Applicability of *Aegilops tauschii* drought tolerance traits to breeding of hexaploid wheat

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Few genes are available to develop drought-tolerant bread wheat (*Triticum aestivum* L.) cultivars. One way to enhance bread wheat's genetic diversity would be to take advantage of the diversity of wild species by creating synthetic hexaploid wheat (SW) with the genomic constitution of bread wheat. In this study, we compared the expression of traits encoded at different ploidy levels and evaluated the applicability of *Aegilops tauschii* drought-related traits using 33 *Ae. tauschii* accessions along with their corresponding SW lines under well-watered and drought conditions. We found wide variation in *Ae. tauschii*, and even wider variation in the SW lines. Some SW lines were more drought-tolerant than the standard cultivar Cham 6. *Aegilops tauschii* from some regions gave better performing SW lines. The traits of *Ae. tauschii* were not significantly correlated with their corresponding SW lines, indicating that the traits expressed in wild diploid relatives of wheat may not predict the traits that will be expressed in SW lines derived from them. We suggest that, regardless of the adaptability and performance of the *Ae. tauschii* under drought, production of SW could probably result in genotypes with enhanced trait expression due to gene interactions, and that the traits of the synthetic should be evaluated in hexaploid level.

Key Words: wheat, *Aegilops tauschii*, synthetic hexaploid wheat, wild relatives of wheat.

Introduction

Feeding the world's growing population is becoming a huge challenge. Food prices, food shortages, and malnutrition are increasing (Webb 2010). Climate change is expected to worsen the current situation through its effects on global agricultural systems (Battisti and Naylor 2009, Bloem *et al.* 2010). Severe scenarios such as significant drying in some regions, leading to an increased frequency and severity of extreme droughts, are expected (Allen *et al.* 2010, Carnicer *et al.* 2010, Soussana *et al.* 2010). Bread wheat (*Triticum aestivum* L.) is affected by periodic drought in around 50% of its cultivated area (Rajaram 2001), and its productivity is often limited because there is insufficient water to maximize biomass and complete grain-filling (Aprile *et al.* 2009).

Few genes have been identified in bread wheat that can be used to develop drought-tolerant cultivars. Millions of years ago, a natural hybridization may have occurred between the wild diploid wheat *Triticum urartu* (genome AA) and the wild grass *Aegilops speltoides* (SS), resulting in the

AABB tetraploid emmer wheat, *Triticum dicoccoides* (Mujeeb-Kazi *et al.* 1996). Later, the domestication of emmer wheat led to the evolution of durum wheat, *Triticum durum* ($2n=28$, AABB), which was in turn hybridized with the diploid wild goat grass *Aegilops tauschii* (genome DD) to produce hexaploid bread wheat, *Triticum aestivum* (AABBDD) about 8000 to 10 000 years ago (Feldman 2001, Helbaek 1959, Kihara 1944, Mujeeb-Kazi *et al.* 1996). Although considerable genetic diversity was preserved in the land races grown by farmers since ancient times, before the spread of modern cultivars with a narrow genetic base, modern wheat breeders have increasingly narrowed this genetic diversity by emphasizing pure-line cultivars. As increasing emphasis was placed on pure lines with higher yields during the Green Revolution, considerable genetic diversity was lost.

Improving wheat drought tolerance through selection and breeding requires a reasonably high level of heritable variation among wheat genotypes or the incorporation of variation from wild relatives, which may serve as a rich source of appropriate genetic variation (Ashraf 2010). As a widely adaptable direct ancestor of bread wheat, *Ae. tauschii* appears to be the most desirable species for wheat improvement among the more than 300 wild species in the tribe

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Triticeae. This species grows on sandy seashores, at the margins of deserts, on stony hills, in grasslands and wastelands, along roadsides, and even in humid temperate forests (van Slageren 1994). Many useful sources of disease and pest resistance are available in this species (Zaharieva *et al.* 2001). The genetic diversity within the DD genome of *Ae. tauschii* is much higher than that of bread wheat (Naghavi and Mardi 2010, Reif *et al.* 2005). The DD genome is also a rich source of resistance to various biotic and abiotic stresses and could therefore contribute to the improvement of wheat cultivars (Assefa and Fehrman 2000, Colmer *et al.* 2006, Cox *et al.* 1994). Many allohexaploid wheat lines can be produced by artificial hybridization between tetraploid wheat and *Ae. tauschii*, and the resulting amphidiploid lines are called “resynthesized” or “synthetic hexaploid” wheat (SW) (Mujeeb-Kazi *et al.* 1996).

However, most breeders use only a limited number of *Ae. tauschii* lines due to the difficulties associated with creating many interspecific hybrids in conventional breeding programs and due to its weedy morphology, which discourages breeders. Even the SW which has same ploidy as the common wheat, the morphology is quite different from that of hexaploid wheat, and it is difficult to deduce the performance of some traits from SW in hexaploid wheat. Although *Ae. tauschii* and SW lines are agronomically inferior to modern wheat cultivars, they may possess superior genes that provide important resources for expanding the available genetic variation in bread wheat. SW lines are therefore being used to transfer exotic genes into bread wheat, and crosses between elite common wheat cultivars and SW lines have resulted in lines with improved drought adaptation. It is estimated that one-third of all new advanced bread wheat lines produced by the International Center for the Improvement of Wheat and Maize (CIMMYT) for use in irrigated and low-rainfall areas are SW derivatives (van Ginkel and Ogbonnaya 2007).

