African Journal of Agricultural Research Vol. 7(46), pp. 6191-6196, 5 December, 2012
Available online at http://www.academicjournals.org/AJAR
DOI: 10.5897/AJAR11.1931
ISSN 1991-637X ©2012 Academic Journals

Full Length Research Paper

Identification of seed dormancy on chromosome 2BS from wheat cv. Chinese Spring

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Accepted 13 June 2012

Seed dormancy, a main factor contributing to preharvest sprouting (PHS) tolerance, is an adaptive trait largely affected by environmental conditions, such as temperature and moisture, during seed development and after ripening. PHS reduces the end-use of wheat by declining grain quality, which leads to further economic losses. The wheat cultivar 'Chinese Spring' (CS) has *ph* and *kr* genes, and was always used as bridge parent to cross with related species in order to transfer good genes from other species. The wheat cultivar CS has moderate seed dormancy level. However, it was widely used to be crossed with stronger dormant varieties to characterize the dormant genes of strong dormancy varieties, the dormant traits of CS itself have not been indicated enough. Germination index (GI) and Germination percent (GP) of CS and its 36 ditelosomics were tested. It suggested that 3AS, 4AS, 6AS, 2BS and 1DS carry major gene(s) associated with wheat seed dormancy. Furthermore, CS and its five corresponding ditelosomics were crossed with an undormancy wheat accession YY2. The lines obtained from DT3AL, DT4AL, DT6AL and DT2BL showed statistically (at 5% level) higher in both GP and GI than that from CS × YY2 line. It indicated that 3AS, 4AS, 6AS and 2BS in CS carry major dormancy gene(s) relative to YY2. A QTL map of GP and GI was carried out at the different region on the short arm of chromosome 2B, which ranged the order as Xgwm510, Xgwm210, Xgwm50, QTL_{GI}, QTL_{GE} and QTL_{GP}, and the genetic distance were 28.5, 2.6, 25.7, 16.4 and 13.7 cM, respectively.

Key words: Wheat, Ditelosomics analyses, seeds dormancy, quantitative trait locus (QTL) mapping.

INTRODUCTION

Seed dormancy is an important characteristic for seeds to survive until conditions are suitable for germination. In cereal crops, pre-harvest sprouting (PHS), which is induced easily in seeds with a low level of dormancy, reduces end-use grain quality, which leads to further economic losses, has been widely recognized by wheat (*Triticum* species) producers throughout the world. Seed dormancy, a main factor contributing to PHS tolerance, is an adaptive trait largely affected by environmental conditions, such as temperature and moisture, during seed development and after ripening (Hagemann and Ciha, 1987; Mares, 1993; Biddulph et al., 2005).

Quantitative trait loci (QTL) for PHS have been found on all 21 wheat chromosomes. The role of seed integument is not investigated enough, although it has been reported that Red-alleles are localized in 3AL, 3BL, 3DL and determine red coloration of seed (Flintham, 2000; Warner et al., 2000). The contribution in seed dormancy of each Red-allele is usually small and hard to

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define (Flintham, 2000). The red-grained genotypes susceptible to pre-harvest sprouting are also known to exist. It is not entirely clear that the role of a seed coat in seed dormancy and resistance to pre-harvest sprouting (Mares et al., 2009). It is possible that in seed coat, some other genes are expressed to determine seed dormancy in addition to Red-genes (Gu et al., 2006, 2008; Barrero et al., 2009). In wheat, three homologous genes *TaVp-A1*, *TaVp-B1* and *TaVp-D1* are localized in the long arm of 3rd group of chromosomes (3AL, 3BL, 3DL) at the distance of approximately 30 cM from Red-loci (McKibbin et al., 2002). Germination usually correlates with activity of alpha-amylase (Amy), which initiates starch to dissolve in the endosperm. Three genes-orthologues (*a-Amy-A1, a-Amy-B1 ua-Amy-D1)* were identified and localized on the long arms of 6AL, 6BL, and 6DL (McIntosh et al., 2009). There are two key hormones affecting the regulation of seed dormancy, germination-abscisic acid (ABA) and gibberellins (GA). ABA is the main signal factor for embryogenesis, the start of seed dormancy and its maintenance (Finkelstein et al., 2008; Gubler et al., 2005). Gibberellins induce the activity of Amy-1, while ABA, apparently, prevents alpha-amylase expression and the programmed cell death in aleurone (Walker-Simmons, 1987; Sabelli and Larkins, 2009).

