute, Cambridge and Ciano 79 by Centro Internacional de Mejoramiento do Maiz y Trigo.

TABLE 2. MAJOR ION CONTENTS OF WHEAT ANCESTORS SUBJECTED TO SALT (NaCl) STRESS[1].

	Shoot ion contents (mmol kg^{-1} plant water)				
	Low salt controls		Salt treated plants (100 mol m^{-3})		
Species	K^+	Na^+	K^+	Na^+	K/Na
T. monococcum	183	6	160	301	0.54
A. searsii	198	4	92	377	0.24
T. dicoccoides	179	4	84	332	0.25
A. squarrosa	166	4	158	154	1.03
T. aestivum cv. Flanders	199	3	169	114	1.48

[1] Plants grown as outlined in Table 1.

Table 3. EFFECT OF SALT (NaCl) STRESS ON THE FRESH WEIGHT YIELD OF SHOOTS OF 4 CULTIVARS OF *T. AESTIVUM*, ONE TETRAPLOID WHEAT AND ONE TRITICALE CULTIVAR.[1]

Variety	Comments	Shoot fresh weight as % of low salt controls at different NaCl treatments (mol m^{-3})			
		75	150	200	250
T. aestivum cv.					
Chinese spring	Used in cytogenetic research	49	41	25	15
Capelle-Desprez	French winter wheat	45	40	38	15
Kogo II	European spring wheat	72	45	17	*
Cheyenne	North American frost resistant winter wheat	50	43	35	15
Atou	High vigour winter wheat	77	54	50	29
T. turgidum cv.					
Cocorit 71		70	27	27	38
Triticale cv.					
GLT 176		(80)[2]	71	64	N.D.

[1] Growth conditions as outlined in Table 1.
[2] Extrapolated from another experiment.
N.D. not determined.
* no survivors.

TABLE 4. COMPARISON OF THE EFFECTS OF CONSTANT AND VARIABLE $Na^+:Ca^{2+}$ RATIOS ON THE SALT TOLERANCE OF *T. AESTIVUM* cv. FLANDERS AND *T. DICOCCOIDES*.

	Shoot yield (fresh weight in g) of plants grown at different NaCl levels (mol m^{-3})				
	0	25	75	150	225
T. aestivum cv. Flanders					
changing ratio	62 ± 7	-	48 ± 7	22 ± 2	14 ± 1
constant Na:Ca[2]	-	64 ± 9	56 ± 7	20 ± 4	15 ± 3
T. dicoccoides					
changing ratio	31 ± 2	-	9 ±3	8 (2 reps)	*
contant Na:Ca[2]	-	30 ± 4	14 ± 2	6 (1 rep)	*

[1] Values are means of 5 replicates except where stated

[2] A constant ratio of Na^+ to Ca^{2+} (10:1) was maintained by adding $CaCl_2$

* no survivors

TABLE 5. INFLUENCE OF SALINITY ON THE GROWTH (FRESH WEIGHT) AND ION CONTENT OF VARIOUS ACCESSIONS OF AGROPYRUM ELONGATUM[1] AND T. AESTIVUM cv. FLANDERS (accession no. 10030).

Accession number	Origin	Fresh weight at 200 mol m^{-3} as % of controls	Ion contents (mmol kg^{-1} plant water) of plants grown in 200 mol m^{-3} NaCl			
			K^+	Na^+	Cl^-	K/Na
20003	U.S.S.R.	41	177 (182)[2]	161	184	1.1
20004	Turkey	16	152 (157)	140	214	1.1
20014	China	80	222 (159)	213	230	1.0
20007	Iran	44	-	-	-	-
20010	Israel	34	186 (278)	466	494	0.4
10030	U.K.	23	133 (193)	164	219	0.8

[1] Kindly supplied by the Germplasm Resources Laboratory.
[2] Figures in brackets are low salt control potassium contents.

TABLE 6. GLYCINEBETAINE CONTENTS OF SOME WHEAT CULTIVARS AND AGROPYRUM SPECIES.