Biomass, biomass-related traits, and vegetative growth rates can be used as indicators of drought tolerance (Entz and Fowler 1990), and they are significantly correlated with grain yield under drought conditions (van Ginkel *et al.* 1998). Various physiological parameters such as the photosynthetic rate, transpiration rate, leaf water potential and root and shoot dry weights are not only important criteria to select for drought tolerance, but also reflect photosynthate production during certain growth stages (Shirazi *et al.* 2010).

We performed the present study (1) to investigate whether the morphological and physiological traits of *Ae. tauschii* related to drought adaptation could be expressed at the hexaploid level, (2) to study the usefulness of *Ae. tauschii* as a tool for predicting the performance of SW lines and (3) to examine whether the drought-related traits of the SW lines were correlated with the respective traits of their wild parents. To accomplish these goals, we analyzed the expression of several drought-related traits encoded in the DD genome of 33 *Ae. tauschii* accessions and their corresponding SW lines.

Materials and Methods

Plant materials

We used 33 *Ae. tauschii* accessions and 33 SW lines obtained from crossing these lines with *T. durum* cv. Langdon (Matsuoka and Nasuda 2004, Matsuoka *et al.* 2007). The SW lines were found to be stable (Takumi *et al.* 2009). Two varieties (*T. durum* cv. Langdon and *T. aestivum* cv. Cham 6) were included as checks. Cham 6 is drought tolerant bread wheat cultivar with synthetic wheat in its pedigree developed in ICARDA (Table 1). The *Ae. tauschii* accessions were collected from five groups of locations: West Asia (Armenia, Syria and Turkey), Iran, Georgia, Central Asia (Afghanistan, Kazakhstan, Kyrgyzstan, India's Jammu and

Table 1. *Aegilops tauschii* accessions and the corresponding synthetic hexaploid wheat (SW) lines used in this study

Serial no.	Accession	Country	<i>Ae. tauschii</i> reference. no.	Synthetic wheat reference no.
1	AE 1090	Kazakhstan	T1	SW1
2	AE 454	Georgia	T2	SW2
3	AE 929	Georgia	T3	SW3
4	AT 55	China	T4	SW4
5	AT 76	China	T5	SW5
6	AT 80	China	T6	SW6
7	IG 126387	Turkmenistan (Ashkhabad)	T7	SW7
8	IG 131606	Kyrgyzstan (Talas)	T9	SW9
9	IG 47259	Syria (Raqqqa)	T11	SW11
10	IG 48042	India (Jammu & Kashmir)	T12	SW12
11	KU-2039	Afghanistan	T14	SW14
12	KU-2069	Iran	T15	SW15
13	KU-2074	Iran	T16	SW16
14	KU-2076	Iran	T18	SW18
15	KU-2078	Iran	T19	SW19
16	KU-2079	Iran	T20	SW20
17	KU-20-8	Iran	T21	SW21
18	KU-2080	Iran	T22	SW22
19	KU-2088	Iran	T23	SW23
20	KU-2103	Iran	T33	SW33
21	KU-2109	Iran	T37	SW37
22	KU-2111	Iran	T38	SW38
23	KU-2132	Turkey	T41	SW41
24	KU-2136	Turkey	T42	SW42
25	KU-2155	Iran	T44	SW44
26	KU-2158	Iran	T46	SW46
27	KU-2160	Iran	T48	SW48
28	KU-2816	Armenia	T49	SW49
29	KU-2826	Georgia	T50	SW50
30	KU-2829A	Georgia	T52	SW52
31	PI 476874	Afghanistan	T53	SW53
32	PI 499262	China (Xinjian)	T54	SW54
33	PI 508262	China (Xinjian)	T55	SW55
34	Cham 6	ICARDA cultivar		
35	Langdon	<i>Triticum durum</i> (parent of all SW)		

Kashmir state, and Turkmenistan), and China. Cham 6 is a drought-tolerant bread wheat cultivar developed by the International Center for Agricultural Research in the Dry Areas (ICARDA).

Experimental conditions

All accessions were grown in pots under fully controlled conditions, with a day length of 14 h, a light intensity of 80 000 lux, a temperature regime of 25°C day/20°C night and a relative humidity of 50% day/60% night. Trials were performed at the Arid Land Research Center, Tottori University, Japan. To break seed dormancy, we first kept the dry seeds at 4°C for 48 h. Seeds that did not germinate were treated with 1% H₂O₂ and kept at 4°C for a further 16 h; then, fresh H₂O₂ was added and the seeds were kept at 25°C for a further 30 h. Five seedlings from each accession were transferred into plastic pots containing 1 kg of dune sand from Tottori City, Japan, and were later thinned to two per pot. Three inorganic fertilizer compounds were added to each pot: N : P : K (13 : 6.5 : 12.5), Ca : Mg (21 : 0.6) and Mg : Mn : B (8.4 : 0.3 : 0.3) at 858, 1431 and 572 mg/pot, respectively. The 66 accessions were grown under either well-watered or drought conditions in a factorial experiment using a completely randomized design with three replicates. The pot weight was recorded daily, and an amount of water equal to the loss was added during the initial establishment period. The volumetric moisture content of the soil was initially maintained at 9 to 12%. Seventeen days after sowing, drought was induced in half of the plants by allowing the moisture content to fall to between 6 and 8%, while the well-watered treatment was maintained as described above.