The highest frequency of QTL occurrence was detected in the chromosomes 3A, 3B, 3D, followed by QTLs on 4A, 4B, 4D (Ogbonnaya et al., 2008; Mares et al., 2002; Mohan et al., 2009; Anderson et al., 1993; Noda et al., 2002; Ohnishi et al., 2008). This group includes the second highest number of identified major and minor *QphsR* loci. The major *QphsR* locus localized in 4AL was found in both white- and red-grained genotypes of various origins (Groos et al., 2002; Kato et al., 2001; Mares et al., 2005; Osa et al., 2003; Mori et al., 2005; Kulwal et al., 2004; Lohwasser et al., 2005; Torada et al., 2005; Chen et al., 2008). In the short arms of 2A, 2B and 2D, there are three identified genes (*TaAFPs*) involved in regulation of ABA-signaling-*TaAFP-A*, *TaAFP-B* and *TaAFP-D*, respectively (Ohnishi et al., 2008). Besides, some *QTL* loci were identified and mapped onsomes of the 1st group (Imtiaz et al., 2008; Flintham et al., 2002; Mohan et al., 2009; Knox et al., 2005), 5th group (Groos et al., 2002; Zanetti et al., 2000; Kulwal et al., 2004; Fofana et al., 2009) and 7th group (Zanetti et al., 2000; Miura et al., 2002; Mares et al., 2005; Rasul et al., 2009; Mohan et al., 2009) of homeologues among different wheat genotypes.

The wheat cultivar 'Chinese Spring' (CS) has *ph* and *kr* genes, and was always used as parent to cross with related species in order to transfer good genes from other species. It's important that characteristics from CS should be understood. The wheat variety CS has moderate seed dormancy level. It was usually crossed with stronger dormant varieties, to analysis the dormant genes from opposite varieties (Miura et al., 2002). The dormant traits of CS itself have not been indicated enough. The objectives of our study were to identify QTLs for seed dormancy in wheat CS.

MATERIALS AND METHODS

Plant materials and evaluation of seed dormancy

Triticum aestivum L. cv. Chinese Spring, its 36 ditelosomics were grown on the experimental field of Sichuan Agricultural University, and their seeds were harvested at wax maturity. One hundred seeds of each line were incubated in a Petri dish (9 cm diameter) with 6 ml of distilled water at 25°C for a week. The number of germinated seeds was counted daily. The germination index (GI), which gave maximum weight to seeds that germinated first and less weight to those that germinated subsequently, was calculated according to Walker-Simmons and Sesing (1990) and multiplied by 100. GI was measured in replicate experiments. GI values were transformed to arcsin √ and tested statistically by Duncan's multiple range tests.

CS and 5 ditelosomics of CS were crossed with wheat line YY2 (undormancy). In crosses with ditelosomics, F_1 plants were grown on the experimental field and were harvested at wax maturity. One hundred seeds of CS, YY2, F_1 between CS and YY2, and each crosses of F_1 between ditelosomics × YY2 were incubated in water at 25°C for 7 days. Measurements were done in triplicate. Both parents and each of 148 F_2 plants between CS and YY2 were incubated in water at 25°C for 7 days. GI was calculated.

SSR analysis

Genomic DNA of the parents and F_2 plants of CS × YY2 was extracted from leaves using the CTAB protocol (Rogers and Bendich, 1985). A total of 28 pairs of SSR primers covering the 2BS genome were synthesized according to the sequences published in the GrainGenes database (http://www.wheat.pw.usda.gov). SSR analysis followed the procedure of Röder et al. (1998) with minor modifications. PCR was performed in a Gene Amp PCR system 9700 (ABI) in 25 µl reaction volumes containing 1 × buffer, 80 ng of template DNA, 250 nmol of each primer, 1.5 mM of $MgCl_2$, 200 µM of each dNTP and 1U of Taq DNA polymerase. The cycling program consisted of 95°C for 5 min, followed by 45 cycles of 94°C for 1 min, 55 to 61°C (depending on annealing temperature for each primer pair) for 1 min, 72°C for 2 min, and a final extension at 72°C for 7 min. PCR products were separated on 6% denaturing polyacrylamide gels and visualized by silver staining (Tixier et al., 1997) with some modifications (Chen et al., 2008). All marker data were scored by visual inspection and double checked to remove ambiguous data.

