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Detection of loci controlling seed dormancy on group 4 chromosomes of wheat and comparative mapping with rice and barley genomes

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Abstract Three quantitative trait loci (QTLs) controlling seed dormancy were detected on group 4 chromosomes of wheat (*Triticum aestivum* L.) using 119 doubled haploid lines (DHLs) derived from a cross between AC Domain and Haruyutaka. A major QTL, designated *QPhs.ocs-4A.1*, was identified within the marker interval between *Xcdo795* and *Xpsr115* in the proximal region of the long arm of chromosome 4A. Two minor QTLs, *QPhs.ocs-4B.2* on 4B and *QPhs.ocs-4D.2* on 4D, were flanked by common markers, *Xbcd1431.1* and *Xbcd1431.2* in the terminal region of the long arms, suggesting a homoeologous relationship. These three QTLs explained more than 80% of the total phenotypic variance in seed dormancy of DHLs grown in the field and under glasshouse conditions. The AC Domain alleles at the three QTLs contributed to increasing seed dormancy. Comparative maps across wheat, barley and rice demonstrated the possibility of a homoeologous relationship between *QPhs.ocs-4A.1* and the barley gene SD4, while no significant effects of the chromosome regions of wheat and barley orthologous to rice chromosome 3 region carrying a major seed dormancy QTL were detected.

Keywords Seed dormancy · Wheat · Barley · Rice · Comparative map

Introduction

Seed dormancy, an important trait in breeding programs of cereal crops because it is associated with pre-harvest sprouting (Seshu and Sorrells 1986); is defined as the inability of a viable seed to germinate under environmental conditions favorable to germination. It is affected by environmental conditions during the ripening stage and storage conditions, as well as by complex genetic factors (Anderson et al. 1993; Oberthur et al. 1995). Molecular markers have made it possible to identify individual genetic factors controlling such complex traits as seed dormancy (Tanksley 1993), and several genes or chromosomal regions affecting seed dormancy in barley (Oberthur et al. 1995; Larson et al. 1996), wheat (Anderson et al. 1993; Flintham et al. 1999; Roy et al. 1999) and rice (Lin et al. 1998; Takeuchi et al. 1999) have been mapped via linkage to molecular markers.

A remarkable level of synteny has been observed between the genomes of a number of cereals. Comparative mapping of wheat and other cereals using common restriction fragment length polymorphic (RFLP) markers has shown that the genetic maps of different species can be aligned (Ahn et al. 1993; Kurata et al. 1994) with several major genes of agronomic importance showing synteny across the cereals (Van Deynze et al. 1995; Devos and Gale 1997; Laurie 1997). This will allow the identification and tagging of genes for seed dormancy. In barley, four quantitative trait loci (QTLs) controlling seed dormancy, designated SD1 to SD4, were identified using Steptoe/Morex doubled haploid lines (DHLs) (Oberthur et al. 1995; Han et al. 1996). In rice, five *Sdr* QTLs affecting seed dormancy were mapped using Kasalath/Nipponbare backcross inbred lines (Lin et al. 1998). Comparative maps have demonstrated that wheat group 4 chromosomes are homoeologous with barley chromosome 4H carrying the SD4 gene (Oberthur et al. 1995) and partially orthologous with rice chromosome 3 (Kurata et al. 1994) in which there is a major *Sdr1* QTL (Lin et al. 1998; Takeuchi et al. 1999).

The objectives of the study reported here were to detect the wheat loci controlling seed dormancy on the group 4 chromosomes and to investigate their syntenious relationships with the barley SD4 or rice *Sdr1*.

