

Tolerance of Prolonged Drought among a Set of Bread Wheat Chromosome Substitution Lines

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Variation in tolerance of prolonged drought was identified among a set of single chromosome bread wheat substitution lines, involving the replacement of each cv. Chinese Spring chromosome in turn with its homologue from a synthetic hexaploid (*Triticum dicoccoides* × *Aegilops tauschii*). Water stress was applied under controlled conditions by limiting the supply of water to 30% from 100% aqueous soil. The reaction to the resulting long-term drought stress was quantified by three indices, based on grain yield components. Enhanced drought tolerance was associated with the presence of donor chromosomes 1A, 5A, 1D, 3D, 5D and 6D, and enhanced susceptibility with chromosomes 3A, 4B and 7D.

Keywords: bread wheat, single chromosome substitution, synthetic hexaploid, yield components, indices of tolerance and sensitivity to drought

Introduction

Drought is one of the most damaging environmental stresses affecting grain yield of bread wheat throughout almost the full geographic range of the crop's production. The genetic enhancement of drought tolerance probably represents the most sustainable means of alleviating the loss in economic yield caused by drought, but little breeding progress has been made over the last century in this direction, mainly because tolerance is an ill-defined trait, and its inheritance is complex (Collard and Mackill 2008; Witcombe et al. 2008; Richards et al. 2010).

Marker assisted selection, where variation at the DNA sequence level is used as a surrogate for variation at the phenotypic level, has considerable potential for applying selection pressure for this sort of trait (Varshney and Tuberosa 2008). The definition of the necessary markers requires mapping in customized populations constructed from crosses between lines contrasting in their response to drought stress (Quarrie et al. 2005; Kuchel et al. 2007; Dashti et al. 2007; Kirigwi et al. 2007; Kordenaej et al. 2008).

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In wheat, the technical difficulty of this process is to a degree simplified by the availability of specialized genetic stocks, which allow for the chromosomal, and in some cases the intra-chromosomal location of quantitative trait loci (QTL). Such lines have, for example, been used to identify the chromosomes responsible for determining relative leaf water content (Farshadfar et al. 1995), stomatal density (Dylenok et al. 1981; Davydov 2001; Davydov and Pshenichnikova 2008), and polyamine accumulation (Galiba et al. 1993).

Bread wheat germplasm includes a measure of variation in drought tolerance, reflected by its cultivation under a wide array of climatic and edaphic conditions. Among its wild relatives are species naturally adapted to droughted environments, and these offer some potential for extending the genetic variability of wheat via wide hybridization and introgression (Hajjar and Hodgkin 2007; Halloran et al. 2008). Introgression lines have already been exploited by Peleg et al. (2009) to identify genetic factors in durum wheat associated with the whole plant response to drought stress, as well as to map bread wheat QTL associated with various characteristics of germination and seedling growth (Landjeva et al. 2009).

The set of single chromosome substitution lines involving a synthetic hexaploid (Syn) as donor and the cultivar Chinese Spring (CS) as recipient was developed by C.N. Law and A.J. Worland at the Plant Breeding Institute, Cambridge, U.K. (Nicholson et al. 1993). Syn is a chromosome-doubled hybrid between the AB tetraploid *Triticum dicoccoides* and the D genome progenitor *Aegilops tauschii* (McFadden and Sears 1946). The substitution line set and various derivatives have been used to genetically analyse variation in a number of agronomic traits (Nicholson et al. 1993; Pestsova et al. 2001, 2006; Arraiano et al. 2001; Simon et al. 2007; Navakode et al. 2009).

Here, we present an analysis of the effect on various grain yield components of artificially imposed and controlled drought on the CS/Syn single chromosome substitution set. Our aim was to reveal which chromosome(s) carry genes responsible for adaptation to drought.