Linkage analysis

A genetic linkage map was constructed with SSR markers using JoinMap version 3.0 (Van Ooijen and Voorrips, 2001). Recombination fractions were converted into centiMorgans (cM) using the Kosambi function (Kosambi 1944).

RESULTS

CS ditelosomics analysis

Seeds of all CS and 36 ditelosomics incubated in water for 7days germinated well. GPs and GIs of CS were 11.33 and 10.38; the means of seeds of 36 ditelosomics were

Table 1. The Germinating data of CS ditelosomics.

Ditelocentric lines	Germination percent	Germination Index	Ditelocentric lines	Germination percent	Germination Index
DT1AS	9.17±1.44	5.79±0.99	DT6BS	27.55±9.25	21.45±5.62
DT1AL	6.67±2.08	4.33±1.70	DT6BL	17.00±3.61	8.68±2.97
DT2AS	7.00±1.73**	2.38±0.59 **	DT7BS	9.36±2.48	7.32±2.96
DT3AS	33.67±15.04	20.43±10.34	DT7BL	9.28±5.96	3.92±2.38*
DT3AL	88.45±6.87**	88.20±14.94**	DT1DS	13.00±3.00	6.87±2.12
DT4AL	45.17±2.27**	37.79±3.06**	DT1DL	36.00±2.00*	29.27±3.51**
DT5AL	10.00±3.46	6.83±2.30	DT2DS	4.67±3.43**	1.87±1.81**
DT6AS	22.14±11.00	13.09±6.10	DT2DL	60.53±14.60	41.89±13.34
DT6AL	57.58±5.57**	48.07±3.01**	DT3DS	41.33±6.03	25.06±7.58
DT7AS	27.44±6.19	16.39±8.22	DT3DL	25.54±15.37	20.74±13.69
DT7AL	19.49±2.35	9.55±1.93	DT4DS	16.23±5.00	12.17±6.27
DT1BS	9.67±2.52	6.19±2.41	DT4DL	6.33±4.1*	4.13±2.24*
DT1BL	28.94±13.05	23.52±10.54	DT5DL	7.39±2.11	6.86±3.12
DT2BL	60.67±13.58**	44.17±10.42**	DT6DS	11.54±5.95	4.30±1.81*
DT3BS	22.90±14.11	14.23±9.33	DT6DL	37.28±8.71	25.97±7.78
DT3BL	20.67±2.31	12.32±2.14	DT7DS	6.04±4.42*	4.22±2.89*
DT4BS	27.42±18.99	17.02±14.77	DT7DL	8.00±3.46	4.41±1.82*
DT4BL	14.67±4.04	4.84±0.63*	Ave	23.70	16.71
DT5BL	17.00±5.29	7.29±2.24	CS	11.33	10.38
			YY2	76.33	74.51

*Statistically significance level at 5%; ** statistically significance level at 1%.

23.70 and 16.71, respectively, indicating that CS seeds were moderate dormant. Seeds of the ditelosomics showed various GP values from the highest of 88.45% in DT3AL to the lowest of 4.67% in DT2DS, similarly, GI values from the highest of 88.20% in DT3AL to the lowest of 1.87% in DT2DS. Among the ditelosomics, DT2AS, DT2DS, DT4DL, DT7DS and 5E(5B) showed statistically (at 5% level) lower than the mean of CS, 7.00, 4.67, 6.33, 6.04 and 5.00 in GP, 2.38, 1.87, 4.13, 4.22 and 3.27 in GI, respectively. The deficient chromosome arms 2AL, 5BL, 2DL, 4DS and 7DL of these ditelosomics appear to carry major gene(s) for germination. On the other hand, DT3AL, DT4AL, DT6AL and DT2BL statistically (at 1% level) higher than the mean of all ditelosomics, 88.45, 45.17, 57.58 and 60.67 in GP, 88.20, 37.79, 48.07 and 44.17 in GI, respectively. DT1DL showed significance level at 5% (36.00) in GP and significance level at 1% (29.27) in GI. The deficient chromosome arms 3AS, 4AS, 6AS, 2BS and 1DS of these ditelosomics appear to carry major gene(s) for dormancy and suggest that the deficient arms of these ditelosomics carry genes which suppress germination. The chromosome arms involved in seed germination are listed in Table 1.

