Theor Appl Genet (1992) 84: 714–719

THEORETICAL AND APPLIED GENETICS

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The expression of salt tolerance from *Triticum tauschii* in hexaploid wheat

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Received September 25, 1991; Accepted February 26, 1992
Communicated by G. S. Khush

Summary. Accessions of *Triticum tauschii* (Coss.) Schmal. (D genome donor to hexaploid wheat) vary in salt tolerance and in the rate that Na$^+$ accumulates in leaves. The aim of this study was to determine whether these differences in salt tolerance and leaf Na$^+$ concentration would be expressed in hexaploid wheat. Synthetic hexaploids were produced from five *T. tauschii* accessions varying in salt tolerance and two salt-sensitive *T. turgidum* cultivars. The degree of salt tolerance of the hexaploids was evaluated as the grain yield per plant in 150 mol m^{-3} NaCl relative to grain yield in 1 mol m^{-3} NaCl (control). Sodium concentration in leaf 5 was measured after the leaf was fully expanded. The salt tolerance of the genotypes correlated negatively with the concentration of Na$^+$ in leaf 5. The salt tolerance of the synthetic hexaploids was greater than the tetraploid parents primarily due to the maintenance of kernel weight under saline conditions. Synthetic hexaploids varied in salt tolerance with the source of their D genome which demonstrates that genes for salt tolerance from the diploid are expressed at the hexaploid level.

Key words: Wheat – Salinity – Genetics

Introduction

Hexaploid wheat (*Triticum aestivum*, AABBDD) is significantly different from tetraploid wheat (*T. turgidum*, AABB) in many phenotypic characters. These differences may be due to the addition of nuclear genes from *T. tauschii* (the D genome donor), to physiological changes caused by increases in ploidy level, and/or to the interaction between genes on the A, B and D genomes. One example of the effect of nuclear genes from *T. tauschii* on hexaploid wheat is the composition of seed storage proteins. Storage proteins, controlled by genes on the D genome, play a critical role in producing a flour that is suitable for bread baking (Orth and Bushuk 1973).

Genes for salt tolerance may also be located on the D genome. Many studies have shown that *T. aestivum* is more salt-tolerant and accumulates less Na$^+$ in leaves than *T. turgidum* (Francois et al. 1986; Rawson et al. 1988). Shah et al. (1987) examined the changes in growth and ion accumulation due to the addition of different accessions of the diploid D genome to tetraploid wheat of plants grown under saline conditions. The synthetic hexaploids (containing the D genome) had lower leaf Na$^+$ concentrations and were more tolerant of salinity than the tetraploid parent. Specific D genome effects were difficult to separate from effects due to increased ploidy level because of the narrow range of diploids that was used to synthesize the hexaploids. In a survey of ditelocentric lines of *T. aestivum* cv. Chinese Spring the 4DS line was less salt-tolerant and had higher leaf Na$^+$ concentration than the euploid line (Gorham et al. 1987, 1990). Although those results support the hypothesis that genes for salt tolerance are on the D genome, pleiotropic effects due to aneuploidy may also affect salt tolerance.

To confirm that there are genes on the diploid D genome that confer salt tolerance to hexaploid wheat, synthetic hexaploids were produced from *T. tauschii* accessions that were moderately tolerant to salinity and had a low rate of Na$^+$ accumulation; and from others that were sensitive to salinity and had a higher rate of Na$^+$ accumulation (Schachtman et al. 1991). The synthetic hexaploids, their tetraploid parents, and two culti-

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vars of known salt tolerance were grown under saline and non-saline conditions. Some of the plants were harvested when leaf 5 was fully expanded for sodium analysis, and others at maturity for the analysis of the components of grain yield. Salt tolerance is defined here as relative grain yield which is the yield in saline relative to non-saline conditions. Grain yield is emphasized because it may be of greater agronomic significance than dry matter yield, and incorporates processes such as fertility and carbon mobilization to grain. Differences in salt tolerance and Na^+ accumulation between synthetic hexaploids with salt-tolerant and salt-sensitive D genomes would suggest that there are specific nuclear genes from *T. tauschii* for reduced Na^+ accumulation and enhanced salt tolerance.