Morphological and physiological measurements

Physiological parameters were recorded using the uppermost fully expanded leaf of the 30- and 37-day-old plants. Photosynthesis (the net photosynthetic rate), stomatal conductance, intercellular CO₂ concentration, and transpiration rate were measured using an LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA). Leaf water potential (LWP) in 42-day-old plants was measured 19 to 20 h after irrigation using a model 600 pressure chamber (PMS Instrument Company, Albany, OR, USA). Chlorophyll content was estimated using a Minolta SPAD-502 leaf chlorophyll meter (Minolta Camera Co. Ltd., Osaka, Japan). Plants were harvested on day 52 and the roots and shoots were collected separately, dried at 65°C for 2 days, weighed, and then used to calculate the total dry weight (TDW), root dry weight (RDW), shoot dry weight (SDW) and the root:shoot ratio (RSR). Water-use efficiency (WUE) was calculated as the weight (g) of dry matter produced per kg of water applied. The partitioning of dry matter to the roots (PDR, %) was calculated as the root weight divided by the total weight, then multiplied by 100%.

Statistical analysis

Data were analyzed using ANOVA for a completely

randomized design. Fisher's protected LSD was used to test differences among genotypes and differences within genotypes between the well-watered and drought conditions. Genotypic variance of the SW lines (from the ANOVA results) was standardized (SW values were divided by *Ae. tauschii* and multiplied by 100) to produce a value of 100 for *Ae. tauschii*, thereby facilitating comparisons with the SW lines.

Correlations of the morphological and physiological traits were estimated based on Pearson correlation coefficient.

Euclidean measure of diversity was used to compare the diversity of the *Ae. tauschii* and SW lines. The Euclidean distance is the square root of the sum of squared differences between the different trait values for a pair of genotypes. As the data had different units, the data were statistically standardized (by subtracting the mean from the data and then dividing it by the standard deviation) and the distances were calculated using the following formula (Teknomo 2011):

$$D_{ij} = \sqrt{\sum_{k=1}^n ((X_{ik} - X_{jk})^2)}$$

Where D_{ij} represents the Euclidean distance between i and j genotypes, k represents the traits from 1 to n and X_{ik} represents the k th trait of i th genotype and X_{jk} represent the k th trait of the j th genotype. From the standardized distances, which fall within the range [0, 1], we calculated the mean, maximum, minimum, variance and standard deviation (SD) of the 528 [= (33 × [33 – 1])/2] distances for all *Ae. tauschii* and SW lines under well-watered and drought conditions.

To test the significance of any differences between the mean distances (the 528 paired values) for the *Ae. tauschii* and SW lines under well-watered and drought conditions separately, we used a t -test based on unequal variances because the variances of the two groups under each water regime were significantly different based on the results of an F -test. The inequality of the variances of the distances also showed significant diversity between the two groups of genotypes.

$$F = \frac{\text{Variance SW}}{\text{Variance AT}}$$

$$t = \frac{\text{Mean SW} - \text{Mean AT}}{\sqrt{(\text{Pooled variance}/528)}}$$

Where SW represents the value for the SW lines and AT represents the value for the *Ae. tauschii* lines.

Results

The SW lines inherited useful morphological and physiological variation

We observed a high degree of variation for most morphological and physiological traits studied in the *Ae. tauschii* and SW lines under both well-watered and drought conditions.

Table 2. Mean squares (MS) from the ANOVA results for morphological and physiological traits of the *Ae. tauschii* lines and their corresponding SW lines grown under well-watered and drought conditions

Trait ^b	Water regime ^a	Group	Photosynthesis	Stomatal conductance	Inter-cellular CO ₂	Transpiration rate	SPAD reading	LWP	RDW	SDW	TDW	RSR	PDR	WUE
Genotypes (G)	WWC	AT ^d	38.779**	0.028 ns	93632**	8.426*	72.94**	10.05**	1.791**	0.606**	3.668**	0.528 ns	167.38 ns	1.082**
		SW	27.940**	0.031**	54676**	2.600 ns	173.16**	10.35**	2.303**	0.811**	5.195**	0.349 ns	168.39 ns	1.823**
	DC	AT	34.166**	0.037 ns	13488*	4.051 ns	46.81**	16.36**	0.431**	0.114 ns	0.702 ns	0.573 ns	269.63 ns	0.461 ns
		SW	28.252 ns	0.040 ns	10339**	1.648 ns	61.49**	18.55**	1.669**	0.352**	3.019**	1.075**	334.68**	1.735**
Error	WWC	AT	18.046	0.019	5976	4.534	16.16	1.97	0.635	0.186	0.797	0.614	159.34	0.239
		SW	13.721	0.014	5243	2.279	11.92	1.49	0.413	0.177	0.814	0.353	137.17	0.281
	DC	AT	10.064	0.035	7739	2.761	17.25	7.34	0.178	0.157	0.476	0.677	221.66	0.384
		SW	19.317	0.035	4947	1.826	21.28	3.44	0.249	0.104	0.453	0.517	136.07	0.351
LSD ^c	WWC	AT	6.929	0.224	126	3.47	6.6	2.3	1.3	0.703	1.457	–	–	0.798
		SW	6.039	0.191	118	–	5.6	2.0	1.048	0.687	1.473	–	–	0.865
	DC	AT	5.181	–	144	–	6.8	4.4	0.689	–	1.128	–	–	–
		SW	7.171	–	115	–	7.5	3.0	0.813	0.527	1.099	1.174	19.1	0.969

^a WWC, well-watered conditions; DC, drought conditions.

^b LWP, leaf water potential; RDW, root dry weight; SDW, shoot dry weight; TDW, total dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency.

^c LSD, least significant difference.

