Theor Appl Genet (2005) 111: 1052–1059
DOI 10.1007/s00122-005-0021-4

ORIGINAL PAPER

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Mapping of a major QTL for pre-harvest sprouting tolerance on chromosome 3A in bread wheat

Received: 21 April 2005 / Accepted: 14 June 2005 / Published online: 18 August 2005
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Abstract Quantitative trait loci (QTL) analysis was conducted for pre-harvest sprouting tolerance (PHST) in bread wheat for a solitary chromosome 3A, which was shown to be important for this trait in earlier studies. An intervarietal mapping population in the form of recombinant inbred lines (RILs) developed from a cross between SPR8198 (a PHS tolerant genotype) and HD2329 (a PHS susceptible cultivar) was used for this purpose. The parents and the RIL population were grown in six different environments and the data on PHS were collected in each case. A framework linkage map of chromosome 3A with 13 markers was prepared and used for QTL analysis. A major QTL (*QPhs.ccsu-3A.1*) was detected on 3AL at a genetic distance of ~183 cM from centromere, the length of the map being 279.1 cM. The QTL explained 24.68% to 35.21% variation in individual environments and 78.03% of the variation across the environments (pooled data). The results of the present study are significant on two counts. Firstly, the detected QTL is a major QTL, explaining up to 78.03% of the variation and, secondly, the QTL showed up in all the six environments and also with the pooled data, which is rather rare in QTL analysis. The positive additive effects in the present study suggest that a superior allele of the QTL is available in the superior parent (SPR8198), which can be used for marker-aided selection for the transfer of this QTL allele to obtain PHS-tolerant progeny. It has also been shown that the red-coloured grain of PHS tolerant parent is not associated with the QTL for PHST identified during the present study, suggesting that PHS tolerant white-grained cultivars can be developed.

Electronic Supplementary MaterialSupplementary material is available for this article at http://dx.doi.org/10.1007/s00122-005-0021-4

Communicated by R. Hagemann

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Introduction

In bread wheat (*Triticum aestivum* L.), pre-harvest sprouting (PHS) is a major problem in various parts of the world, including India. It leads to yield losses and reduction in the quality of kernels, thus limiting their end use. In our initial study on the genetics of this trait, we identified two molecular markers (one each on chromosomes 6B and 7D) to be associated with pre-harvest sprouting tolerance (PHST) (Roy et al. 1999). In this study, as also in several other earlier studies, PHST was treated as a qualitative trait. However, several studies in the past including our own recent study conducted using International Triticeae Mapping Initiative population (ITMI*pop*), demonstrated that PHST is a quantitative trait controlled by many quantitative trait loci (QTLs)/genes, so that a number of QTLs controlling this trait have been identified (Anderson et al. 1993; Zanetti et al. 2000; Mares et al. 2001; Kato et al. 2001; Flintham et al. 2002; Groos et al. 2002; Osa et al. 2003; Kulwal et al. 2004).

In bread wheat, 20 chromosomes with the solitary exception of chromosome 1D are now known to carry QTLs/genes for PHST/dormancy. However, chromosomes 3A, 3B, 3D and 4A have been considered to be more important than other chromosomes for the study of genetics of PHST/dormancy (Flintham and Gale 1996; Bailey et al. 1999; Zanetti et al. 2000; Warner et al. 2000; Watanabe and Ikebata 2000; Kato et al. 2001; Flintham et al. 2002; Groos et al. 2002; Himi et al.

2002; Gale et al. 2002; Osa et al. 2003; Kulwal et al. 2004; Mori et al. 2005). In our recent study on PHST (Kulwal et al. 2004) utilizing ITMI*pop*, we also detected QTLs on the long arms of chromosomes 3B and 3D. However, no QTL was detected on chromosome 3A in this study, perhaps because the parents of ITMI*pop* did not differ for the QTL alleles for any of the PHST loci on chromosome 3A. In contrast to this study, QTLs for PHST on chromosome 3A have been identified in several other studies (Zanetti et al. 2000; Groos et al. 2002; Osa et al. 2003; Mori et al. 2005), utilizing different independent mapping populations. A preliminary analysis of our own data of an intervarietal population using single marker analysis also suggested the presence of a major QTL on 3AL (unpublished results). Apart from this, chromosome 3A is also known to contain QTLs for various other important agronomic traits (Shah et al. 1999a, b; Campbell et al. 2003, 2004), making chromosome 3A important for QTL studies. This background knowledge prompted us to conduct QTL analysis for PHST involving 3A using a trait-specific intervarietal recombinant inbred mapping population derived from a cross SPR8198 (a PHS tolerant genotype) × HD2329 (a PHS susceptible cultivar). This mapping-population was evaluated for PHST at three different locations for two years, and a framework map for chromosome 3A was constructed through genotyping of this mapping population. A major QTL for PHST was identified on this chromosome, which explained up to 78.03% of variation. In two earlier studies, QTLs for PHST on 3AL explained only 5.5% and 13% of the phenotypic variation (Groos et al. 2002; Osa et al. 2003). The results of the present study suggested that in future wheat breeding programmes in India and elsewhere, the bread wheat genotypes (including SPR8198), which carry the desired allele of the major QTL detected during the present study, might be exploited for developing PHS-tolerant varieties of bread wheat.