Analysis of partial F_1 of CS ditelosomics × YY2

Lower germination in ditelosomics was probably related to deficiency in whole chromosome arms, not only the gene(s) on the arm. In order to discover seed dormant genes of CS, 5 ditelosomics which showed evidently higher germination levels than that of population were crossed with YY2 (Table 2). F_1 population between CS and YY2 showed high germination (75.33 in GP and 45.66 in GI). All the five crosses had higher GP and GI than that of CS × YY2, but crosses with DT3AL, DT4AL, DT6AL and DT2BL showed statistically (at 5% level) higher, 100.00, 95.33, 96.66 and 98.67 in GP, 83.52, 80.95, 78.86 and 88.14 in GI, respectively. The crosses with DT1DL did not showed statistically (at 5% level) significance level, 84.00 in GP and 56.10 in GI, respectively.

Genetic map construction and QTL mapping

CS has the strongest dormant on 2B chromosome, which had highest GI in this research, so we carried out analysis of genetic linkage map on 2BS. After screening a total of 32 SSR primers, 6 showed polymorphism, and were further used to screen 128 plants F_2 with the cross of CS × YY2 in the mapping population. A genetic map was constructed with 3 SSR markers distributed the linkage groups covering a genetic distance of 42.1 cM, another 3 SSRs were not lingked togather. QTLs of GP and GI were localized to the different region on the short arm of chromosome 2B, which ranged the order as Xgwm510, Xgwm210, Xgwm50, QTL_{GI}, QTL_{GE} and QTL_{GP},

Table 2. The germinating data of F_1 ditelosomics.

Ditelocentric lines	Germination percent	Germination Index
DT3AL	100.00±0.00**	83.52±1.86**
DT4AL	95.33±1.16*	80.95±0.59**
DT6AL	96.00±4.00*	78.86±2.97**
DT2BL	98.67±1.16**	88.14±2.76**
DT1DL	84.00±13.12	56.10±8.60
CS× YY2	75.33	45.66
CS	11.33	8.86
YY2	76.33	62.70

*Statistically significance level at 5%; ** statistically significance level at 1%.

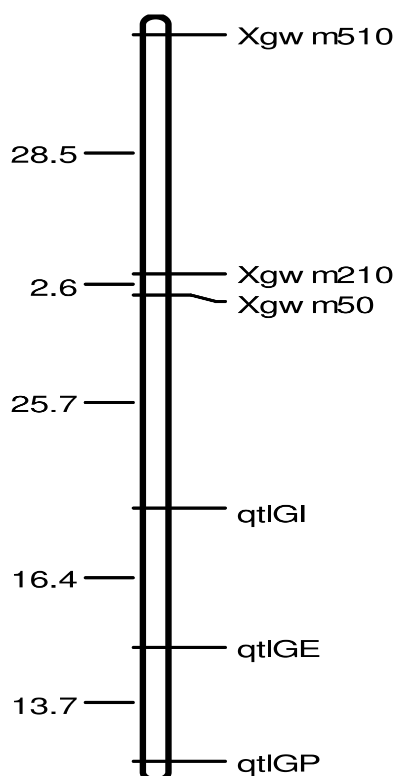

Figure 1. QTLs for GP, GE and GI on the short arm of chromosome 2B.

and the genetic distance were 28.5 cM, 2.6 cM, 25.7 cM, 16.4 cM and 13.7 cM, respectively (Figure 1).

DISCUSSION

Preharvest sprouting and seed dormancy in wheat are expressed as quantitatively inherited traits that are strongly influenced by the environment. QTL studies are useful to identify the genome regions that control PHS and seed dormancy and their relative importance for further studies such as fine mapping. Several chromosomes suggested carrying genes that make dormancy or nondormancy (Table 1). Anderson et al. (1993) and Sorrells and Anderson (1996) identified RFLP markers for pre-harvest sprouting resistance of white wheat in chromosomes 1AS, 2S, 2L 3BL, 4AL, 4L, 5DL, 5L and 6BL and reported that the effects of these QTLs were influenced by interaction of genes on these chromosomes and the environment. This present results also suggested that seed dormancy is expressed in total by these genes that act positively or negatively.