Species	Glycinebetaine content[1] ($mmol\ kg^{-1}$ fresh weight) Low salt controls	salt treated (200 $mol\ m^{-3}$ NaCl)
T. aestivum cv.		
Chinese spring	0.6	10.0
Flanders	1.7	2.8
Triticale	3.8	17.0
A. elongatum		
20003	6.2	8.8
20014	2.9	9.8
A. intermedium	1.8	2.6
A. scirpeum	6.5	8.7
A. junceum	3.5	2.1
A. curvifolium	1.9	2.5
A. dasystachyum	3.3	4.6

[1] Determined by the method of Gorham *et al.*, 1982.

TABLE 7. INFLUENCE OF SALINITY ON THE GROWTH (FRESH WEIGHT) AND ION CONTENTS OF VARIOUS AGROPYRUM SPECIES.

Species, origin and chromosome number	Fresh weight at 200 mol m^{-3} NaCl as % of controls	Ion content kg^{-1} plant water) of plants grown at 200 mol m^{-3} NaCl			
		K^{+}	Na^{+}	Cl^{-}	K/Na
A. intermedium Latvia, 2n=42	26	186 (180)[1]	215	377	0.9
A. scirpeum Aegean, 2n=48	60	156 (212)	209	235	0.7
A. junceum U.S.S.R., 2n=14	106	173 (185)	102	184	1.7
A. curvifolium Spain, 2n=28	64	262 (194)	128	252	2.1
A. dasystachyum Canada, 2n=28	31	159 (173)	156	225	1.0

[1] control values.

TABLE 8. INFLUENCE OF SALINITY ON THE GROWTH (FRESH WEIGHT) AND ION CONTENTS OF VARIOUS ELYMUS SPECIES.

Species, origin and chromosome number	Fresh weight at 200 mol m^{-3} NaCl as % of controls	Ion contents (mmol kg^{-1} plant water) of plants grown at 200 mol m^{-3} NaCl			
		K^{+}	Na^{+}	Cl^{-}	K/Na
E. giganteus U.S.S.R., 2n=63	63	192 (290)[1]	151	216	1.3
E. dahuricus U.S.S.R., 2n=67	67	90 (176)	217	245	0.4
E. angustus U.S.S.R., 2n=78	78	254 (301)	106	170	2.4
E. sabulosus U.S.S.R., 2n=70	70	232 (275)	60	125	3.8
E. triticoides unknown, 2n=28	46	220 (199)	72	157	3.1

[1] control values.

TABLE 9. EFFECTS OF SALINITY ON THE GLYCINEBETAINE AND PROLINE CONTENTS (mmol kg^{-1} fresh weight) OF SOME *ELYMUS* SPECIES.

Species	Glycinebetaine		Proline	
	low salt control	NaCl 200 mol m^{-3}	low salt control	NaCl 200 mol m^{-3}
E. giganteus	4.4	4.4	0.2	1.9
E. dahuricus	4.5	5.6	0.3	6.2
E. angustus	4.3	3.2	0.2	1.0
E. sabulosus	3.9	4.0	0.3	0.2
E. triticoides	7.4	14.2	0.6	1.8

Legends to Figures

Figure 1. Details of growth habit and genetics for the different genera within the Triticeae (redrawn from Feldman and Sears, 1981).