Materials and methods

Plant material

Pollen from *Triticum tauschii* accessions CPI 110756, CPI 110649, CPI 110813, CPI 110791, and AUS 18905 was used to fertilize emasculated florets of *T. turgidum* cv. Langdon or *T. turgidum* cv. Algeria 33. CPI 110756, CPI 110649 and CPI 110813 are moderately tolerant to salinity, CPI 110791 and AUS 18905 are sensitive to NaCl salinity (Schachtman et al. 1991). *T. turgidum* cv. Langdon and 'Algeria 33' are sensitive to salinity (Shah et al. 1987; Schachtman, unpublished). Hybrid embryos (triploid) were rescued and grown on sterile medium. After the second leaf emerged, plants were transferred to soil and after the fifth leaf emerged plants were treated for 5 h with 0.05% colchicine to double the chromosome number. The leaves of plants were trimmed, then repotted and put under a translucent covering until they began to recover from the colchicine treatment. Plants were selfed and then grown to maturity. Seeds from the 'Langdon' × *T. tauschii* CPI 110756 cross used in the following experiment were C_2 (progeny of the first generation after colchicine treatment) whereas the other synthetic hexaploids were C_3. The successful hybridization and colchicine treatment was shown by the change in head morphology accompanied by a high seed set.

No data are presented for the synthetic hexaploid produced from the 'Langdon' × *T. tauschii* AUS 18905 cross. The C_3 generation of these synthetic hexaploids exhibited the characteristics of grass clump (Worland and Law 1980). They grew poorly under saline conditions and died without setting seed. In control conditions these hybrids also grew poorly with only a few plants producing seed.

T. aestivum cv. Kharchia (salt-tolerant) and *T. turgidum* cv. Modoc (salt-sensitive) were used as standards as their salt tolerance has been documented in other experiments (Schachtman et al. 1991; Schachtman and Munns 1992). 'Kharchia' is more salt-tolerant and accumulates less than Na^+ in leaf five on the main stem than 'Modoc'. Wide crosses were attempted between 'Modoc' and the *T. tauschii* accessions without success.

Growth experiment

Seeds were surface-sterilized in 1% sodium hypochlorite for 30 min and placed in Petri dishes at 20 °C. After the plumule had emerged, seedlings were planted into 8.5/16 cm tubes containing gravel in 60 l tanks. At emergence they were watered with an automatic sub-irrigation system every 30–90 min, depending on ambient conditions, for approximately 9 min. Plants were grown in nutrient solutions containing in mol m^{-3}6.5 KNO_3, 4.0 $Ca(NO_3)_2$, 1.0 $NH_4H_2PO_4$, 2.0 $MgSO_4$ and in mmol m^{-3}: 71 $FeSO_4$, 4.6 H_2BO_3, 0.5 $MnCl_2$, 0.2 $ZnSO_4$, 0.2 $CuSO_4$, 0.1 $(NH_4)_6Mo_7O_{24}$ in mol m^{-3}. Quarter-strength nutrients were added incrementally on alternate days so that the solutions reached full strength 7 days after emergence. Solutions either contained 1 mol m^{-3} NaCl or 150 mol m^{-3} NaCl. After the second leaf on half the plants was fully expanded (8–10 days after plant emergence) NaCl was added to a concentration of 1 mol m^{-3} or in daily increments of 25 mol m^{-3} to a final concentration of 150 mol m^{-3}. Supplemental Ca^{2+} (6 mol m^{-3}) was added to the 150 mol m^{-3} NaCl treatment to adjust the molar ratio of Na : Ca to 15. Nutrient solutions were renewed weekly. The electrical conductivity and water levels were monitored between solution changes to ensure all tanks within the same treatment were at the same salinity level. At maturity, 12 plants of each genotype were harvested from the saline (150 mol m^{-3}) tanks and ten plants from the control (1 mol m^{-3}) tanks. Straw, leaves and grain were dried at 70 °C and then weighed. Kernel weight was determined by weighing two lots of 100 seeds or by weighing all the seeds that a plant produced.

Na^+ analysis

When the fifth leaf on the main stem was fully expanded, eight plants from each genotype were harvested, the lamina of leaf 5 was rinsed in deionized water and oven dried at 70 °C. Leaves were extracted in 50 ml of 500 mol m^{-3} HCl at 35 °C (Hunt 1982) and analyzed for Na^+ with an atomic absorption spectrophotometer (Varian Spectra AA-300). Leaf 5 was chosen for analysis rather than earlier leaves, because leaf 5 started to expand after the NaCl concentration in the nutrient solution reached 150 mol m^{-3} and was previously shown to be negatively correlated with the salt tolerance of *T. tauschii* accessions (Schachtman et al. 1991).