^d AT, *Ae. tauschii*; SW, synthetic hexaploid wheat; **, $P < 0.01$; *, $P < 0.05$; ns, not significant.

Under well-watered conditions, highly significant differences were observed in all the studied morphological and physiological traits except for stomatal conductance, transpiration rate, root-shoot ratio, and PDR in the *Ae. tauschii* and SW lines (Table 2). Neither group differed significantly with regard to the root-shoot ratio and PDR. Although the SW lines showed high and significant differences for stomatal conductance, no differences were observed among the *Ae. tauschii* accessions. In contrast, only the *Ae. tauschii* lines showed significant differences in transpiration rate under well-watered conditions. The *Ae. tauschii* lines transpired more but produced more dry matter per unit water than the SW lines under well-watered conditions. These observations were consistent with the averages of the stomatal conductance, transpiration rate, and TDW values shown in Table 3.

When exposed to drought, large differences were observed between the two groups in the traits related to water use and biomass production. Only the SW group exhibited a highly significant difference for SDW, TDW, RSR, PDR and WUE (Table 2). Moreover, the SW lines had higher averages than the *Ae. tauschii* lines for these traits (Table 3), which indicates their ability to use water more efficiently for biomass production under drought conditions.

SW lines showed greater drought tolerance than *Ae. tauschii* lines

The *Ae. tauschii* lines had higher RDW, SDW, and TDW under well-watered conditions, but they sustained a greater reduction in these traits under drought conditions (Table 3). The SW group showed better tolerance of drought conditions both in terms of the actual RDW, SDW, and TDW values and in terms of the percent reduction in these values due

to drought (Table 3). This was clearly reflected in the RSR and the PDR, which both decreased in *Ae. tauschii* under drought conditions but increased in the SW group (Table 3). The SW group showed a smaller percent reduction in average TDW (33.8%) than the *Ae. tauschii* group (51.8%) and Langdon (42.6%), but Cham 6 showed the least reduction (12.4%). Interestingly, SW5 had 18.4% greater TDW under drought conditions. Although SW2 had a 29.2% reduction in TDW under drought conditions, it produced the highest TDW (3.8 g/pot) among all the genotypes. Under drought conditions, RDW decreased by 53.0% in the *Ae. tauschii* group, versus 30.1% in the SW group. Despite the general reduction in RDW with drought, Cham 6, SW19 and SW5 produced 105.0, 22.6 and 44.3% more RDW, respectively.

Although the *Ae. tauschii* group had higher average photosynthetic rates than the SW group under both well-watered and drought conditions, the SW accessions had a smaller reduction in photosynthetic rate (20.4% vs. 21.8%) (Table 3). The standard check line Cham 6 maintained the highest average photosynthetic rate (26.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and sustained the smallest reduction (5.7%) under drought conditions.

The *Ae. tauschii* accessions used water more efficiently than the SW accessions under well-watered conditions (Table 3), but exhibited a greater reduction in their average WUE under drought conditions (30.6 and 2.7%, respectively). Cham 6, SW5 and SW6 used water more efficiently (23, 81 and 28%, respectively) under drought conditions than under well-watered conditions (Table 3).

The *Ae. tauschii* group maintained higher transpiration rates and higher stomatal conductance under both conditions, and responded to drought by exhibiting a higher reduction in their transpiration and stomatal conductance than in the SW group (Table 3). Although the chlorophyll content

Table 3. Consolidated table showing the mean values of the morphological and physiological characteristics of the *Ae. tauschii* lines and their corresponding SW lines under well-watered and drought conditions

Traits ^b	Group	WWC	DC	% reduction with drought	WWC ^a		DC	
					Min	Max	Min	Max
TDW (g per pot)	AT ^c	3.59	1.73	51.8	1.23	6.04	0.93	2.88
	SW	3.11	2.06	33.8	0.92	5.35	0.32	3.78
RDW (g per pot)	AT	2.00	0.94	53.0	0.52	4.23	0.31	2.01
	SW	1.66	1.16	30.1	0.35	3.21	0.11	2.60
SDW (g per pot)	AT	1.59	0.80	49.7	0.57	2.38	0.50	1.39
	SW	1.44	0.90	37.5	0.57	2.33	0.12	1.73
RSR	AT	1.35	1.29	4.4	0.57	2.32	0.17	2.40
	SW	1.16	1.32	-13.8	0.60	1.80	0.51	3.10
PDR	AT	53.7	51.7	3.7	36.0	69.1	13.2	69.5
	SW	50.6	52.4	-3.6	34.9	64.2	32.2	71.9
Photosynthesis ($\mu\text{mol m}^{-2}\text{ s}^{-1}$)	AT	30.7	24.0	21.8	24.8	38.6	17.4	32.7
	SW	27.0	21.5	20.4	19.6	32.9	14.8	27.9
WUE (g kg ⁻¹)	AT	2.09	1.45	30.6	0.72	3.45	0.81	2.33
	SW	1.85	1.80	2.7	0.59	3.32	0.32	3.33
Transpiration rate mmol H ₂ O m ⁻² s ⁻¹	AT	5.03	3.9	22.5	1.43	9.30	1.78	7.6
	SW	3.69	3.1	16.0	1.71	5.8	2.23	4.30
Stomatal conduct. (mol m ⁻² s ⁻¹)	AT	0.30	0.27	10.0	0.15	0.57	0.13	0.58
	SW	0.25	0.23	8.0	0.13	0.59	0.09	0.56
Inter cellular CO ₂ (ppm)	AT	370	253	31.6	146	648	153	453
	SW	268	211	21.3	127	533	109	357
Chlorophyll content (SPAD reading)	AT	48.1	49.3	-2.5	39	59.2	40.5	55.8
	SW	53.1	53.2	-0.2	38.4	69.1	45.8	63.5
LWP	AT	-8.52	-10.27	-20.5	5.17	14.5	6.67	16.3
	SW	-7.6	-9.78	-28.7	4.67	10.5	4.33	16.5

^a WWC, well-watered conditions; DC, drought conditions.