Materials and methods

Plant material and data recording

A mapping population in the form of recombinant inbred lines (RILs) derived from a cross SPR8198 (a PHS tolerant genolype) × HD2329 (white-grained; PHS susceptible) was initially developed at Punjab Agricultural University, Ludhiana, India. More details about the plant material used in the present study are available elsewhere (Roy et al. 1999). During 2000–2001, the mapping population along with the two parental genotypes was evaluated in replicated trials at Meerut, Pantnagar and Ludhiana, which are the major wheat-growing areas of Northern India. During 2001–2002, the population was raised in a simple lattice design with replications at the same three locations. Thus, data from six environments were utilized in the present study. At each location, five spikes (per replication) from each of the two parents and from each of the 100 RILs were harvested as and when they reached physiological maturity, characterized by the loss of green colour from the spike (Trethowan 1995). There were no rains during the period of harvesting at any of the locations and the mean day/night temperatures for the six environments varied (Table 1). The laboratory test of Baier (1987) was used to test the level of PHS in harvested spikes, as was also done in our earlier study (Kulwal et al. 2004). Data on PHS were scored on the scale of 1 through 9 with score of 1 for genotypes with no visible sprouting and a score of 9 for the genotypes with complete sprouting. This scale corresponds to 1 through 10 scale of McMaster and Derera (1976) with slight modifications. Phenotypic data on red/white kernel colour were also recorded on maturity in all the six environments.

Table 1 Mean day and night temperatures for six different environments

Environment[a]	Mean temperature (°C)	
	Day	Night
I	36.0	19.1
II	35.0	18.6
III	34.7	18.0
IV	38.9	21.2
V	35.0	18.6
VI	36.6	18.9

[a] Environment I = Meerut 2001; II = Pantnagar 2001; III = Ludhiana 2001; IV = Meerut 2002; V = Pantnagar 2002; VI = Ludhiana 2002

DNA isolation

DNA was isolated from one-month-old field-grown plants using a modified CTAB method (Saghai Maroof et al. 1984).

SSR, AFLP and SAPML markers for framework map

The SSR, AFLP and SAMPL primers used during the present study are listed in Table 2. The sequences of these primers are available elsewhere (http://wheat.pw.usda.gov; Vos et al. 1995; Witsenboer et al. 1997; Röder et al. 1998).

DNA amplification was carried out for SSR markers following Röder et al. (1998) and Prasad et al. (1999), and for AFLP/SAMPL following Vos et al. (1995) with some modifications. The PCR products for SSR were resolved manually on 10% PAGE, while those for AFLP/SAMPL were resolved on 4% PAGE using ABI Prism 377 DNA sequencer (PE/Applied Biosystems); AFLP/SAMPL data were analysed using GeneScan analysis software version 3.2.4 (PE/Applied Biosystems) and Genotyper analysis software version 2.5.

Table 2 A summary of SSR, AFLP and SAPML primers used for genetic mapping

Class of markers	Primers
SSR	gwm2, gwm4, gwm5, gwm30, gwm155, gwm162, gwm269, gwm369, gwm480, gwm497, gwm666, wmc11, wmc96, wmc153, wmc169, wmc173, wmc215, wmc261, wmc388, wmc428, wmc594
AFLP	16 primer combinations (two *Eco*RI primers, E35 and E36, each in combination with eight *Mse*I primers)
SAMPL	Nine primer combinations (SAMPL primers S6 in combination with four *Mse*I primers, and SAMPL primer S7 in combination with five *Mse*I primers)

Construction of framework linkage map and QTL analysis

The genotyping data on 100 RILs for polymorphic markers were used for constructing a framework linkage map of chromosome 3A using MAPMAKER/EXP v 3.0b (Lander et al. 1987) with Kosambi's mapping function (Kosambi 1944) and using a minimum LOD score of 2.0 and maximum recombination frequency of 50%.