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Materials and methods

RFLP mapping of wheat

For mapping, 119 DHLs were developed by the anther culture method using the F_1 plants of a cross between AC Domain and Haruyutaka. AC Domain is a Canadian hard red spring wheat developed by Agriculture and Agri-Food Canada that shows a high level of seed dormancy (Depauw et al. 1995). Haruyutaka is a Japanese hard red spring wheat with a low level of seed dormancy (Miura et al. 1997). All of the DHLs are red-grained. To determine the chromosomal or chromosomal arm locations of RFLP fragments, we used Chinese Spring (CS) and its aneuploid stocks including the CS nullisomic 4A tetrasomic 4B line, the CS ditelosomic 4BL and 4BS lines and the CS nullisomic 4D tetrasomic 4B line (Sears 1954). The wheat aneuploid stocks were kindly provided by Dr. H. Tsujimoto, Kihara Institute for Biological Research, Yokohama City University, Japan. Genomic DNA was extracted from leaves of 2- to 4-week-old glasshouse-grown plants by the modified CTAB method (Murray and Thompson 1980). Southern blotting was carried out as described by Kato et al. (1998). Thirty-two clones known to hybridize to DNA fragments located on the group 4 chromosomes of wheat were used. The cDNA and gDNA clones used as probes were kindly provided by the USDA-ARS central probes repository, Albany, Calif., USA, constructed by Dr. M.E. Sorrells (prefixed with BCD, CDO, WG) and Dr. M.D. Gale, John Innes Centre, UK (prefixed with PSR). Thirty clones closely linked to the rice seed dormancy QTL, *Sdr1* (Takeuchi et al. 1999), by less than 10 cM on rice chromosome 3 (Harushima et al. 1998) were kindly provided by Dr. T. Sasaki, Rice Genome Research Program, NIAR, Japan (prefixed with R, C and S). Probes showing polymorphism in the parents were used to characterize the genotype of each line of the mapping population and aneuploid stocks. The linkage maps were generated using MAPMAKER/EXP 3.0 (Lander et al. 1987) using the Kosambi mapping function (Kosambi 1944). These maps were compared with published ITMI maps for chromosomes 4A, 4B and 4D (Dvorak and Luo 1997).

QTL analysis of seed dormancy and ear emergence time of wheat

Parents and DHLs were evaluated under the three conditions – field, glasshouse and growth chamber – at Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan. All trials were spring-sown experiments. Field trials contained parents and DHLs in plots consisting of single 1-m rows with two replications in 1998. A glasshouse trial was conducted by growing 2 plants of each parent and each DHL under natural daylength in 1998. A growth chamber trial was conducted by growing 2 plants of each parent and each DHL from flowering to harvesting, conditioned at 15°C (6:00 to approx. 18:00: 18°C, 18:00 to approx. 6:00: 13°C) under natural daylength in 1999. For glasshouse and growth chamber trials, plants were arranged at random and re-randomized weekly to minimize positional effects.

Seven spikes from the field, five from the glasshouse and four from the growth chamber trial were harvested at physiological maturity as indicated by a loss of green color from the glumes of the basal spikelets. Harvested spikes were allowed to air-dry for 10 days under room conditions. Dried spikes were carefully hand-threshed. Germination tests were performed on paper filters moistened with distilled water placed in sterile plastic petri dishes at 20°C in the dark for 10 days. The germination rate of each line was scored as the percentage of germinated seeds relative to the total number of seeds on each trial spike. To reduce inequalities in variance, we transformed the percentage germination rate of each individual into arc sine [=arc sine $(\chi)^{1/2}$] and then used the latter for QTL analyses.

To evaluate an association between seed dormancy and heading time, we scored the average number of days for the first ear to emerge in each plant as the ear emergence time of each plant. The number of days required from seeding to ear emergence were used in the QTL analysis.

QTL mapping analyses for each trait were performed using the interval mapping method implemented by the software package MAPMAKER/QTL (Lander and Botstein 1989; Lincoln et al. 1993). A log-likelihood (LOD) score threshold of 2.0 was used to identify regions containing putative loci associated with each trait. The total LOD score and variance explained (r^2) in each trait were determined in a multiple QTL model that included all of the significant QTLs (Lander and Botstein 1989).

RFLP mapping of barley

Probes mapped on wheat chromosomes 4A, 4B and 4D in the present study were localized on the barley chromosome map using a mapping population of 60 DHLs, DH1–DH60, derived from a cross between Steptoe and Morex (Kleinhofs et al. 1993). The barley DHLs were developed by the North American Barley Genome Mapping Project, and seed was multiplied by Dr. K. Sato, Okayama University, Japan. Genomic DNA extraction and Southern blotting were conducted using the same method described for wheat. A new locus was identified by the 'try' and 'compare' commands of Mapmaker/Exp 3.0 (Lander et al. 1987) on the previous map (Kleinhofs et al. 1993) using genotype data and map data obtained from the Internet; gopher://greengenes.cit.cornell.edu:70/00/maps/Hordeum/Barley%20Steptoe%20x%20Morex 20mapping%20data. The recombination frequencies were converted to centiMorgans (cM) using the Kosambi mapping function (Kosambi 1944).