^b TDW, total dry weight; RDW, root dry weight; SDW, shoot dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency; LWP, leaf water potential.

^c AT, *Ae. tauschii*; SW, synthetic hexaploid wheat.

in both groups was not greatly affected by drought, the SW group maintained higher chlorophyll contents under both conditions (Table 3). The intercellular CO₂ concentration was higher and water potential was lower (more negative) in the *Ae. tauschii* group than in the SW group under both conditions.

The SW lines had higher genotypic variance than the Ae. tauschii lines

We analyzed the genotypic variance of the two groups of lines based on their morphological and physiological performance, using the ANOVA mean squares of *Ae. tauschii* for each characteristic as the standard of comparison (with a standardized value of 100 for each characteristic). Although the SW lines showed remarkably less genotypic variance in photosynthetic rate, intercellular CO₂ concentration, and transpiration rate under both well-watered and drought conditions (Table 4), the SW lines showed higher genotypic variance in all other parameters except the RSR (i.e., higher variance in stomatal conductance, chlorophyll content, wa-

ter potential, RDW, SDW, TDW, PDR and WUE). Interestingly, although the SW lines showed less variation than the *Ae. tauschii* lines in the RSR under well-watered conditions, they showed higher variation in this parameter under drought conditions.

Greater variation in the SW genotypes based on the Euclidian distance

To study the degrees of variation among the *Ae. tauschii* and SW lines, we adopted the Euclidian distance, standardized to [0, 1] according to the method of Teknomo (2011). The mean Euclidean distance revealed more variation in the SW group than in the *Ae. tauschii* group under both conditions (0.539 compared to 0.486 under well-watered conditions and 0.593 compared to 0.475 under drought conditions). Within the *Ae. tauschii* group, greater variation was observed under well-watered conditions (0.486) than under drought conditions (0.475). In contrast, the SW accessions showed more variation under drought conditions (0.593) than under well-watered conditions (0.539).

Correlations among the morphological and physiological traits

Under well-watered conditions, the transpiration rate and intercellular CO₂ concentration were significantly correlated with the photosynthetic rate in the *Ae. tauschii* group but not in the SW group (Table 6). Similarly, the three biomass traits (RDW, SDW and TDW) were correlated with the photosynthetic rate in the *Ae. tauschii* group but not in the SW group. Although the RSR and PDR were not significantly correlated with LWP in the *Ae. tauschii* group, they were significantly correlated in the SW group (Table 6). In both groups, WUE was significantly correlated with the intercellular CO₂ concentration, transpiration rate, chlorophyll content, and the three biomass traits (Table 6). For all other pairs of parameters, the correlations showed similar patterns for the morphological and physiological traits within SW or *Ae. tauschii*.

Under drought conditions, the photosynthetic rate was significantly correlated with the chlorophyll content, RDW, and the root-shoot ratio in the *Ae. tauschii* group but not in the SW group (Table 7). Although stomatal conductance was not significantly correlated with any trait in the *Ae. tauschii* group, it was significantly correlated with the chlorophyll content, LWP, SDW and TDW in the SW group (Table 7). The intercellular CO₂ concentration was significantly correlated with the transpiration rate, RDW, the RSR and PDR in the *Ae. tauschii* group, and it was significantly correlated with the three biomass-related traits and WUE in the SW group under drought conditions (Table 7). Transpiration was significantly correlated with RDW, the RSR and PDR in the *Ae. tauschii* group but not in the SW group.

Correlation of traits of the *Ae. tauschii* lines with those of the corresponding SW genotypes

No morphological or physiological traits of the SW lines were significantly correlated with the corresponding traits of their parental *Ae. tauschii* lines under drought conditions (Table 8). Under well-watered conditions, highly significant correlations were found for the intercellular CO₂ concentration and significant correlations were found for the transpiration rate, RDW, TDW and WUE. The other traits were not significantly correlated between the two groups under well-watered conditions.

SW lines from the Central Asian and Georgian groups had better performance

The *Ae. tauschii* accessions were categorized into five different groups based on their geographic origin. The SW lines derived from *Ae. tauschii* collected from Central Asian countries and Georgia produced significantly higher TDW than in their corresponding *Ae. tauschii* lines and Langdon under drought condition (Fig. 1). Although not significant, these SW lines produced more TDW under well-watered conditions but less TDW under drought conditions compared to Cham 6. The *Ae. tauschii* accessions from West Asian countries and Iran produced higher TDW than their

Fig. 1. Production of total dry weight of *Ae. tauschii* accessions and their corresponding SW based on the five geographic groups of origin of *Ae. tauschii*.*, $P < 0.05$

corresponding SW lines (Fig. 1). Although the *Ae. tauschii* accessions from China produced the highest TDW under well-watered conditions, their corresponding SW lines produced far less TDW.