Results

Synthetic hexaploids produced from moderately salt-tolerant and salt-sensitive T. tauschii parents

Under control (non-saline) conditions the addition of the D genome (*T. tauschii* CPI 110756, 110649, 110791) to *T. turgidum* cv. Langdon resulted in synthetic hexaploids that had about 50% more dry matter (i.e., stems, leaves and chaff) than the tetraploid 'Langdon'. Because the winter-habit characteristic of *T. tauschii* was retained, synthetic hexaploids grew for a longer period, produced more tillers and therefore accumulated more dry matter than 'Langdon'. Although the dry matter under control conditions of the synthetic hexaploids was greater than 'Langdon', the grain yields were about the same and, therefore, the harvest index was lower for the synthetic hexaploids (Table 1). The similar yield was mainly due to a lower kernel number per spike in the synthetic hexaploids than 'Langdon' that was not compensated by the slightly higher kernel weight in the synthetic hexaploids (Table 1).

The different synthetic hexaploids were more salt-tolerant than 'Langdon'. Although dry matter was reduced to about 20% by salt in 'Langdon' and the three synthetic hexaploids (Table 1) both relative grain yield (Fig. 1)

Table 1. Mean of yield components (±standard error) for individual plants grown in 1 mol m^{-3} NaCl (ctrl) and 150 mol m^{-3} NaCl (salt)

Genotype	Dry matter[a] (g/plant)		Grain yield (g/plant)		Harvest index		Kernel weight (mg)		Number of kernels per spike		Number of spikes	
	Ctrl	Salt	Ctrl	Salt	Ctrl	Salt	Ctrl	Salt	Ctrl	Salt	Ctrl	Salt
Lang756[b]	95±22	21±1	28.0±6	12.6±1	0.23±0.02	0.37±0.01	46±2	44±2	30±1	24±1	20±5	12±1
Lang649[b]	93±29	22±2	30.5±8	11.8±1	0.25±0.07	0.35±0.03	49±3	41±2	26±3	24±1	28±7	13±1
Lang791[b]	99±22	18±1	37.2±6	7.8±1	0.27±0.04	0.31±0.01	51±1	38±2	35±3	25±1	20±3	7±1
T. turgidum 'Langdon'	48±3	10±1	27.0±3	1.7±0.2	0.36±0.01	0.15±0.02	38±2	10±1	53±2	29±2	14±1	6±1
T. aestivum 'Kharchia'	42±7	13±1	33.1±4	8.3±1	0.44±0.05	0.40±0.06	42±2	28±2	45±2	41±6	17±1	5±1
T. turgidum 'Modoc'	19±3	5±0.5	11.0±2	1.3±0.2	0.37±0.03	0.22±0.03	25±3	12±1	42±4	23±2	10±1[c]	8±1

[a] Dry matter = stems, leaves and chaff

[b] *T. turgidum* 'Langdon' × *T. tauschii* CPI 110756, CPI 110649, or CPI 110791

[c] Tiller number in 'Modoc' was low due to competition from taller genotypes

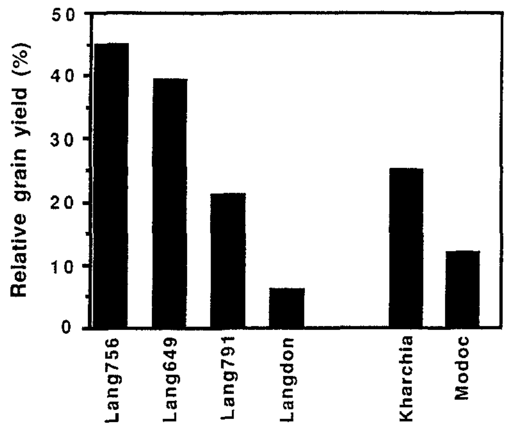

Fig. 1. Relative grain yield of selected wheat varieties. See Fig. 3 legend for full description of varieties. Relative refers to the quantity measured in saline versus the quantity in control conditions

and absolute grain yield (Table 1) were higher in the three synthetic hexaploids. Kernel number per spike and kernel weight were reduced more by salinity in 'Langdon' than the synthetic hexaploids (Fig. 2). The number of spikes was reduced by about 50% in 'Langdon' and the three synthetic hexaploids (Table 1).