Materials and Methods

Of the 21 possible CS/Syn single chromosome substitution lines, four were excluded from the analysis as their constitution has been previously shown to be incorrect (Salina et al. 2003). Also, included were recipient and donor lines Syn and cv. CS. Before germination, all grains were surface-sterilized by immersion for 1–2 min in 96% ethanol. A one month period of vernalization (low temperature, low light intensity) was given to seedlings of Syn and substitution line CS/Syn 5D in order to ensure that all lines reached flowering at much the same time. A sample of 10–12 grains per line was sown into each of four Mitcherlich vessels containing a humus, sand, peat (1:1:1) mixture, and the plants were maintained under a 16 h day/8 h night at 20–25/10–15°C air and $19 \pm 1^\circ\text{C}$ soil temperature. Additional lighting was supplied at 260 W/m². Two contrasting moisture regimes were applied: in two vessels, moisture stress was avoided by regular watering, while in the other two, once the plants had reached the three leaf stage, water regime was restricted till 30% from 100% aqueous soil (full soil drought). Plants of the control group received 60%

moisture from 100% aqueous soil which was determined according a standard method (Zhurbitzkiy 1968). The amount of water supplied was determined three times per week by weighing the vessels and adjusting the volume of supplementary water accordingly.

At maturity, the leading spike of five to eight plants per vessel was harvested, and analysed for the number of grains (NG), the grain weight in g (GW) and the individual grain mean weight in mg (MGW = GW/NG). Drought tolerance/sensitivity was assessed by calculating the indices ITF (Fernandez 1992), IT (Kuol 2004) and SSI (Fischer and Maurer 1978). These indices are derived from the parameters \bar{T}_d (global trait mean of all droughted plants), \bar{T}_c (global trait mean of all non-droughted plants), T_d and T_c (trait mean of, respectively, droughted and non-droughted plants of a given line). ITF is given by the expression $(T_c \times T_d)/(\bar{T}_c)^2$; IT by $T_d/T_c \times 100$, and SSI by $[1 - (T_d/T_c)]/[1 - (\bar{T}_d/\bar{T}_c)]$. Means, standard errors and the significance of differences according the Student *t*-test were calculated within Microsoft Excel.

Results

In the absence of moisture stress, Syn was the least productive line for all the yield components measured, while the presence of a single Syn chromosome pair in an otherwise cv. CS background had a variable effect (Table 1). Thus the presence of Syn chromosomes 2B, 5B and 5D depressed both NG and GW, but did not affect MGW. The presence of Syn chromosomes 1A, 4B, 1D, 4D, 6D and 7D increased GW, while in CS/Syn 3D GW was significantly lower than in CS. The range in GW was from 0.18 g (CS/Syn 5D) to 1.64 g (CS/Syn 1A), that of NG from 4.8 (CS/Syn 5D) to 45.2 (CS) and that of MGW from 25.7 g (CS/Syn 3D) to 38.3 g (CS/Syn 6D). Most of the Syn chromosomes had a deleterious effect on grain productivity (Table 1).

Of the four A genome substitution lines analyzed, CS/Syn 1A and CS/Syn 5A both developed speltoid spikes under both well-watered and moisture stressed conditions, as did Syn itself. Under well-watered conditions, the GW of these lines did not differ from that of CS, but the CS/Syn 1A MGW was noticeably higher in both well-watered and droughted conditions (Table 1), with a consequential increase in its ITF for this trait (Table 2). CS/Syn 5A showed a good level of tolerance in terms of NG, while CS/Syn 3A yielded poorly and had a lower tolerance than CS with respect to both GW and MGW. CS/Syn 6A showed a rather high IT, but was less productive than CS with respect to NG.

The B genome was represented by six of the possible seven lines. The GW of CS/Syn 2B and CS/Syn 5B under well-watered conditions was below that of CS, but the other four lines were as productive as the recipient. CS/Syn 4B developed particularly large grains. The spike productivity of all these B genome chromosome substitution lines was reduced by drought (decrease in ITF), but they were all more tolerant than CS with respect to NG (except for CS/Syn 5B) and MGW (Table 2). CS/Syn 4B was not able to fully fill its large size grains under droughted conditions; it produced a low ITF, IT and SSI for both WG and MGW, revealing this line to be the most drought susceptible of the set.

