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Journal of Plant Breeding and Genetics



ROOT WATER-UPTAKE AND PLANT GROWTH IN TWO SYNTHETIC HEXAPLOID WHEAT GENOTYPES GROWN IN SALINE SOIL UNDER CONTROLLED WATER-DEFICIT STRESS

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ABSTRACT

A key breeding objective for bread wheat grown in the dry regions of Western Asia and North Africa is to enhance its adaptation to drought and its related salinity. Two newly-developed genotypes of synthetic hexaploid wheat, 'SW-3' and 'SW-4', their parental durum wheat variety 'Jennah Khetifa' and a dry-land bread wheat variety 'Cham 6', were compared for plant growth in saline hydroponic culture. They were also compared for root water-uptake and growth in soil culture in pots under combined water deficit and salinity stresses. Under saline hydroponic culture for five weeks, 'SW-3' developed a larger leaf area than the other genotypes. In saline soils for the period up to maturity, 'SW-4' and 'Cham 6' had higher root water uptake than the others. Only 'SW-4' developed normal grains and was clearly tolerant of soil salinity. 'Cham 6' developed normal spikes but ceased to fill the grains after heading. It may be assumed that salinity stress depressed root water-uptake at the early stages of growth, but the toxic effects of salinity stress whereas water-deficit stress resulted in relatively few genotypic differences. 'SW-4' was more tolerant of soil salinity than its durum wheat variety parent 'Jennah Khetifa'. This could be a useful genetic resource for improving 'Cham 6', which was relatively tolerant of water-deficit stress but sensitive to salinity stress after heading.

Keywords: *Triticum aestivum, Triticum durum, Aegilops tauschii*, synthetic wheat, drought, salinity, genetic resource, pre-breeding.

INTRODUCTION

Global climate change will affect the use of soil water by field crops. This is particularly likely in the Mediterranean climates of the arid agricultural regions of West Asia and North Africa (Thomas 2008). Changes in soil water use, in combination with soil salinity, are likely to influence crop yields (de Oliveira *et al.*, 2013). A key breeding objective for bread wheat (*Triticum aestivum* L.) grown in these dry regions is to enhance its adaptation to climate change.

In these regions, rainfall is seasonal and concentrated in the winter and spring periods, which overlap with the wheat growing season. Wheat plants grown under rainfed conditions often suffer water-deficit stress during the reproductive stage, both before and after flowering.

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In many such regions the subsoil contains salts, so wheat plants growing on stored soil moisture can also suffer severe salinity stress under water-deficit conditions because in these drier soils the migration of salts to the soil surface is accelerated. This results in increased concentrations of salts in the topsoil (Gowing *et al.*, 2009). The combination of these drought and salinity effects can impose a special stress on plants and thus have a strongly adverse effect on productivity. Enhanced salt tolerance can allow roots to take up more water and thus increase crop productivity on saline soils. Under water-deficit stress in a saline soil, root water-uptake for transpiration is a critical factor affecting both total biomass and also grain production.

Passioura (1977) indicated that there are three related components: water use (WU), water use efficiency (WUE) and harvest index (HI), which are critical for grain yield in wheat grown under conditions of limited water supply. In Australia, where a considerable proportion of the wheat crop is grown on stored soil moisture, grain yield has been improved by selection for genotypes having high WUE (Condon et al., 2002). Blum (2009) reviewed dehydration avoidance as a strategy for obtaining increased drought tolerance, suggesting that a major avenue for yield improvement is the reduction in WU during the early vegetative stage of growth in order to conserve soil moisture for use during the later reproductive stage. Wheat plants that allow optimized use of soil moisture may express high WUE for grain yield because of their relatively moderate WU and high HI. Mori and Inagaki (2012) recently confirmed that the drought-adaptive wheat genotypes achieved water savings through reduced WU and compensated for these through higher WUE and higher HI. WU, as effective use of water, may be the determinant for grain yield under water-deficit stress.