Results and discussion

Genetic map of wheat group 4 chromosomes

Eight marker loci covering 136.5 cM were mapped on chromosome 4A. The marker order revealed was comparable with that of the maps previously compiled by the International Triticeae Mapping Initiative (ITMI; Dovorak and Luo 1997). The centromere was assigned within the marker interval between *Xcdo795* and *Xbcd1265* from the ITMI maps of homoeologous group 4 chromosomes (Dvorak and Luo 1997).

RFLP analyses of ditelosomic stocks demonstrated that *Xbcd1265*, *Xbcd1431.1* and *Xbcd1431.2* hybridized to fragments on the long arm of chromosome 4B, while a break is shown between *Xbcd1265* and *Xbcd1431.1* due to a recombination frequency of greater than 0.40 in constructing our map. Of the 30 rice cDNA clones closely linked to *Sdr1* (Takeuchi et al. 1999), only R2184 showed polymorphism in the parents and mapped in the proximal region of the long arm, being linked to *Xbcd1265* by 4.5 cM. The semi-dwarf *Rht-B1* gene from Haruyutaka was located in the terminal region of 4BS. Hence, five markers were mapped on chromosome 4B. Based on ditelosomic analyses and the ITMI map, the centromere was assigned within the marker interval between *Rht-B1* and *Xrgr2184*. For chromosome 4D, only *Xbcd1431.1* and *Xbcd1431.2* were mapped on the long arm. This chromosome segment of 26.1 cM was estimated to be located in the terminal region of 4DL from Nelson et al. (1995).

The germination rates of AC Domain were 60.8% (field), 51.8% (glasshouse) and 19.1% (growth chamber). When Haruyutaka was grown in the field and under glasshouse conditions, a perfect loss of dormancy was found, as indicated by germination rates of 97.4% in the field and 99.0% in the glasshouse. These results confirmed a distinctive difference in the level of seed dormancy between the parents. The germination rates of DHLs ranged from 27.0% to 100% (field), 29.3% to 100% (glasshouse) and 0.9% to 100% (growth chamber) (Fig. 1).

Three putative QTLs associated with seed dormancy were detected (Fig. 2). A major QTL, designated *QPhs.ocs-4A.1*, was identified within the marker interval between *Xcdo795* and *Xpsr115* in the proximal region of 4AL. The percentages of phenotypic variation explained by *QPhs.ocs-4A.1* were 77.2% (field), 70.8% (glasshouse) and 33.0% (growth chamber) (Table 1). QPhs.ocs-4B.2 was detected within the marker interval between *Xbcd1431.1* and *Xbcd1431.2* in the terminal region of 4BL. This *QPhs.ocs-4B.2* showed minor and inconsistent effects on seed dormancy of seed produced in the glasshouse and growth chamber trials but not in the field trial. The percentages of phenotypic variation explained by *QPhs.ocs-4B.2* were 13.9% (glasshouse) and 14.8% (growth chamber). Likewise, *QPhs.ocs-4D.2* within the marker interval between *Xbcd1431.1* and *Xbcd1431.2* of 4DL had a minor but significant effect on seed dormancy and explained 19.1% (field), 36.5% (glasshouse) and 14.8% (growth chamber) of the total phenotypic variance. There were no significant effects on seed dormancy linked to *Rht-B1*. Based on the multiple QTL model of MAPMAKER/QTL, phenotypic varia-

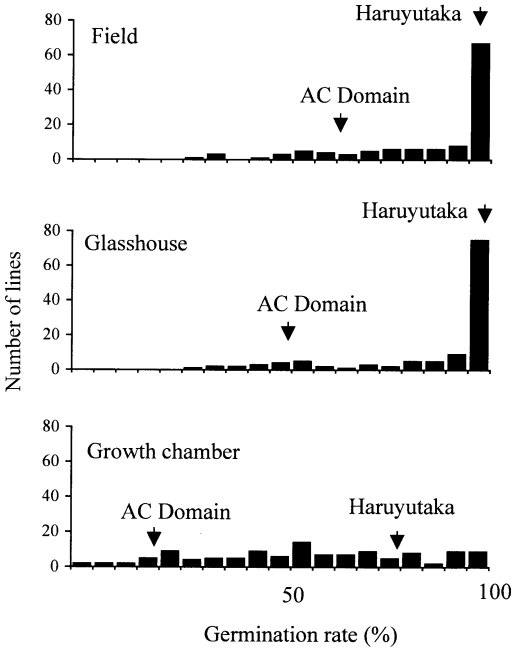

Fig. 1 Distribution of germination rates in 119 DHLS developed from F_1 plants of a cross between AC Domain and Haruyutaka under field, glasshouse and growth chamber conditions, respectively