Under well-watered conditions, both GW and NG were lower for all the D genome chromosome substitution lines than for CS (Table 1). However, both CS/Syn 1D and

Table 1. Mean values (m_s) and standard error (σ) of spike yield components among the CS/Syn chromosome substitution lines and their parents. Plants were grown under both well-watered (control) and limited moisture (drought) conditions

Lines	Weight of grain		Number of grains		Mean weight of one grain, mg	
	Control	Drought	Control	Drought	Control	Drought
CS	1.41 ± 0.25	0.59 ± 0.04	45.2 ± 9.0	17.6 ± 1.7	31.4 ± 1.4	29.3 ± 1.5
Syn	0.47 ± 0.09**	0.22 ± 0.03***	18.4 ± 1.4**	10.2 ± 1.1**	26.6 ± 2.5*	21.5 ± 2.8*
1A	1.64 ± 0.06	0.59 ± 0.05	43.4 ± 2.9	18.0 ± 1.4	37.8 ± 2.3**	33.5 ± 1.2*
3A	1.44 ± 0.14	0.43 ± 0.05*	43.8 ± 5.9	18.8 ± 1.8	33.4 ± 1.8	24.6 ± 1.3*
5A	1.39 ± 0.10	0.60 ± 0.02	40.8 ± 4.2	20.0 ± 1.1	33.8 ± 1.9	28.9 ± 1.6
6A	1.17 ± 0.06	0.52 ± 0.06	33.8 ± 2.6	17.8 ± 2.8	34.6 ± 1.6	29.1 ± 1.7
1B	1.10 ± 0.18	0.49 ± 0.04*	32.6 ± 2.1	18.3 ± 0.9	33.4 ± 4.3	27.5 ± 3.1
2B	1.01 ± 0.12*	0.51 ± 0.06	32.2 ± 4.6	18.4 ± 1.6	32.0 ± 3.8	28.8 ± 0.6
3B	1.09 ± 0.15	0.59 ± 0.05	35.4 ± 5.1	21.5 ± 0.5	31.0 ± 2.1	27.4 ± 1.7
4B	1.41 ± 0.11	0.25 ± 0.02***	40.0 ± 2.4	17.3 ± 1.3	35.3 ± 1.1**	13.2 ± 1.2***
5B	0.91 ± 0.18*	0.47 ± 0.05	26.4 ± 4.6**	15.7 ± 1.3	34.6 ± 3.7	30.0 ± 1.7
7B	1.29 ± 0.15	0.48 ± 0.03	42.0 ± 4.0	16.9 ± 1.4	30.5 ± 1.4	25.9 ± 2.8
1D	1.28 ± 0.20	0.62 ± 0.09	33.8 ± 4.7	20.4 ± 2.8	37.8 ± 1.0**	30.7 ± 0.7
2D	1.08 ± 0.18	0.50 ± 0.06	30.2 ± 4.6*	16.5 ± 0.9	35.0 ± 1.7	30.0 ± 3.3
3D	1.01 ± 0.08*	0.59 ± 0.09	39.6 ± 3.3	25.0 ± 2.8*	25.7 ± 2.8*	25.1 ± 0.8
4D	0.93 ± 0.23*	0.49 ± 0.07	26.2 ± 6.6**	15.2 ± 2.1	35.9 ± 2.0*	29.6 ± 1.6
5D	0.18 ± 0.14***	0.23 ± 0.09***	4.8 ± 2.2***	8.0 ± 3.2*	31.8 ± 2.1	27.1 ± 0.9
6D	1.19 ± 0.29	0.54 ± 0.05	31.2 ± 2.6*	4.2 ± 1.9	38.3 ± 3.0***	35.8 ± 2.3*
7D	1.25 ± 0.11	0.43 ± 0.05*	35.8 ± 3.4	15.2 ± 1.9	34.6 ± 1.7*	24.7 ± 1.5*