The early breakage of seed dormancy was proposed as a major cause of PHS (Mares, 1987). However, the QTL mapping evidence did not fully support this hypothesis. QTLs for PHS resistance were mapped to chromosomes 2BS (http://maswheat.ucdavis.edu/), 3A (Kulwal et al., 2005), 4AL (Anderson et al., 1993; Flintham et al., 2002; Sorrells and Anderson, 1996) 3B, 5A, 6A, 7B (Zanetti et al., 2000), 1AS, 3BL, 4AL, 5DL and 6BL (Anderson et al., 1993; Sorrells and Anderson, 1996), 6B and 7D (Roy et al., 1999), 5A and all group 3 chromosomes (Groos et al., 2002), whereas the major QTLs for seed dormancy were mapped to chromosomes 4A (Kato et al., 2001; Noda et al., 2002; Mares et al., 2005; Torada et al., 2005) and 3A (Osa et al., 2003; Mori et al., 2005). In this study, several seed dormant loci in CS were detected. In order to validate if it was precise to the results on ditelosomics location, we carried out analysis of genetic linkage map on 2BS. One of major QTLs significantly associated with seed dormancy was identified on the short arm of chromosome 2B. Our result confirmed that seed dormancy is the major component of PHS resistance and that the QTL on chromosome 2BS controls both PHS resistance and seed dormancy in wheat. The QTL is homeologous to that on 2DS in our previous research (Ren et al., 2008).

PHS resistance or seed dormancy is most likely controlled by several QTLs. In this study, we identified one major QTL on 2BS. Due to the lack of polymorphism in the markers used, or the lack of available markers closely linked to other QTLs, we did not detected relative to LOD and contribution rate in this study. Further studies to add other markers may improve the map resolution to

facilitate identification of the QTL.

The association between PHS and grain color in red wheat may be due to either a pleiotropic effect of the genes controlling grain color or to genetic linkage between seed color genes and the genes affecting PHS (Gale, 1989; Watanabe and Ikebata, 2000). Flintham et al. (1999), using nulli-tetra series and ditelocentric (ditelo) lines of a red grained wheat cultivar, Chinese Spring, reported that chromosome 7D is involved in the development of dormancy besides genes on chromosomes group 3. Noda et al. (2002), Using ditelocentric lines of wheat cv. Chinese Spring (as nondormant and ABA insensitive), F_2 seeds between monosomic lines of CS and a wheat line Kitakei-1354 (as dormant, ABA sensitive) and deletion lines of CS chromosome 4A, germinability of seeds and embryo-half seeds incubated in water and ABA were examined. The results indicated that the long arm of chromosome 4A carried major gene(s) for the embryo sensitivity to ABA and dormancy. Chromosome 2D might be also involved in the sensitivity to ABA. In this study, crosses between ditelosomics of CS (red grain) and YY2 (white grain) were used to develop the chromosome location population. CS has a similar level of PHS as some red PHS-resistant wheat cultivars, and it has significantly longer seed dormancy than the sensitive parent YY2. Therefore, the difference in seed dormancy between CS and YY2 was detected on 3A, 4A and 6A, besides on 2B.

PHS resistance in wheat is a complex trait. Many factors may affect PHS resistance. Phenotyping methods and many environmental factors can affect accurate identification of QTLs for PHS resistance. A suitable method for phenotypic evaluation is critical to the successful mapping of QTLs. In our study, GI, GP and GE were used to estimate seed dormancy at the same time. However, the three values were not identical, and the QTL loci were mapped at different locations. Germination index (GI), measured as the germination level, was most close to marker Xgwm50. It provides a more accurate phenotypic data for QTL mapping.

Conclusion

This percent study indicated that 3AS, 4AS, 6AS and 2BS in CS carrying major dormancy gene(s). Among them, the major QTL on the short arm of chromosome 2B was identified. However, the three parameters, *viz*. GI, GP and GE were mapped at different locations. Germination index (GI), measured as the germination level, should be the most credible to provide an accurate phenotypic data for QTL mapping.

ACKNOWLEDGEMENTS

The authors are thankful to the National Natural Science Foundation of China (30471088; 30370883), and the National High Technology Research and Development Program of China (863 program 2011AA100103).

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