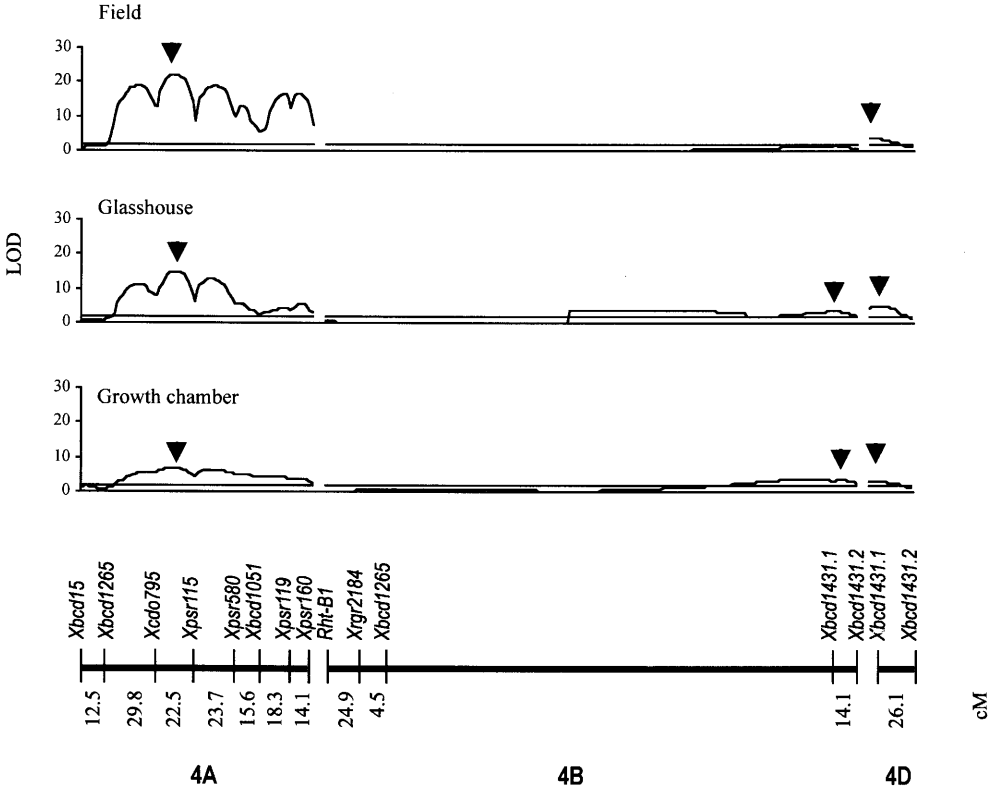

Fig. 2 QTL-likelihood curves of LOD scores for arc sine of germination rates on group 4 chromosomes of wheat under field, glasshouse and growth chamber conditions, respectively

Table 1 Location of QTLs controlling seed dormancy of DHLs derived from a cross between AC Domain and Haruyutaka

Trial	Chromosome arm	Marker interval	LOD	r^2	Weight[a]
Field	4AL	*Xcdo795/Xpsr115*	22.2	77.2	33.7
	4DL	*Xbcd1431.1/Xbcd1431.2*	3.5	19.1	10.4
	Multiple QTL model		25.0	86.0	
Glasshouse	4AL	*Xcdo795/Xpsr115*	14.8	70.8	26.2
	4BL	*Xbcd1431.1/Xbcd1431.2*	3.6	13.9	2.3
	4DL	*Xbcd1431.1/Xbcd1431.2*	5.1	36.5	13.0
	Multiple QTL model		18.3	81.2	
Growth chamber	4AL	*Xcdo795/Xpsr115*	6.8	33.0	17.9
	4BL	*Xbcd1431.1/Xbcd1431.2*	3.4	14.8	8.0
	4DL	*Xbcd1431.1/Xbcd1431.2*	3.0	14.8	8.2
	Multiple QTL model		9.0	37.6	

[a] Additive effects (1/2 weight) of the AC Domain allele increasing seed dormancy by arc sine of germination rate

tion explained by the three putative QTLs were 86.0%, 81.2% and 37.6%, in the field, glasshouse and growth chamber trials, respectively. The AC Domain alleles at the three putative QTLs contributing to increasing seed dormancy ranged from 2.3 to 33.7 in the arc-sine transformation of germination rate. It needs a further mapping study to determine the precise loci of *QPhs.ocs-4B.2* and *QPhs.ocs-4D.2*.