The salt tolerance of the three synthetic hexaploids differed according to the source of their D genome. 'Langdon' × *T. tauschii* CPI 110756 (Lang756) and 'Langdon' × *T. tauschii* CPI 110649 (Lang649) contained *T. tauschii* genomes that were moderately salt-tolerant and 'Langdon' × *T. tauschii* CPI 110791 (Lang791) contained a *T. tauschii* genome that was sensitive to saline conditions. The absolute yield under saline conditions (Table 1) and the relative yield (Fig. 1) of Lang756 and Lang649 was higher than that of Lang791. A higher harvest index for Lang756 and Lang649 under saline conditions was due to a more effective maintenance of kernel weight and kernel number (Fig. 2). The effect of salinity on kernel weight, kernels per spike, and number of spikes per plant, differed among the three hexaploids. In Lang791, with the sensitive D genome, both kernel number and kernel weight were reduced by salinity (Fig. 2). In the other two synthetic hexaploids either kernel weight or kernel number was reduced, not both (Fig. 2). The number of spikes per plant was reduced more in Lang791 than in the other synthetic hexaploids or 'Langdon' (Table 1).

Synthetic hexaploids from a moderately tolerant T. tauschii in two tetraploid wheat backgrounds

Hexaploids were synthesized with *T. turgidum* cv. Langdon or 'Algeria 33' and *T. tauschii* CPI 110813. CPI 110813 was moderately tolerant of salinity. The *T. turgidum* cv. Langdon × *T. tauschii* CPI 110813 (Lang813) hexaploids differed in height in the second generation. Under control conditions some were only 0.8 m while others were similar to the other synthetic hexaploids produced with 'Langdon', about 1.2 in height. The shorter Lang813 synthetics were used in this study because they were more similar in height to the synthetic hexaploid produced from the *T. turgidum* cv. Algeria 33 × *T. tauschii* CPI 110813 cross (Alg813) (Table 2). Data are not presented for synthetic hexaploids with CPI 110813 grown in control conditions because these hexaploids were unable to compete with the taller plants they were growing amongst. Competition was not a problem in the saline treatment because the height and tillering of all the genotypes was sufficiently reduced by the salinity. Therefore,

Table 2. Mean of yield components (±standard error) for individual plants grown in 150 mol m^{-3} NaCl

Genotype	Dry matter[a] (g/plant)	Grain yield (g/plant)	Stem height (m)	Harvest index	Kernel weight (mg)	Number of kernels per spike	Number of spikes
Alg813[b]	18±2	10.5±1.3	0.8±0.01	0.34±0.02	39±4	31±1	9±1
T. turgidum 'Algeria 33'	12±1	3.0±0.5	0.7±0.02	0.20±0.04	14±1	26±2	8±1
Lang813[c]	8±2	4.6±0.8	0.6±0.04	0.32±0.06	33±3	20±4	7±1
T. turgidum 'Langdon'	10±1	1.7±0.2	1.0±0.02	0.15±0.02	10±1	29±2	6±1

[a] Dry matter = stems, leaves and chaff
[b] *T. turgidum* 'Algeria 33' x *T. tauschii* CPI 110813
[c] *T. turgidum* 'Langdon' x *T. tauschii* CPI 110813

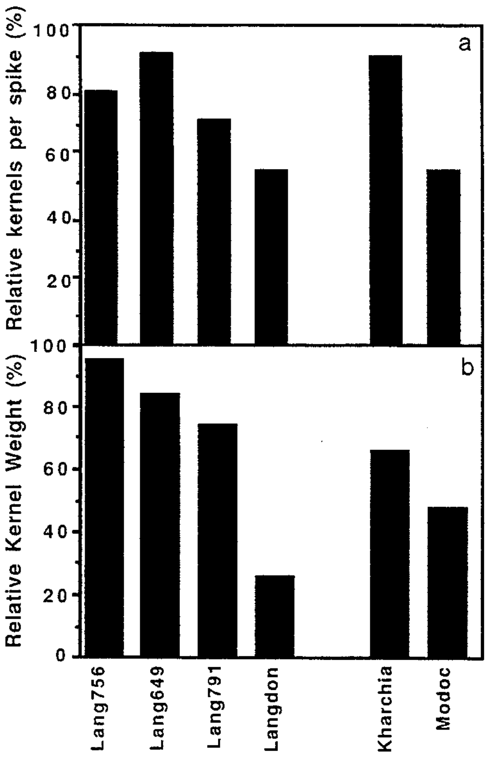

Fig. 2. Relative number of kernels per spike (**a**) and kernel weight (**b**) of selected wheat varieties. See Fig. 3 for full description of varieties. Relative refers to the quantity measured in saline versus the quantity in control conditions

no conclusions can be made about salt tolerance based on relative yields for these two synthetic hexaploids.