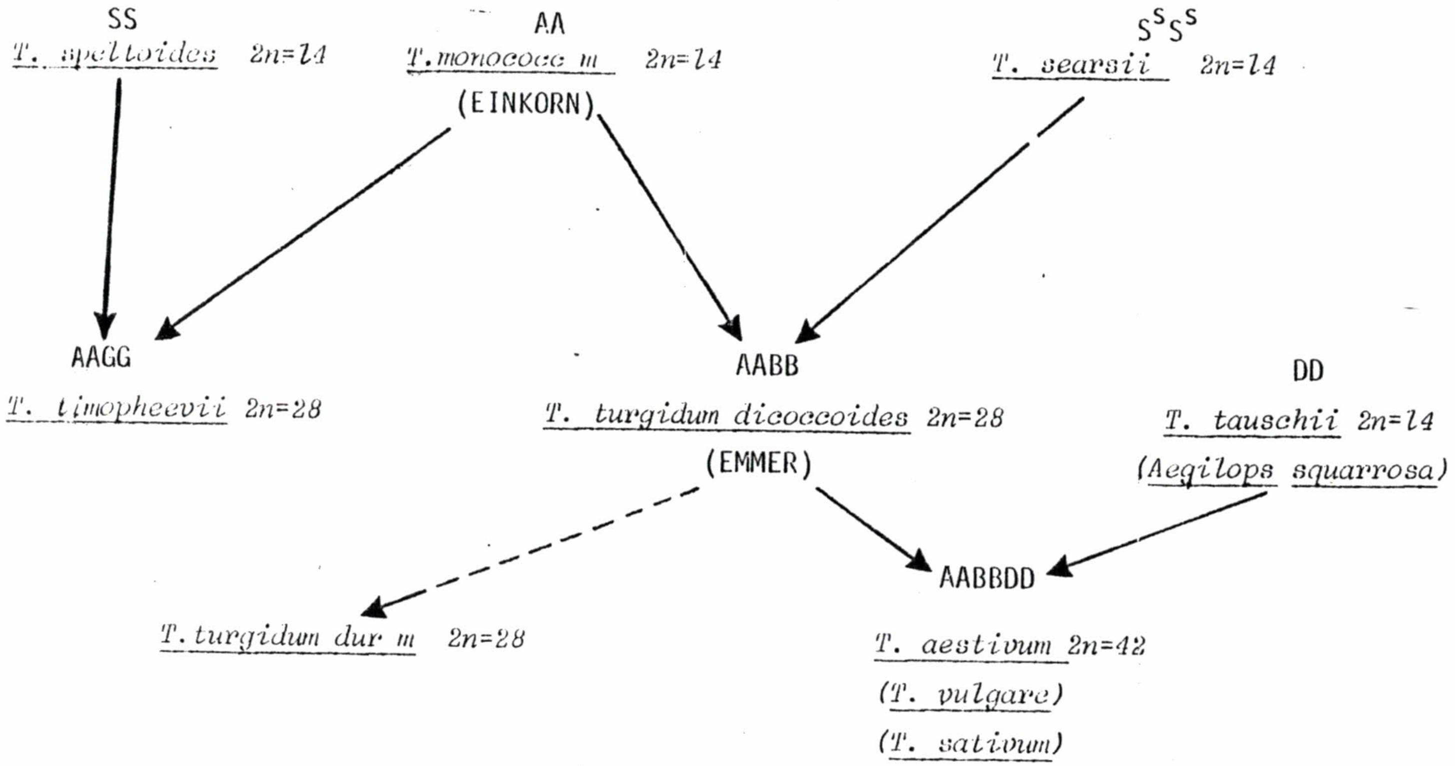
Figure 2. Probable evolutionary pathways of hexaploid wheat (from Feldman and Sears, 1981; Sears, 1981).

Figure 3. Inorganic ion contents of T. *monococcum* and *T. dicoccoides* grown at different NaCl levels (for growth conditions see Table 1).