Discussion

Marked morphological and physiological variation exhibited in *Ae. tauschii* and SW

We observed wide and statistically significant variation in most of the morphological and physiological characteristics we measured in the *Ae. tauschii* accessions (Table 2). Dudnikov and Kawahara (2006) also reported wide genotypic variation among *Ae. tauschii* collected from regions with various agricultural and climatic conditions. These genotypic differences might result from different adaptation mechanisms to cope with unique aspects of local management techniques and environmental stresses. Therefore, the morphological and physiological variations observed in *Ae. tauschii* could result from wide differences in the agricultural and climatic conditions among their diverse origins. On the other hand, the SW genotypes derived from the 33 different *Ae. tauschii* lines exhibited wide variation in their morphological and physiological responses to drought (Table 2). These results appear to be consistent with the wide genotypic variation in their parental *Ae. tauschii* lines.

SW showed marked drought tolerance

The SW lines exhibited greater drought tolerance than the *Ae. tauschii* accessions; that is, they showed a smaller reduction in the values of most traits when exposed to drought (Table 3). In particular, the biomass-related traits (TDW, RDW and SDW) showed clearly lower reductions under drought, and the RSR and PDR values increased under drought, versus a decrease for *Ae. tauschii*.

Increased PDR in the SW lines under drought resulted in an increased RDW and root-shoot ratio in the SW lines, which suggests the higher capacity of these plants to exploit soil water by expanding their root distribution. These results

are in good agreement with those of Reynolds *et al.* (2007), who reported that SW lines performed better under moisture stress due to their increased partitioning of root mass to deeper soil layers and their increased ability to extract moisture from deeper depths.

Higher WUE is considered crucial for resistance to drought stress. In this study, WUE provided the clear difference in drought tolerance among the genotypes. The SW lines used water more efficiently than the *Ae. tauschii* lines under drought conditions and showed a much smaller reduction compared with well-watered conditions (Table 3). Some SW lines such as SW5, SW2 and SW19 had a higher WUE (3.3, 3.0 and 3.0 g kg⁻¹, respectively) than the standard drought-tolerant cultivar Cham 6 (2.3 g kg⁻¹). Our results are in line with those of Huang *et al.* (2007), who reported increased WUE at higher ploidy levels. Higher yield is associated with high WUE (Angus and van Herwaarden 2001), therefore these SW lines may represent useful resources for breeding high-yield cultivars.

The overall photosynthetic rates of the *Ae. tauschii* lines were higher than those of the SW lines under both drought and well-watered conditions (Table 3), which agrees with earlier reports that *Ae. tauschii* was capable of maintaining a satisfactory rate of net photosynthesis even at lower relative soil water contents (Dulai *et al.* 2006, Wang *et al.* 2008).

Some SW lines were more drought-tolerant than the standard cultivar (Cham 6), and these lines may be good candidates for breeding programs to develop drought-tolerant cultivars (Reynolds *et al.* 2005). Other lines were less drought-resistant, but showed better physiological traits that are associated with drought tolerance; these lines may still be useful materials if those traits can be transferred into commercial wheat cultivars, as suggested by van Ginkel and Ogbonnaya (2007). Wild species are not always tolerant or

resistant to certain stresses, but they may still have the potential to create tolerant hexaploids. The SW lines in our study that were not drought-tolerant can still be used for breeding programs with other goals, such as rust resistance, salinity or other abiotic stresses as reported by Colmer *et al.* (2006), Liu *et al.* (2010) and Valkoun (2001).

SW showed greater variation than Ae. tauschii

In comparison with the *Ae. tauschii* lines, the SW genotypes generally showed more genotypic variance under drought conditions than under well-watered conditions (Table 4), and the differences were often large (more than 300%). Moreover, except for the photosynthetic rate, intercellular CO₂ concentration, and transpiration rate, the SW group had higher variation in all morphological and physiological traits under both conditions.

The Euclidean distance revealed great genetic diversity between the two groups under both conditions (Table 5). Greater variation was observed in the SW lines than in the *Ae. tauschii* lines under both conditions. Moreover, the SW lines exhibited more variation under drought than under well-watered conditions. These results reflect the ability of the SW lines to cope with drought conditions, which represents variation that could be exploited in breeding programs. Despite this rich diversity, not all of the SW lines would be useful, since some showed less variation in the photosynthetic rate, intercellular CO₂ concentration, and transpiration rate (Table 4).

The interaction between the AABB and DD genomes in the SW lines may therefore have enhanced the response to drought in some lines. These results generally agree with those of Reynolds *et al.* (1999), who suggested an increase in the probability of favorable traits being expressed in hexaploid and tetraploid combinations.

Table 4. Genotypic variance in the SW lines (from the ANOVA variances) in comparison with the genotypic variance in the *Ae. tauschii* lines (standardized to a value of 100)

Water regime ^a	Photosynthesis	Stomatal conductance	Intercellular CO ₂	Transpiration rate	Chlorophyll content	LWP ^b	RDW	SDW	TDW	RSR	PDR	WUE
WWC	72.0	110.7	58.4	30.9	237.4	103.0	128.6	133.8	141.6	66.1	100.6	168.5
DC	82.7	108.1	76.7	40.7	131.4	113.4	387.2	308.8	430.1	187.6	124.1	376.4

^a WWC, well-watered conditions; DC, drought conditions.

^b LWP, leaf water potential; RDW, root dry weight; SDW, shoot dry weight; TDW, total dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency.