The physiological mechanisms through which salinity impacts wheat growth have mainly been studied using saline hydroponic culture, however, this does not allow for a combined water-deficit treatment. Munns et al., (1995, 2006) indicated that salinity has a two-phase effect - osmotic (water-stressed) and toxic (salt accumulation). Salt tolerance is often associated with a trait for a low rate of sodium (Na) accumulation in the plant and an enhanced potassium/sodium (K/Na) discrimination (Gorham et al., 1987; Gorham 1990; Munns and Tester 2008). For example, bread wheat has this trait, which is determined by a locus (Kna1) located on chromosome 4DL (Gorham et al., 1987; Dubcovsky et al., 1996). Durum wheat (T. turgidum L. ssp. durum (Desf.) Husn.) has a higher rate of Na accumulation and a lower K/Na discrimination, and is less saline tolerant than bread wheat (Gorham 1990; Munns and James 2003). Gorham (1990) reported that the enhanced K/Na discrimination was originally found in bread wheat and its wild relative Aegilops tauschii Coss. (common name, goat grass). It is thus clear how soil salinity in combination with water-deficit decreases root wateruptake for transpiration.

Breeding research for improvements in salinity tolerance in wheat, therefore, focuses on the use of wild relatives (Colmer *et al.*, 2006; Nevo and Chen 2010). Hexaploid bread wheat (ABD genomes) is thought to have originated spontaneously some 8000 years ago from natural crosses of tetraploid wheat (AB genomes) with diploid *Ae. tauschii* (D genome) (Feldman 2001),

and can be artificially synthesized from interspecific crosses between durum wheat and *Ae. tauschii*. This approach is providing an emerging genetic resource in bread wheat improvement, not only for increasing resistance to various biotic stresses, but also to resistance to abiotic ones, such as drought and salinity (Trethowan and van Ginkel 2009). *Ae. tauschii* is one of the wild relatives having high salinity tolerance (Farooq *et al.*, 1989; Dreccer *et al.*, 2004). A large number of the synthetic hexaploid wheat genotypes have been so far developed from crosses between durum wheat genotypes and *Ae. tauschii* accessions that enjoy high cross-compatibility (Ogbonnaya *et al.*, 2013).

This study, using soil in pots under controlled soil moisture conditions, has two objectives, 1) to compare the root water-uptake and growth of synthetic hexaploid wheat genotypes under conditions that combine both water deficit and salinity stress, and 2) to examine whether drought and salinity tolerance are enhanced by incorporating the D genome of *Ae. tauschii* into durum wheat. Two newly-developed genotypes of synthetic hexaploid wheat, a parental durum wheat variety and a dry-land bread wheat variety, were selected for experiments involving both hydroponic culture and soil culture in pots.

MATERIALS AND METHODS

Plant materials: Two synthetic hexaploid wheat genotypes, 'SW-3' and 'SW-4', were developed from crosses between the durum wheat 'Jennah Khetifa' with two Ae. tauschii accessions (ICARDA Genebank accession numbers 'ig48677' and 'ig47259') (Inagaki et al., 2014). 'Jennah Khetifa' is a landrace grown in the dry regions of North Africa showing tall stature and strong rootpenetration ability (Kubo et al., 2007). Ae. tauschii accession 'ig48677' was originally received as 'K7-8-6a (KU-2080)' in 1990. It was collected in 1955 by the Kyoto University Scientific Expedition (Japan) from Semnan Province in Iran. The accession 'ig47259' was collected by ICARDA from a heat-affected and low-rainfall site in Ragga Province, Syria in 1988 (Valkoun 2001). In addition to the two synthetic wheat genotypes, a parental durum wheat variety, 'Jennah Khetifa', and a leading bread wheat variety in dry regions, 'Cham 6', were used as the checks. The four genotypes were examined for their growth response to drought and salinity stresses using hydroponic culture and soil culture in pots.

Experiment 1 - hydroponic culture: Three germinated seeds from each of the four wheat genotypes, with four

replications, were used as the plant material. The culture solution contained 5 g of 'HYPONeX' (Hyponex Japan, Osaka, N:P:K 6.5:6.0:19.0) in 10 L of water. Hydroponic cultures were placed in a growth chamber under controlled conditions of 20°C, 12 h days and 20,000 lux fluorescent light-intensity. After one week of incubation with tap water, a culture solution having a concentration of 150 mM NaCl was added. Shoots and roots were harvested after five weeks of incubation and then spread on clear plastic film for measurement of the total leaf area using a leaf area meter (AAC-410, Hayashi Denko, Japan), and total root length using a scanner and image analysis program (WinRhizo, Regent Instruments Inc., Canada).