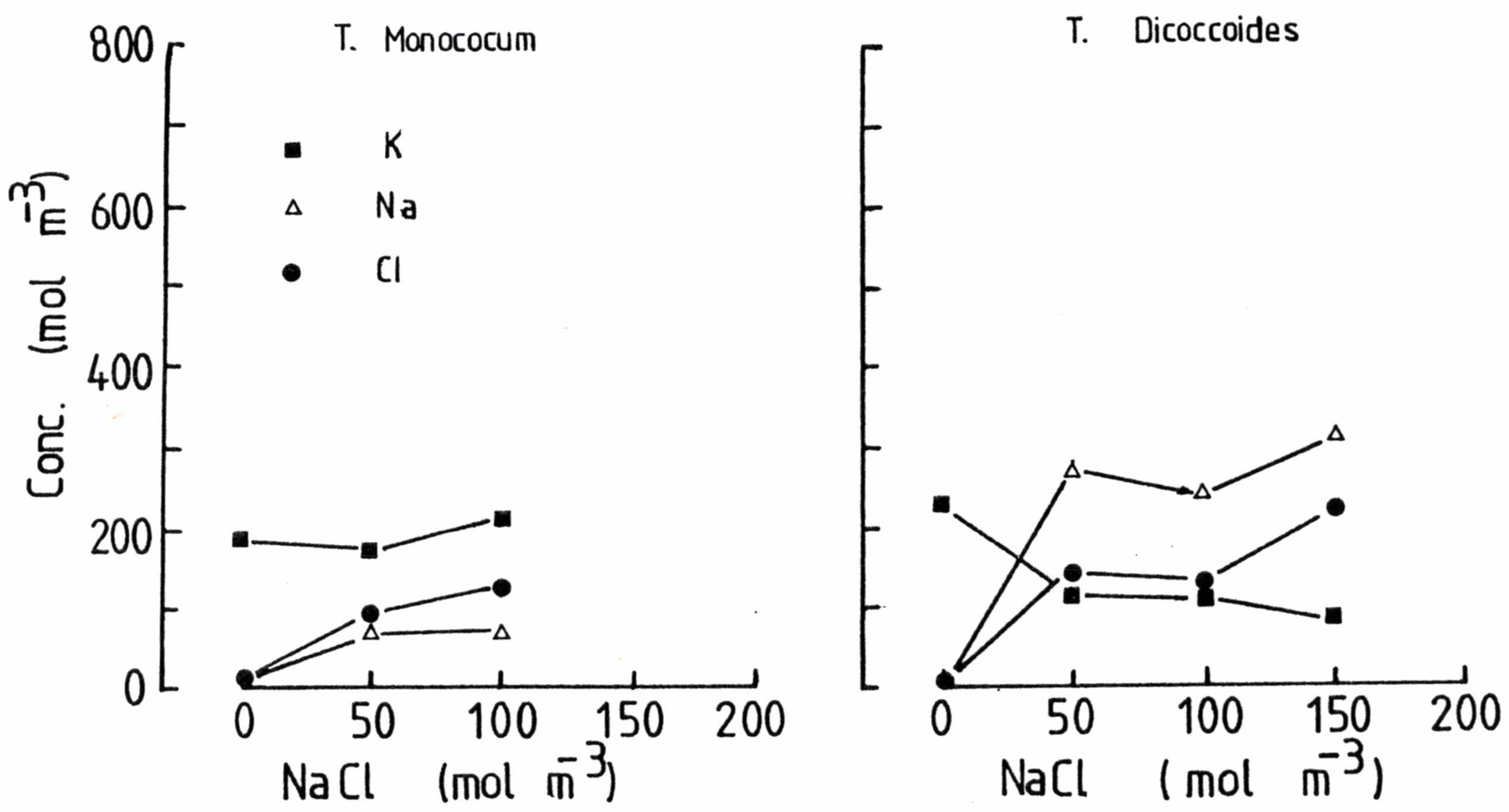
Figure 4. Inorganic ion contents of cultivated tetraploid and hexaploid wheats and a Triticale grown at different levels of NaCl (for growth conditions see Table 1).