Table 5. Euclidean distance standardized to [0, 1] to show the morphological and physiological diversity for *Ae. tauschii* and SW under drought and well-watered conditions based on the averages of the 12 morphological and physiological traits shown in Tables 2 and 3

Water regime ^a	Group	Mean	Minimum	Maximum	Range	Variance	SD	Median	CV
WWC	AT ^b	0.486	0.173	1.000	0.827	0.022	0.147	0.491	30.243
	SW	0.539	0.139	1.000	0.861	0.025	0.158	0.543	29.391
DC	AT	0.475	0.146	1.000	0.854	0.020	0.143	0.464	30.073
	SW	0.593	0.175	1.000	0.825	0.033	0.180	0.588	30.422

^a WWC, well-watered conditions; DC, drought conditions; SD, standard deviation; CV, coefficient of variation.

^b AT, *Ae. tauschii*; SW, synthetic hexaploid wheat.

Table 6. The correlations among the morphological and physiological traits of 33 *Ae. tauschii* (upper part) and SW (lower part) lines under well-watered conditions

	Photo-synthesis	Stomatal cond. ^a	Inter. CO ₂ ^b	Transp. Rate ^c	Chl. con. ^d	LWP ^e	RDW	SDW	TDW	RSR	PDR	WUE
Photosynthesis	1.0	-0.2917	0.6080**	0.5429**	0.1187	-0.2127	0.4161*	0.4376*	0.4594**	0.0477	0.1238	0.4183**
Stomatal cond. ^a	-0.2053	1.0	-0.2298	-0.0351	-0.2510	0.3826*	-0.0601	-0.1724	-0.1163	0.1116	0.1498	-0.1080
Inter. CO ₂ ^b	0.1884	-0.3374	1.0	0.8689**	-0.1967	-0.2417	0.6754**	0.6163**	0.7104**	0.1426	0.3793*	0.6613**
Transp. rate ^c	0.1906	0.3294	0.4515**	1.0	-0.1510	-0.2636	0.5511**	0.3594*	0.5224**	0.2521	0.4393*	0.4747**
Chl. con. ^d	0.1974	-0.2559	-0.3330	-0.2407	1.0	-0.3171	-0.4252*	-0.4202*	-0.4639*	-0.0670	-0.2890	-0.4458**
LWP ^e	-0.2658	0.3482*	-0.3246	0.2783	-0.1197	1.0	0.0952	0.1465	0.1316	0.1190	0.1265	0.1969
RDW	-0.0091	-0.1235	0.5867**	0.4311*	-0.4414**	0.2324	1.0	0.6360**	0.9495**	0.5646**	0.7229**	0.9264**
SDW	0.0876	-0.0823	0.6849**	0.5007**	-0.4995**	0.0921	0.8454**	1.0	0.8443**	-0.1651	0.0332	0.8334**
TDW	0.0242	-0.1165	0.6477**	0.4711**	-0.4758**	0.1830	0.9772**	0.9387**	1.0	0.3340	0.5161**	0.9832**
RSR	-0.1740	-0.1231	0.2210	0.2553	-0.1732	0.3820*	0.6826**	0.2785	0.5530**	1.0	0.8919**	0.3642**
PDR	-0.2192	-0.0584	0.2816	0.2836	-0.3130	0.3810*	0.8049**	0.4378*	0.6955**	0.9512**	1.0	0.5159**
WUE	0.0159	-0.1394	0.6748**	0.4607**	-0.4624**	0.1495	0.9713**	0.9260**	0.9918**	0.5561**	0.6999**	1.0

^a Stomatal conductance.^b Inter-cellular CO₂.^c Transpiration rate.^d chlorophyll content.^e LWP, leaf water potential; RDW, root dry weight; SDW, shoot dry weight; TDW, total dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency.**, $P < 0.01$; *, $P < 0.05$.**Table 7.** The correlations among the morphological and physiological traits of the 33 *Ae. tauschii* and SW lines under drought conditions

	Photo-synthesis	Stomatal cond. ^a	Inter. CO ₂ ^b	Transp. Rate ^c	Chl. con. ^d	LWP ^e	RDW	SDW	TDW	RSR	PDR	WUE
Photosynthesis	1.0	-0.0161	0.5463**	0.4965**	0.3947*	0.0417	0.3478*	-0.1236	0.2046	0.3665*	0.3321	0.1589
Stomatal cond. ^a	0.1796	1.0	0.0211	0.2515	-0.0441	0.1717	0.0247	-0.1414	-0.0401	0.0486	0.1105	-0.0520
Inter. CO ₂ ^b	0.4835**	0.1352	1.0	0.6524**	0.1925	0.2937	0.5138**	-0.0969	0.2477	0.4719**	0.5284**	0.1251
Transp. rate ^c	0.5613**	0.0669	0.3271	1.0	0.0554	0.1410	0.3444*	-0.3172	0.0694	0.5659**	0.5084**	-0.0062
Chl. con. ^d	-0.0614	-0.4161*	-0.3030	-0.2192	1.0	-0.2660	-0.0223	-0.2349	-0.0644	0.0911	-0.0121	-0.0162
LWP ^e	0.0715	0.4061*	0.3292	0.2420	-0.3261	1.0	0.4101*	0.2600	0.3879*	0.3211	0.4128*	0.2938
RDW	-0.0063	0.3115	0.3985*	0.1102	-0.1826	0.5310**	1.0	0.3600*	0.8634**	0.7684**	0.7804**	0.7700**
SDW	0.0941	0.3608*	0.4402**	0.1344	-0.2645	0.5344**	0.8010**	1.0	0.7107**	-0.0793	0.0727	0.7566**
TDW	0.0352	0.3476*	0.4334*	0.1292	-0.2259	0.5519**	0.9799**	0.9031**	1.0	0.5145**	0.6111**	0.9575**
RSR	-0.0786	0.2350	0.1899	-0.0078	-0.1029	0.3228	0.7876**	0.3266	0.6745**	1.0	0.8762**	0.4484**
PDR	0.0684	0.2851	0.2963	0.0886	-0.2038	0.3603*	0.8087**	0.4244*	0.7264**	0.9300**	1.0	0.5283**
WUE	0.0150	0.3221	0.3909*	0.1096	-0.1985	0.5454**	0.9735**	0.8876**	0.9904**	0.6810**	0.7163**	1.0

^a Stomatal conductance.^b Inter-cellular CO₂.^c Transpiration rate.^d chlorophyll content.^e LWP, leaf water potential; RDW, root dry weight; SDW, shoot dry weight; TDW, total dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency.**, $P < 0.01$; *, $P < 0.05$.