Experiment 2 - pot culture in soil: Wheat plants of the same four genotypes were established in pots with three plants per pot and four replicate pots per genotype. The plastic pots were 16 cm diameter giving sufficient volume to hold 2.7 kg dry weight of soil. The soil was a mixture of field soil, sand and peat moss having a field capacity (FC) of 45.4% and a permanent wilting point (PWP) of 13.3% by weight. Four pots of soil without plants were included to estimate evaporation from the soil surface. To accelerate growth, each pot was charged with 10 g of chemical fertilizer (N:P:K 8.0:8.0).

The pots were then irrigated to the soil top surface once or twice per week to maintain mean soil moistures up to 35% by weight. At three weeks of establishment, plants at three-tiller growth stage were subjected to drought and salinity stresses. A water-stress treatment was achieved by maintaining two ranges of soil moisture: 25 to 35% (well-irrigated) and 15 to 20% (water-stressed). The salinity-stress treatment was done by irrigating with saline water at a concentration of 150 mM NaCl. The four treatments consisted of C (well-irrigated with tap water, control), D (water-stressed with tap water), S (well-irrigated with saline water) and DS (waterstressed with saline water). The pot layout was randomly rearranged within and among treatment blocks once a week to minimize any shading effects among pots. The pots were placed in a naturally lit shade house with an average temperature of 17.3°C from January to June 2014 in Tunis, Tunisia. The shade house was covered with semi-transparent polycarbonate plates and overlaid with black shade net to reduce sunlight intensity.

Measurements: Root water-uptake (transpiration) was determined by weighing and calculated as the mean difference between the water consumption of pots with

plants (evapotranspiration) and that of pots without plants (evaporation). At the heading and maturity stages, the roots were separated from the soil. The roots were then spread on clear plastic film and the total root length (RL, $m \cdot pot^{-1}$) at heading was obtained using an image analysis program. Total transpiration (TA, L·pot⁻¹) was assumed equal to root water-uptake and this was accumulated for two periods from germination to heading and from germination to maturity. Data for root weight (RW, g·pot⁻¹) and shoot/leaf biomass (BM, g·pot⁻ 1) were collected at heading and maturity, after ovendrying to constant weight at 90°C. Plants under the DS treatment were harvested at the same time as those under the S treatment because most did not achieve heading. Data for grain weight (GW, g·pot⁻¹), number of grains per pot (n·pot⁻¹) and kernel weight (KW, mg·grain-1) were obtained at maturity. Transpiration efficiency g·L⁻¹) was expressed (TE, as (RW+BM+GW)·TA-1 and the HI (%)as GW·(RW+BM+GW)⁻¹. The soil salinity, expressed as electrical conductivity (EC, $dS \cdot m^{-1}$) and the acidity (pH) of the pot soils were estimated from 1:5 soil:water (g:g) extracts before planting and again after harvest. Comparisons of the wheat genotype means were carried out using Tukey's multiple range test derived from analyses of variance.

RESULTS

Plant growth under saline hydroponic culture: In the control (not salinity-stressed) of Experiment 1 hydroponic culture, 'Cham 6' had the largest leaves (16.25 cm²) and longest roots (500.0 cm) while 'SW-4' had the smallest leaves (10.34 cm²) and shortest roots (349.3 cm) (Fig. 1). Salinity treatment severely reduced both leaf development and root elongation in all genotypes tested, with large genotypic differences in leaf area (2.02 to 4.84 cm²) and root length (74.6 to 131.0 cm). 'SW-3' developed a significantly larger leaf area than the other genotypes. In contrast, 'SW-4' showed the smallest plants with the lowest leaf areas. This suggests that 'SW-3' is more tolerant to salinity stress than the controls, while 'SW-4' was more sensitive.

Root water-uptake and plant growth under waterdeficit and salinity treatments in soil in pots: In Experiment 2 of the pot culture in soil, the well-irrigated treatments (C and S) gave soil moistures of 35 to 25% which lay between FC and PWP, whereas the waterstress treatments (D and DS) had soil moistures slightly higher than PWP.



Figure 1. Leaf and root development in four wheat genotypes grown under salinity-stress conditions in hydroponic culture. Columns labeled with the same letter in each condition for each trait are not significantly different (P<0.05) based on Tukey's multiple range test.