* P < 0.05; ** P < 0.01; *** P < 0.001

Table 2. Drought tolerance indices [ITF (Fernandez 1992); IT (Kuol 2004); SSI (Fischer and Maurer 1978)] based on spike yield components among the CS/Syn chromosome substitution lines and their parents

Lines	Weight of grain			Number of grains			Mean weight of one grain, mg		
	ITF	IT	SSI	ITF	IT	SSI	ITF	IT	SSI
CS	0.66	42.5	1.0	0.71	38.5	1.18	0.83	93.4	0.40
Syn	0.08***	45.3	0.95	0.25**	51.9*	0.92*	0.51*	80.9	1.24
1A	0.71	36.0	1.1	0.70	41.5	1.19	1.13*	88.6	0.74
3A	0.44**	30.9*	1.2*	0.74	43.0	1.13	0.83	73.7*	1.60*
5A	0.63	42.5	1.0	0.73	49.0*	1.05	0.88	85.6	0.93
6A	0.47*	43.0	0.99	53.1*	0.93	0.90	0.90	84.1	0.81
1B	0.46*	44.5	0.94	0.54*	56.0**	0.89**	0.82	82.3	1.06
2B	0.39*	51.2	0.86	0.53	56.9*	0.87*	0.83	90.1	0.64
3B	0.49	53.6	0.83	0.69	60.7*	0.83*	0.76	88.4	0.74
4B	0.27***	18.1***	1.42**	0.62	43.3*	0.83	0.42*	37.5**	3.94*
5B	0.32***	51.7	0.93	0.37***	59.4**	0.81**	0.93	86.6	0.84
7B	0.45**	36.6	1.07	0.64	40.2	1.24	0.83	84.7	0.98
1D	0.61	47.8	0.92	0.62	58.4*	0.82*	1.04*	81.2	1.20
2D	0.42**	45.0	0.96	0.46*	53.2*	0.97*	0.95	85.7	0.97
3D	0.34***	54.4	0.79	0.8	59.0*	0.83*	0.62*	97.2	0.28
4D	0.34***	54.4	0.79	0.35***	58.1*	0.83*	0.95	82.4	0.53
5D	0.49*	228.3*	-2.85**	0.03***	200.0*	2.65**	0.78	85.3	0.90
6D	0.49*	45.3	0.95	0.40**	45.4	1.07	1.23*	93.3	0.35
7D	0.42**	32.8*	1.17	0.49*	42.5	1.17	0.92	71.4*	1.75*

* P < 0.05; ** P < 0.01; *** P < 0.001

/Syn 6D produced larger individual grains (MGW), while CS/Syn 3D produced smaller ones. Under drought stress, the yield of most of the lines was reduced, producing a significantly smaller ITF for MG and NG compared to CS. The MGW ITF of CS/Syn 1D and CS/Syn 6D remained significantly higher than that of CS, reflecting the ability of these two lines to maintain large grains even under droughted conditions. In a field experiment the latter genotype also showed a high tolerance for all yield components (unpublished results). Most of the D genome chromosome substitution lines had a high NG IT (Table 2), and among them, the least productive, but the most drought tolerant was CS/Syn 5D.

Discussion

The ITF index reflects the tolerance of a line by comparing its performance to the global mean within a treatment. The Syn GW ITF was eightfold lower than that of CS (Table 2), but Syn showed a greater tolerance with respect to NG. This suggested that while the response of CS to drought stress was to retain GW at the expense of NG, that of Syn was the other way around, consistent with the idea that the genetic basis of variation in drought tolerance is polygenic. This model of genetic control similarly explains why the drought response of the individual single chromosome substitution lines differ from one another.