Correlations among the morphological and physiological traits

The correlations of morphological and physiological traits within the *Ae. tauschii* and within SW lines had some similarities under well-watered and drought conditions, but we noted many differences between the morphological and physiological traits that could indicate different interactions between the parent, genotypes and various environmental conditions. These differences need to be further explored in order to understand their potential usefulness in breeding programs.

The photosynthetic rate was significantly correlated with the intercellular CO₂ concentration and transpiration rate. However, for the SW lines under well-watered conditions, this correlation was not significant (Tables 6, 7). The photosynthetic rate was not significantly correlated with stomatal conductance in both groups and under both conditions, which indicate that stomatal conductance might not be main determinant factor for photosynthetic rate under drought condition. Other possible factors such as photophosphorylation and ATP synthesis have been suggested to affect and limit photosynthetic under drought (Medrano *et al.* 2002).

Stomatal conductance was significantly correlated with LWP in both groups under well-watered conditions (Table 6), but under drought condition a significant correlation was found only in SW group. Under water stress, a good correlation is often observed between leaf water potential and stomatal conductance (Medrano *et al.* 2002). These results indicate the importance of stomatal conductance interaction with LWP for drought tolerance in SW.

WUE was significantly correlated with RDW, SDW, TDW, the root-shoot ratio, and PDR in both groups and under both conditions (Tables 6, 7), which indicates the importance of the WUE in maximizing total biomass in these species regardless of the water availability.

Correlation of the *Ae. tauschii* lines with their corresponding SW genotypes

We found no correlations between the *Ae. tauschii* lines and their corresponding SW lines for any of the studied traits under drought conditions while under well watered condition intercellular CO₂ concentration, transpiration rate, RDW, TDW and WUE were correlated. Kajimura *et al.* (2011) reported that heading, flowering and maturation time of *Ae. tauschii* lines correlated with their corresponding SW lines (Table 8). This indicates that the performance of the SW lines appeared to result from complex interactions between the potential of *Ae. tauschii* itself and the genes in durum wheat, as was reported by Trethowan *et al.* (2005). These results suggest that the *Ae. tauschii* lines and their corresponding SW lines exhibit nearly independent behavior under different conditions. Our results provide supporting evidence for the findings of Fujiwara *et al.* (2010) and Kurahashi *et al.* (2009), who found that the genome variations observed at the diploid genome level (DD) were not necessarily reflected at the hexaploid level in the SW lines.

Table 8. Correlations between the morphological and physiological traits of the *Ae. tauschii* lines and their corresponding SW lines under well-watered and drought conditions

Trait ^b	Under DC ^a	Under WWC
Photosynthesis	0.0247 ns	0.0920 ns
Stomatal conductance	-0.1072 ns	0.1474 ns
Intercellular CO ₂	0.3198 ns	0.4877 **
Transpiration rate	0.0536 ns	0.3686 *
Chlorophyll content	0.3371 ns	0.0655 ns
LWP ^b	0.1996 ns	-0.2439 ns
RDW	0.3049 ns	0.3576 *
SDW	0.1473 ns	0.2482 ns
TDW	0.2881 ns	0.3629 *
RSR	0.1149 ns	-0.0251 ns
PDR	0.1498 ns	0.1721 ns
WUE	0.2430 ns	0.3634 *

^a WWC, well-watered conditions; DC, drought conditions.

^b LWP, leaf water potential; RDW, root dry weight; SDW, shoot dry weight; TDW, total dry weight; RSR, root-shoot ratio; PDR, partitioning of dry matter to roots (%); WUE, water-use efficiency; LSD, least significant difference.

**, $P < 0.01$; *, $P < 0.05$; ns, not significant.

SW lines from the Central Asian and Georgian groups had enhanced performance

We divided the *Ae. tauschii* and SW genotypes into five groups based on their origin. The SW lines developed from *Ae. tauschii* accessions from Georgia and Central Asia performed better than their corresponding *Ae. tauschii* genotypes under both water regimes (Fig. 1). In contrast, the *Ae. tauschii* accessions from West Asia performed better than their corresponding SW lines under both conditions. This emphasizes the importance of utilizing the genetic resources from each region judiciously when breeding wheat for drought resistance.

We suggest that, regardless of the adaptability and performance of the *Ae. tauschii* lines under drought stress, the production of many SW lines would probably result in genotypes with enhanced trait expression due to gene interactions. One way to take advantage of this useful variation would be to use the synthetic wheat derivatives system proposed by Tsujimoto *et al.* (2011). Based on the results of the present study, we recommend that the useful traits of the SW lines observed at the hexaploid level be used not only for improving drought tolerance but also for breeding wheat cultivars capable of resisting other biotic and abiotic stresses.

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