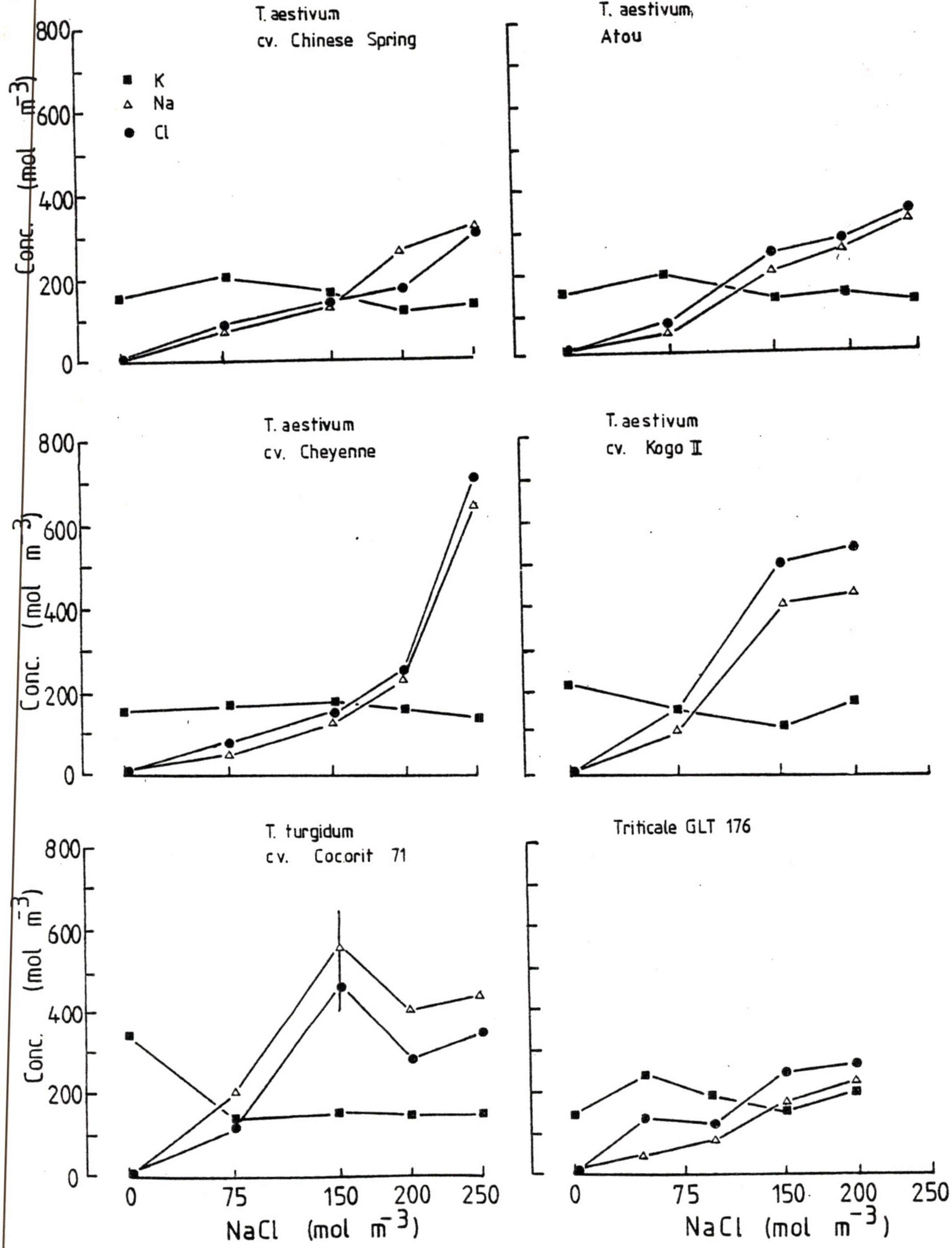
SUBTRIBE	GENUS	NUMBER OF SPECIES	PLOIDY LEVEL (X = 7)	GROWTH HABIT			MODE OF POLLINATION			SUCCESSFUL HYBRIDS WITH TRITICUM
				PEREN-NIAL	PEREN-NIAL ANNUAL	ANNUAL	CROSS	CROSS, SELF	SELF	
HORDEINAE	Hordeum	25	2X-6X		■			■		■
	Elymus	60	2X-12X	■				■		■
	Asperella	7		■			■			
	Sitanion	1	4X	■			■			
	Psathyrostachys	6		■			■			
	Crithopsis	1	2X			■			■	
	Taeniatherum	2	2X			■			■	■
TRITICINAE	Agropyrum	100	2X-10X	■			■			■
	Haynaldia	2	2X,4X		■		■			■
	Secale	6	2X		■		■			■
	Heteranthelium	1	2X			■			■	
	Henrardia	2	2X			■			■	
	Eremopyrum	5	2X,4X			■			■	■
	Triticum	27	2X-6X			■		■	■	■

Fig 2: Probable Evolutionary Pathways of Hexaploid Wheat[1]



[1] Feldman & Sears (1981) Sears (1981)


T. Monococum
T. Dicoccoides
K
Na
Cl
Conc. (mol m^{-3})
800
600
400
200
0
0
50
100
150
200
NaCl (mol m^{-3})
0
50
100
150
200
NaCl (mol m^{-3})


T. aestivum
cv. Chinese Spring
K
Na
Cl
T. aestivum,
Atou
T. aestivum
cv. Cheyenne
T. aestivum
cv. Kogo II
T. turgidum
cv. Cocorit 71
Triticale GLT 176
Conc. (mol m-3)
0
200
400
600
800
0
75
150
200
250
NaCl (mol m-3)