Under saline conditions grain yields of the synthetic hexaploids with the D genome from *T. tauschii* CPI 110813 were higher than the tetraploid parents 'Langdon' or 'Algeria 33'. Grain yields were 3.5 times higher in Alg813 than in 'Algeria 33'. The grain yields of Lang813 were 2.7 times higher than 'Langdon'. Dry matter yields of Alg813 under saline conditions were 1.5 times higher than 'Algeria 33', while Lang813 yielded less dry matter than 'Langdon' (Table 2). Kernel weight was about three times higher in these synthetic hexaploids than the tetraploids. Kernel number per spike was higher in Alg813 than 'Algeria 33', but was lower in Lang813 than 'Langdon' (Table 2). Spike number was not significantly different between either tetraploid parent and the corresponding synthetic hexaploid.

Triticum aestivum cv. Kharchia and T. turgidum cv. Modoc, cultivar standards

These cultivars were shorter in height than many of the synthetic hexaploids, so they completed their life cycle in control conditions with some competition for light ('Kharchia' 1.0 m and 'Modoc' 0.7 m). Competition is reflected in the low spike number for 'Modoc' under control conditions (Table 1). Even though reduced yield under control conditions would lead to an increase in relative salt tolerance, 'Kharchia' was still more salt-tolerant than the tetraploid 'Modoc' in terms of absolute and relative grain yield (Fig. 1, Table 1). In both 'Kharchia' and 'Modoc' the kernel weight was reduced under saline conditions (Fig. 2b). However in 'Kharchia' the number of kernels per spike was almost constant whereas in 'Modoc' the number of kernels per spike dropped by 40% (Fig. 2a). As in the synthetic hexaploids and 'Langdon' comparison, the dry matter of 'Modoc' and 'Kharchia' was reduced 70–80% in saline conditions. The harvest index in 'Kharchia' was stable whereas in 'Modoc' it decreased.

The relative grain yield of 'Kharchia' was as low as that of Lang791, which contained the most sensitive *T. tauschii* genome (Fig. 1). The relative kernel weight of 'Kharchia' was also as low as that of the synthetic hexaploids (Fig. 2b). The tetraploid 'Modoc' was as sensitive to salinity as 'Langdon' in terms of relative grain yield. Under saline conditions 'Modoc', 'Langdon', and 'Algeria 33' produced the smallest grains which were between 12 and 14 mg (Tables 1, 2).

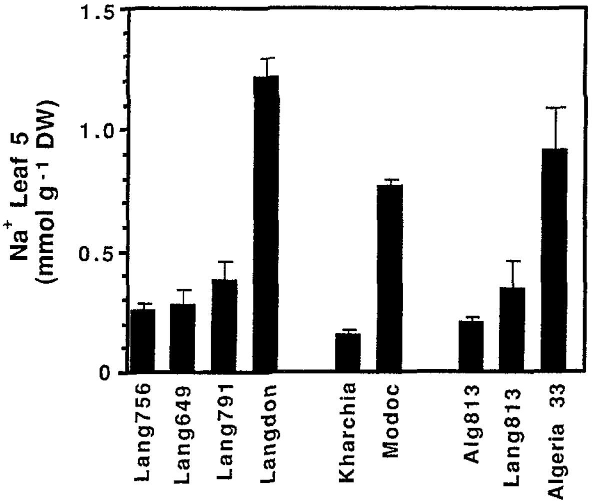

Fig. 3. The Na^+ concentrations in leaf 5 of selected wheat varieties grown in 150 mol m^{-3} NaCl. *T. turgidum* cv. Langdon × *T. tauschii* CPI 110756 (Lang756) or CPI 110649 (Lang649) or CPI 110791 (Lang791) or CPI 110813 (Lang813); *T. turgidum* cv. Algeria 33 × *T. tauschii* CPI 110813 (Alg813); three tetraploids *T. turgidum* cv. Langdon, cv. Modoc, cv. Algeria 33 and *T. aestivum* cv. Kharchia

Na^+ concentrations in leaf 5

The Na^+ concentration in the fifth leaf was related to salt tolerance. The synthetic hexaploids had a 60–80% lower Na^+ concentration in leaf 5 than the tetraploids. The Na^+ concentration in leaf 5 of the more salt-tolerant synthetic hexaploids, Lang756 and Lang649, was slightly lower than the less salt-tolerant Lang791 (Fig. 3). The Na^+ concentration in leaf 5 was lower in 'Kharchia' than in any other genotype. The concentration of Na^+ in leaf 5 of 'Kharchia' was about one-fifth of that in 'Modoc' and about half of that in the synthetic hexaploids (Fig. 3).