QTL analysis involving detection of main effect QTL (M-QTL) was conducted following composite interval mapping (CIM) using QTL Cartographer v. 2.0 (Basten et al. 1994; Basten et al. 2000). A LOD score of 3.0 was used for declaring the presence of a putative QTL. Threshold LOD scores for detection of QTLs were also calculated based on 1,000 permutations (Churchill and Doerge 1994; Doerge and Churchill 1996). The 95% confidence intervals (CI) were obtained through LOD drop-off method as well as through bootstrapping using 1,000 samples. For determination of confidence interval through bootstrapping, and for estimation of QTL detection power and Q×E interaction, MultiQTL package (http://www.multiqtl.com) was used. The QTL for PHST detected in the present study was designated according to the standard nomenclature for QTLs as recommended for wheat and followed in our earlier study on PHST (Kulwal et al. 2004).

Rank correlation coefficients and linkage analysis

Spearman's rank correlations for PHS scores of RILs in 15 pair-wise combinations involving six different environments were calculated using MS Excel.

Results

Mean PHS values and rank correlations

Mean PHS values of RILs ranged from 3.68 (Environment V) to 5.34 (Environment IV); the distributions were skewed towards PHST in each of the six environments, often showing negative kurtosis (ESM, Fig. 1). The 15 possible correlations between the ranks of RILs in six environments arranged in pairs were, however, positive and significant (Table 3).

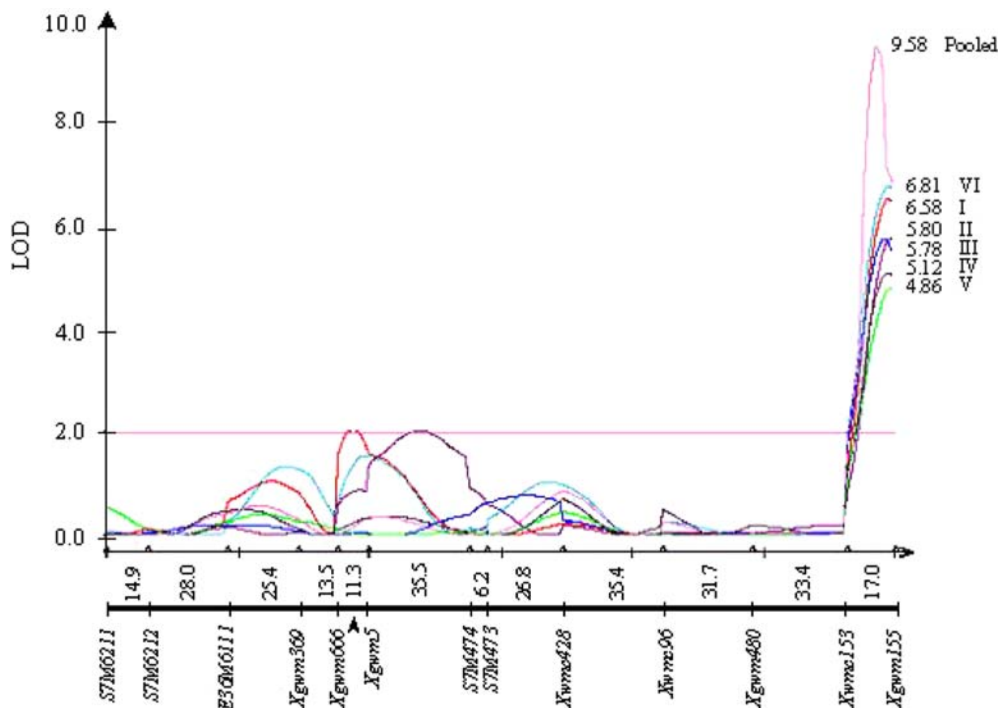

Fig. 1 A QTL Cartographer plot for chromosome 3A obtained following composite interval mapping (CIM) for pre-harvest sprouting tolerance (PHST) for six different environments and the pooled data; LOD score values for each environment along with the environment designations are given in front of the LOD peaks; marker designations are given at the bottom and the genetic distances (cM) are given above the horizontal line; *arrow* indicates centromere

Table 3 Rank correlation coefficients between the PHS scores in six different environments

Environment[a]	II	III	IV	V	VI
I	0.747**	0.640**	0.682**	0.675**	0.688**
II		0.501**	0.559**	0.496**	0.557**
III			0.735**	0.626**	0.846**
IV				0.687**	0.753**
V					0.644**