Table 1 lists the results for the physiological traits of the four wheat genotypes grown from germination to heading under the four treatment conditions combined with water-deficit and salinity stresses. Under the non-saline treatments of C and D, TA, RL, BM and TE were not significantly different among the 'SW-3', 'SW-4' and 'Jennah Khetifa' genotypes. 'Cham 6' was lower in both of TA and BM than the other genotypes. There were similar values for TE among all four genotypes. Under the salinity treatments S and DS, growth was severely depressed to lower TA and BM. Under the S treatment, 'SW-4' and 'Cham 6' had relatively higher TEs than the others. All plants under the DS treatment developed slightly longer

roots and took up more water than those under the S treatment, but ceased to develop before heading. Only 'Cham 6' had a higher TE under the DS treatment.

Growth of the four wheat genotypes after heading, under the four treatments, C, D, S and DS, is shown in Fig. 2. Results for the physiological traits of the four wheat genotypes at maturity are given in Table 2. Under the non-saline treatments of C and D, 'SW-3' and 'SW-4' had significantly lower GWs than 'Cham 6' and 'Jennah Khetifa' because of lower HIs. They also showed less distinct genotypic differences between the C and D treatments. There were no significant differences in TE among genotypes.



Figure 2. Growth of four wheat genotypes (from left to right in each photograph: 'SW-3', 'SW-4', 'Jennah Khetifa' and 'Cham 6') after heading under different stress conditions (C, control; D, water-deficit; S, salinity; DS, water-deficit and salinity).

In contrast, under the saline treatment S, 'SW-4' and 'Cham 6' showed higher TA, lower TE, and higher HI than 'SW-3' and 'Jennah Khetifa', indicating significant differences in these traits between the two groups. Also, 'SW-4' and

'Cham 6' showed reduced GWs while 'SW-3' produced very few grains and 'Jennah Khetifa' had no grains. In addition, 'Cham 6' ceased to develop after heading, with shriveled grains with smaller KW than those of 'SW-4'.

Condition	Transpiration	Root length	Root weight	Biomass	Transpiration efficiency			
Genotype	(L∙pot-1)	(m·pot-1)	(g∙pot-1)	(g∙pot-1)	(g·L-1)			
C (well irrigated)								
SW-3	4.86ª	382ª	2.82ª	33.9ª	7.03ª			
SW-4	4.82ª	328ª	2.24 ^a	35.1ª	7.29ª			
Jennah Khetifa	5.01 ^a	331ª	2.51ª	38.8 ^a	7.74 ^a			
Cham 6	2.78 ^b	250 ^b	1.37 ^b	20.2 ^b	7.26ª			
D (water stressed)								
SW-3	2.81 ^a	175ª	1.23ª	18.5ª	7.04 ^a			
SW-4	2.81 ^a	158ª	1.10 ^a	18.9 ^a	7.13ª			
Jennah Khetifa	2.89ª	178ª	1.05 ^a	21.2ª	7.68ª			
Cham 6	2.00 ^b	113 ^b	0.73 ^b	13.8 ^b	7.25ª			
S (well irrigated with saline water)								
SW-3	1.02ª	70 ^a	0.51ª	9.6ª	9.9 ^b			
SW-4	0.98 ª	77 ^a	0.52ª	10.5ª	11.3 ^{ab}			
Jennah Khetifa	1.04 a	81ª	0.46 ^a	10.6ª	9.8 ^b			
Cham 6	0.87 b	65ª	0.39ª	10.9ª	13.0ª			
DS (water stressed with saline water)								
SW-3	1.21 ^b	76ª	0.43ª	4.7 ^b	4.2 ^b			
SW-4	1.28 ^b	80 ^a	0.44^{a}	5.1 ^b	4.3 ^b			
Jennah Khetifa	1.47ª	87ª	0.45 ^a	5.9 ^{ab}	4.3 ^b			
Cham 6	1.15 ^b	74 ^a	0.40ª	7.2ª	6.6 ^a			

Table 1. Root water-uptake and growth from germination to heading under different stress conditions in four wheat genotypes.

Values followed by the same superscript letter in each condition for each trait are not significantly different (*P*<0.05) based on Tukey's multiple range test.