Ear emergence times of AC Domain were 67.0 days (field), 63.0 days (glasshouse) and 55.0 days (growth chamber), while those of Haruyutaka were 69.0 days (field), 62.0 days (glasshouse) and 55.0 days (growth chamber). Under field conditions, AC Domain showed a significantly earlier heading than Haruyutaka (2.0 days, $P<0.01$). Ranges in ear emergence times of DHLs were about 12 days and consistent across the three growing conditions with near normal distributions (data not shown). QTL analysis revealed that no significant effects were associated with the marker loci or intervals on ear emergence time, and there was no correlation between the variation in the DHLs for seed dormancy and that for ear emergence time across the trials. Hence, the effect of the three QTLs on seed dormancy was found to be independent of the environmental effects during the ripening stage caused by differences in flowering time.

It is known that low temperature during the ripening stage introduces deep seed dormancy (Kuwabara and Maeda 1979). This was the case in our DHLs grown in the growth chamber; transgressive segregants were observed, showing the association of a complex genetic factor to seed dormancy under low temperature conditions during the ripening stage. The percentage of variance of the DHLs under growth chamber conditions explained by three QTLs was only about half of the other two conditions. It is possible that there are additional QTL(s) controlling seed dormancy under a low temperature during the ripening stage.

Anderson et al. (1993) identified one QTL associated with tolerance to pre-harvest sprouting linked to a RFLP marker *Xcdo545* on the long arm of wheat chromosome 4A. *Xcdo545* is located on the translocation segment from the short arm of chromosome 7B in the terminal region of 4AL (Nelson et al. 1995). The *Xcdo545* region is identical to the chromosomal region flanked by *Xpsr160* and *Xpsr119*, apart from *QPhs.ocs-4A.1* by more than 50 cM in the present study. This evidence suggests that *QPhs.ocs-4A.1* and the QTL identified by Anderson et al. (1993) are independent loci, and thus chromosome 4A may carry at least two QTLs for seed dormancy. Further study is necessary using common markers to decide this. In addition, *Xcdo795* (*Xcnl.cdo795*) was also a linked QTL associated with tolerance to pre-harvest sprouting and not assigned to the wheat chromosomes (Anderson et al. 1993). At present, it is difficult to say if *Xcnl.cdo795* and *QPhs.ocs-4A.1* are independent loci or the same locus.

Comparative map

Three clones, BCD1265, BCD15 and BCD1431, were integrated into the previous barley map (Fig. 3) constructed by Kleinhofs et al. (1993) using the Steptoe/Morex DHLs. BCD1265 was mapped in the marker interval between ABR315 and WG464 in the proximal region of the long arm of 4H. BCD15 was mapped at two loci, between ABG397 and ABG319C in the terminal region of the long arm of 4H and between ABR303 and BCD129 on the short arm of 7H in the present study. Kleinhofs et al. (1993) had mapped BCD15 on the long arm of 1H. BCD1431 co-segregated with two markers, Bmy1 (*β-Amy-H1* after McIntosh et al. 1998), in the terminal region of the long arm of 4H, and CDO105B, in the proximal region of the long arm of 1H. Two chromosomal regions linked to both BCD15 and BCD1431 in the barley 4H and 1H chromosomes showed no association with seed dormancy in previous studies (Oberthur et al. 1995; Larson et al. 1996).