Discussion

In this study salt tolerance was greater in all the synthetic hexaploids than in the tetraploid parents. The increased salt tolerance was probably not due to increased ploidy because when ploidy level increases from tetraploid to hexaploid neither growth nor photosynthetic rate increase (Evans and Dunstone 1970). Further evidence that ploidy level alone does not appear to be an important factor in salt tolerance is that diploids have been identified that have the same low Na^+ accumulation characteristics and high salt tolerance as some hexaploids (Schachtman et al. 1991).

Interaction between the entire A, B and D genomes could be as important for salt tolerance as the source of the D genome. The effect of genome interaction was tested by producing a synthetic hexaploid with a common *T. tauschii* parent and different tetraploid parents. Few reports describe the interaction between one *T. tauschii* parent and several *T. turgidum* parents for any trait. No difference was found in resistance to cereal cyst nematode between two synthetic hexaploids produced from different tetraploid parents and a single resistant *T. tauschii* accession (Eastwood et al. 1991). In contrast, crosses between several *T. turgidum* cultivars and one *T. tauschii* accession showed that the interaction between the high molecular-weight subunits of glutenin from *T. tauschii* and from tetraploids resulted in baking quality differences (Lagudah et al. 1987). In our study, depending on the tetraploid parents, the yield increase of the synthetic hexaploids varied slightly under saline conditions. This may indicate that interaction between the 'Algeria 33' (AABB) and *T. tauschii* CPI 110813 (DD) was more favorable in terms of salt tolerance than 'Langdon' and CPI 110813. Lower relative yields of Lang813 than Alg813 could also have been due to lower fertility as evidenced by fewer grains per spike (Table 2), or else be associated with the short height of the *T. turgidum* cv. Langdon synthetic hexaploid used in this study. A gene for reduced height, as well as genes for salt tolerance, may be located on the 4D chromosome and in this event there may be some genetic or physiological linkage between these traits.

The expression of genes for disease resistance from *T. tauschii* in hexaploid wheat has been demonstrated (reviewed by Appels and Lagudah 1990), but the expression of genes for salt tolerance from *T. tauschii* has not. Genes for salt tolerance from other wild species are expressed in amphiploids with hexaploid wheat (Dvorak and Ross 1986; Foster et al. 1987). The expression of genes for salt tolerance from *T. tauschii* was demonstrated in our study by comparing three synthetic hexaploids produced from a common tetraploid parent and several *T. tauschii* accessions differing in salt tolerance. Synthetic hexaploids with moderately tolerant D genomes (Lang756, Lang649) had higher relative grain yields, and lower leaf 5 Na^+ concentrations, than the synthetic hexaploid with the sensitive D genome (Lang791). The larger reduction in spike-bearing tillers, kernel weight, and kernel number, resulted in a lower relative yield of Lang791 as compared to the other synthetic hexaploids. Similar reductions in spike-bearing tillers and kernels per spike, due to salinity, have been reported between a relatively salt-sensitive wheat and a relatively salt-tolerant wheat (Maas and Grieve 1990). The differences among synthetic hexaploids in our study suggest that there are nuclear genes from *T. tauschii* which are expressed at the hexaploid level to limit Na^+ accumulation in leaves and enhance salt tolerance.

Genes that code for reduced Na^+ accumulation in leaves of wheat appear to enhance yield under conditions of high NaCl. In hexaploid wheat, leaf longevity may be increased by limiting the amount of Na^+ taken up by roots and transported to the shoots. Since about 90% of the carbohydrate in grain comes from photosynthesis after anthesis in well-watered plants (Evans et al. 1975), the maintenance of more live leaf area during the later stages of development could partially account for the higher yields of the more tolerant genotypes under saline conditions. This is presumably why kernel weight in the synthetic hexaploids was so high. In tetraploid wheat, where the rates of Na^+ accumulation were very high, a low area of live leaves after anthesis presumably led to the very low kernel weight of the *T. turgidum* cultivars in saline conditions. Mapping the gene(s) that reduce the accumulation of Na^+ in leaves could provide breeders with a tightly linked marker that may hasten the development of salt-tolerant wheat cultivars.

Acknowledgements. This project was partially funded by an Australian National University Postgraduate Scholarship to D. P. S. and by an Australian Wheat Research Council grant (CSP88W). We thank Drs. R. Richards, M. Stapper, U. Hohmann, and R. Appels for helpful discussions during the preparation of this manuscript.

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