Overall, NG was less affected by the imposition of drought among the chromosome substitution lines (and Syn itself) than in CS. The ability to retain fertility and grain number despite the presence of water deficit is a common characteristic of wild cereal species, which are naturally adapted to regions where drought is commonplace. In contrast, the recipient CS tended to retain its grain size in the face of drought stress, which may reflect its history of many generations of man-made selection pressure for this critical end-use trait.

Pestsova et al. (2001, 2006) studied the field performance of the CS/Syn D genome chromosome substitution lines, and showed that the replacement of CS chromosome 5D by its Syn homologue reduced fertility (and therefore the grain yield) by >90%. This effect was ascribed to the action of two independent QTL, one of which co-located with *Vrn-D1*. Since much of this effect was thought to be due to the vernalization requirement inherited from Syn (Pestsova et al. 2006), here we removed this effect by full vernalizing the line prior to the treatment. Nevertheless, in spite of this precaution, the CS/Syn 5D line still performed poorly with respect to both GW and NG (Table 1), producing the lowest levels of ITF (Table 2). But having so low productivity the line had higher mean values for WG and NG under drought. This explains the highest and lowest values for IT and SSI, respectively. This special feature of the line we also observed in a field experiment under more severe drought when plants obtained only 10% of water from the optimal water supply (unpublished results). So, 5D substitution in CS background for the homoeologue from *Ae. tauschii* resulted in genotype being unlike the parents in physiological performance.

Our results are in a good agreement with those reported by Farshadfar et al. (1995), who studied relative water content and water loss in a set of single chromosome substitution lines derived from the cross CS × cv. Cappelle-Desprez. The six chromosomes identified as harbouring the most (or the largest effect) relevant genes were 1A, 5A, 4B, 1D, 3D and 5D, which coincided with the most critical chromosomes in the CS/Syn set.

The dehydrins are a group of proteins which characteristically accumulate under drought stress; they are thought to help prevent tissue dehydration. Some of these proteins in wheat are under the control of genes present on homoeologous group 1 (Ried and Walker-Simmons 1993). Thus the positive effect of both Syn chromosomes 1A and 1D may reflect the presence of favourable alleles at structural genes for dehydrin or for dehydrin accumulation. The importance of the homoeologous group 5 chromosomes in the abiotic stress response has also repeatedly been identified (Cattivelli et al. 2002), and has been associated with the accumulation of polyamines and abscisic acid (Galiba et al. 1993; Quarrie et al. 1994).

The physiological basis of the poor drought tolerance of CS/Syn 4B is unclear. Both structural and regulatory genes encoding enzymes involved in antioxidant production are located on the chromosomes of homoeologous group 4 (Thiele and Siedel 1990; Dudnikov 2002), so it is possible that the alleles of these gene(s) provided by Syn chromosome 4B result in a weakening of the antioxidant system. This notion enjoys some circumstantial support from the performance of a line in which chromosome 4D has been replaced by barley 4H, which suggested that the drought tolerance of wheat was improved by this substitution (Molnar et al. 2007).

We aimed to identify which chromosomes were most critical to the determination of the drought tolerance displayed by CS and Syn. The individual chromosome substitution lines varied with respect to their tolerance, particularly those involving either the A or the D genome (in particular, chromosomes 1A, 5A, 1D, 3D, 5D and 6D). The least tolerant line was CS/Syn 4B, followed by CS/Syn 3A and CS/Syn 7D. The best combination of productivity under well-watered conditions and tolerance to drought was exhibited by CS/Syn 1D. Thus our future strategy will focus on the production of recombinant lines involving the critical chromosomes, with a view to carrying out a formal QTL mapping exercise to identify the intrachromosomal position of the gene(s) responsible. We also intend to search for syntenic to homologous loci with known functions in sequenced plant genomes using bioinformatic approach.

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