Table 2. Root water-up	ptake and growth fro	om germination t	to maturity under	different stress co	nditions in four	wheat genotypes.
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Condition Genotype	Transpiration (L·pot ⁻¹)	Root weight (g•pot ⁻¹)	Biomass (g∙pot⁻¹)	Grain weight (g∙pot¹)	Transpiration efficiency(g·L ⁻¹)	No. grains (n•pot ⁻¹)	Kernel weight (mg•grain ⁻¹)	Harvest index (%)	
C (well-irrigated)								(,,,)	
SW-3	8.13 ª	1.21 ^a	34.7ª	11.4 ^b	5.67ª	230 ^c	49.9 ^a	24.8°	
SW-4	7.71 ª	0.89 ^{ab}	31.7ª	11.7 ^b	5.63ª	287c	40.9 ^a	26.8°	
Jennah Khetifa	8.11 ^a	1.16 ^a	33.8ª	17.1ª	6.28 ^a	355 ^b	48.0 ^a	33.5 ^b	
Cham 6	6.77 ^b	0.69 ^b	23.3 ^b	19.8ª	6.40 ^a	439 ^a	45.2ª	46.1ª	
D (water-stressed)									
SW-3	4.03 ^a	0.79 ^a	18.3ª	4.6 ^c	5.69ª	86 ^c	53.2ª	19.7 ^d	
SW-4	4.00 ^a	0.63ª	16.0ª	5.7c	5.43 ^a	153 ^b	37.7 ^b	26.3 ^c	
Jennah Khetifa	4.41 ^a	0.71 ^a	19.4ª	8.7 ^b	6.37 ^a	182 ^b	48.1 ^a	31.0 ^b	
Cham 6	4.37ª	0.48^{b}	13.6 ^b	12.4 ^a	5.96 ^a	280 ^a	44.3 ^a	47.6 ^a	
S (well-irrigated with saline water)									
SW-3	0.95 ^b	0.62ª	10.4ª	0.0 ^b	11.39ª	4 ^c	-	_	
SW-4	1.44ª	0.67 ^a	12.8ª	1.8 ^{ab}	8.88 ^b	62 ^b	28.7ª	12.3 ^b	
Jennah Khetifa	1.03 ^b	0.44 ^a	12.0ª	0.0 ^b	11.68ª	0 ^c	-	-	
Cham 6	1.34ª	0.49 ^a	11.3ª	3.0ª	9.26 ^b	228ª	12.7 ^b	20.5ª	
DS (water-stressed with saline water)									
SW-3	1.38ª	0.58ª	5.3 ^b	0.0	3.85°	0.0	-	_	
SW-4	1.33ª	0.54ª	5.9 ^b	0.0	4.44 ^{bc}	0.0	-	-	
Jennah Khetifa	1.47ª	0.61ª	6.9 ^b	0.0	4.72 ^b	0.0	_	-	
Cham 6	1.60ª	0.48 ^a	9.5ª	0.0	5.94 ^a	0.0	-	-	

Values followed by the same superscript letter in each condition for each trait are not significantly different (*P*<0.05) based on Tukey's multiple range test.

Under the water-stress/salinity treatment of DS, most of the plants did not achieve heading, although 'SW-3' and 'SW-4' maintained green crowns.

The soil used for Experiment 2 showed an initial EC of 0.22 dS·m⁻¹ and a pH of 8.12. At the maturity stage, the mean soil salinity levels under C, D, S and DS treatments were 2.91, 2.38, 5.15 and 4.46 dS·m⁻¹, respectively, This shows a distinct increase in salinity level following irrigation with tap water and in the salinity treatments, but with no significant differences between wheat genotypes. Mean soil acidities (pH values varied from 7.70 to 7.53) indicated no significant differences among genotypes and treatments.