Comparative maps across wheat, barley and rice suggest two possibilities. Firstly *QPhs.ocs-4B.2* and *QPhs.ocs-4D.2* are homoeologous in the wheat genome, common markers, *Xbcd1431.1* and *Xbcd1431.2*, are associated with these two QTLs in the terminal region of the long arms. Secondly, the wheat *QPhs.ocs-4A.1* is homoeologous to barley gene SD4: these two QTLs are linked to CDO795 (*Xcdo795* in wheat map) and ordered as QTL-CDO795(*Xcdo795*)-R2184(*Xrgr2184*)-

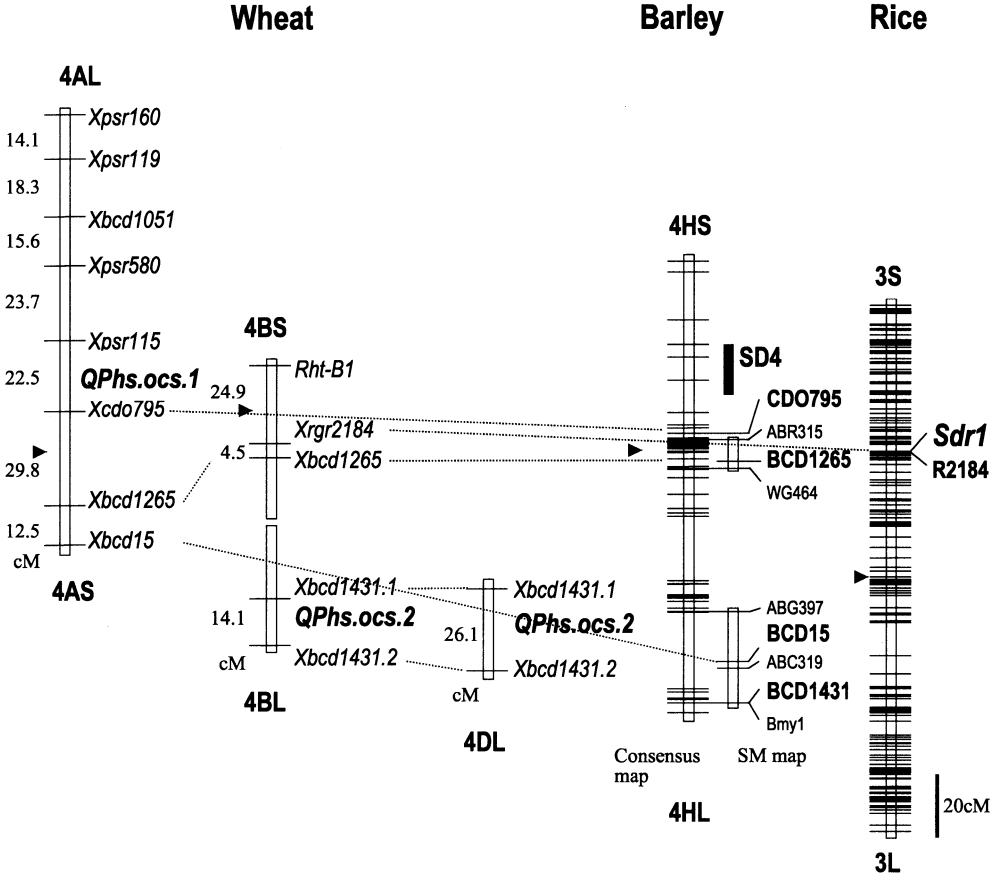

Fig. 3 Comparative mapping of QTLs controlling seed dormancy. The marker order is shown on the *right hand side*, while the genetic distances are on the *left hand side*. A breakage is shown between *Xbcd1265* and *Xbcd1431.1* on the long arm of wheat chromosome 4B. The centromere is designated by an *arrowhead*. Barley consensus map is from Langridge et al. (1995); SD4 was mapped by Oberthur et al. (1995), the barley SM map is from Kleinhofs et al. (1993); BCD1265, BCD15 and BCD1431 were mapped using SM mapping population (Kleinhofs et al. 1993) in this study. Rice chromosome 3 is from Harushima et al. (1998). *Sdr1* was mapped by Lin et al. (1998) and Takeuchi et al. (1999)

BCD1265(*Xbcd1265*)-BCD15(*Xbcd15*). In the wheat group 4 chromosomes and barley 4H, however, no significant effects of chromosome regions orthologous to the rice chromosome 3 region (Oberthur et al. 1995; Larson et al. 1996) carrying a major QTL for seed dormancy *Sdr1* (Lin et al. 1998; Takeuchi et al. 1999) were detected. To interpret these conflicts, we propose two hypotheses: (1) wheat and barley carry the loci orthologous to rice *Sdr1* not detected here because of no segregation in the parents; (2) alternatively, the Triticeae have different mechanisms and genes controlling seed dormancy from rice. Confirmation of one of the above will be achieved by further comparative mapping using multiple mapping populations and an additional understanding of the mechanism of seed dormancy of these crops.

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