DISCUSSION

After five weeks under hydroponic culture, the newlydeveloped synthetic hexaploid wheat genotypes 'SW-3' and 'SW-4' were, respectively, less and more sensitive to salinity stress than the parental durum wheat 'Jennah Khetif. However, these genotypes showed opposite responses up to maturity under saline conditions in soil in pots. 'SW-4' was tolerant to soil salinity and developed normal grains. It is not clear why 'SW-4' expressed a tolerant response to salinity in pot soil culture but was salinity sensitive in hydroponic culture. In addition, 'Cham 6' developed spikes, but ceased to complete grain filling after heading under soil salinity stress. Therefore, it may be assumed that salinity stress depressed root water-uptake at the early stages of growth, but the toxic effects of salinity stress increased in the later stages, resulting in different genotypic responses to salinity stress in grain yield. Munns and Tester (2008) indicated that the toxic effects of sodium ion accumulation were more damaging in terms of early leaf senescence than was osmotic stress to leaf/shoot development. 'SW-4' may be sensitive to osmotic stress and tolerant to toxic stress while 'Cham 6' may be tolerant to osmotic stress, but sensitive to toxic stress. Further study is required to determine the effects of salinity stress on root wateruptake that may be associated with osmotic stress and the effects of salinity stress on biomass production that may be associated with the toxic effect.

Water-deficit stress did not elicit distinctive genotypic responses in this study. Both the synthetic wheat genotypes, 'SW3' and 'SW4', were less productive for grain yield than 'Jennah Khetifa' and 'Cham 6'. This may be attributed to their lower rates of partitioning biomass to grains. 'Cham 6' was relatively tolerant to waterdeficit stress with the highest GW and HI. Grain yield under water-deficit conditions is determined not only by HI but also by WU and WUE (Passioura 1977; Siddique et al., 1990). Sohail et al., (2011) reported that no morphological or physiological traits on drought tolerance in the synthetic wheat genotypes were significantly correlated with the corresponding traits of their parental Ae. tauschii accessions under water-deficit conditions. The low correlation between them was also reported on the abscisic acid responsiveness that was associated with stress tolerance (Iehisa and Takumi 2012). Synthetic wheat is physiologically and morphologically an intermediate form between the cultivated and wild types and should be improved by creating a cultivated form having early heading and of short stature by back-crossing with elite bread wheat varieties. Some of these synthetic wheat derivatives have achieved improved grain yields under water-deficit stress by modifying WU, WUE, and HI (Reynolds et al., 2007; Mori and Inagaki 2012).

Distinct responses were found to soil salinity among the four wheat genotypes. 'SW-4' clearly had improved tolerance to salinity as a consequence of adding the D genome of the Ae. tauschii accession 'ig47259' to the durum wheat variety 'Jennah Khetifa', which was sensitive to salinity. However, another accession, 'ig48677', did not show such an effect in the synthetic wheat genotype 'SW-3'. 'SW-4' developed normal grains, although the number of grains was severely decreased under salinity stress, whereas 'Cham 6' developed a sufficient number of grains, but ceased filling them after heading. Schachtman et al., (1992) examined the grain yields of synthetic wheat genotypes under hydroponic culture and reported that they varied in salt tolerance depending on the source of Ae. tauschii. Their salt tolerance was greater than that of the durum wheat parents primarily because of the maintenance of kernel weight. This suggests that the mechanism of salinity tolerance might be different between the synthetic wheat genotypes and the bread wheat variety 'Cham 6'. A population of recombinant inbred lines derived from back-crosses of 'SW-4' with 'Cham 6', has been developed for further evaluation of the effects of incorporating the salt tolerance of 'SW-4' into a bread wheat.

This study shows that the salinity level of soil in pots was increased by irrigation with saline water and even with tap water. Soil salinity conditions, combined with water deficit, were too severe to allow development of the grains. The depressing effects of salinity stress on growth may be exacerbated by increased concentrations of salts in the soil when combined with a water-deficit stress. Grewal (2010) reported that highly saline subsoil affected root growth, water uptake, grain yield and WUE under temporary water-deficit stress, with a depressing effect on grain yield through a reduced number of kernels per spike.

In conclusion, the four wheat genotypes used in this study responded differently to salinity stress while water-deficit stress gave less genotypic differences. A newly-developed synthetic wheat genotype, 'SW-4', was more tolerant to soil salinity than its parental durum wheat variety, 'Jennah Khetifa', and may represent a genetic resource useful for improving 'Cham 6', which was relatively tolerant to water-deficit stress but sensitive to salinity stress after heading.

ACKNOWLEDGEMENTS

This article is a contribution from the special projects of ICARDA on 'Development of drought-tolerant wheat germplasm through integrated approaches' funded for 2010–2014 by the Government of Japan. The technical support on wheat root analysis from the Arid Land Research Center, Tottori University, Japan is also appreciated.

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