[a] Environment designations are same as given in the footnotes of Table 1 **$P<0.01$

Framework map of chromosome 3A

The genotypic data on 100 RILs using 11 SSR (including six wmc and five gwm), 76 AFLP and 37 SAMPL markers were used for the construction of a framework linkage map of chromosome 3A. A total of 13 markers including 8 SSR, 4 SAMPL, and 1 AFLP were mapped on this chromosome. The tentative position of centromere was assumed to be present in the marker interval *Xgwm666*-*Xgwm5* (deduced from 3A map of ITMI*pop*), thus mapping five markers (1 AFLP, 2 SAMPL and 2 SSR) on 3AS and the remaining 8 markers (2 SAMPL and 6 SSR) on 3AL.

In the framework map for 3A prepared during the present study, the maximum distance (35.5 cM) was between markers *Xgwm5* and *S7M474* and the minimum distance (6.2 cM) was between the markers *S7M474* and *S7M473* with average distance of 21.47 cM between any two markers. The total length of the current genetic map of chromosome 3A is 279.1 cM.

QTL analyses and detection of a major QTL

The CIM conducted using data on PHS in each of the six environments and using data pooled over environments suggested the presence of a major QTL (*QPhs.ccsu-3A.1*) on the long arm of chromosome 3A in the marker interval *Xwmc153*-*Xgwm155*. The LOD scores ranged from 4.86 (environment V) to 9.58 (pooled data) (Table 4, Fig. 1), which were above the threshold LOD scores (ranging from 4.2 in environment I to 5.79 in pooled data) in each of the six environments and also in the pooled data. The phenotypic variation explained (PVE) by the QTL varied from 24.68% (environment V) to 78.03% (pooled data). Positive values of additive effect of the QTL in all the environments suggested that the superior parent (SPR8198) contributed to PHST in the present study.

In order to achieve higher precision, the data were also subjected to QTL analysis using MultiQTL package, which confirmed the presence of a major QTL at the position located through QTL Cartographer. When analysis was conducted across environments using MultiQTL, QTL detection power in this analysis was 100%, even at $P=0.001$. Confidence interval based on LOD-drop-off method ranged from 5.9 cM (pooled data) to 9.5 cM (environment III), while that based on bootstrapping was 6.82 cM across all the environments.

QTL × environment interaction

QTL analysis across environments, conducted using MultiQTL package, also suggested absence of Q×E and "residual variation" × E interactions, although the main trait value × E interaction was significant. These results are in conformity with the fact that the mean values varied significantly among locations ($P<0.001$).

Parents of mapping population did not differ for alleles of R gene on 3A

Attempts to map *R* gene for kernel colour on 3A, using the available mapping population failed, suggesting that the parents differed for *R* genes on chromosomes other than 3A. Test of independence between the grain colour and the marker that was found to be associated with the major QTL for PHST identified during the present study, suggested that grain colour in this population was independent of the QTL for PHST ($\chi^2=2.98$; $P=0.1$).

Alignment of present 3AL map with other available 3AL maps

The 3AL map, which allowed the detection of a major QTL for PHST during the present study, was aligned with other maps available in the literature; these earlier

Table 4 Results of composite interval mapping for pre-harvest sprouting tolerance

Environment	QTL	Closest marker	Position (cM)	LOD	CI[a] (cM)	R^2 (%)	Additive effect
I	*Qphs.ccsu-3A.1*	*Xgwm155*	276.11	6.58	270.4–278.2	35.21	1.48
II	*Qphs.ccsu-3A.1*	*Xgwm155*	278.11	5.80	271.0–278.2	26.02	1.43
III	*Qphs.ccsu-3A.1*	*Xgwm155*	276.11	5.78	269.0–278.5	33.99	1.36
IV	*Qphs.ccsu-3A.1*	*Xgwm155*	276.11	5.12	269.5–278.2	29.49	1.51
V	*Qphs.ccsu-3A.1*	*Xgwm155*	278.11	4.86	270.4–278.2	24.68	1.28
VI	*Qphs.ccsu-3A.1*	*Xgwm155*	276.11	6.81	270.4–278.5	33.39	1.33
Pooled data	*Qphs.ccsu-3A.1*	*Xgwm155*	272.11	9.58	269.0–274.9	78.03	1.29

Environment designations are same as given in the footnotes of Table 2
R^2 phenotypic variation explained

[a] Confidence intervals were obtained by marking positions ±1 LOD from the peak

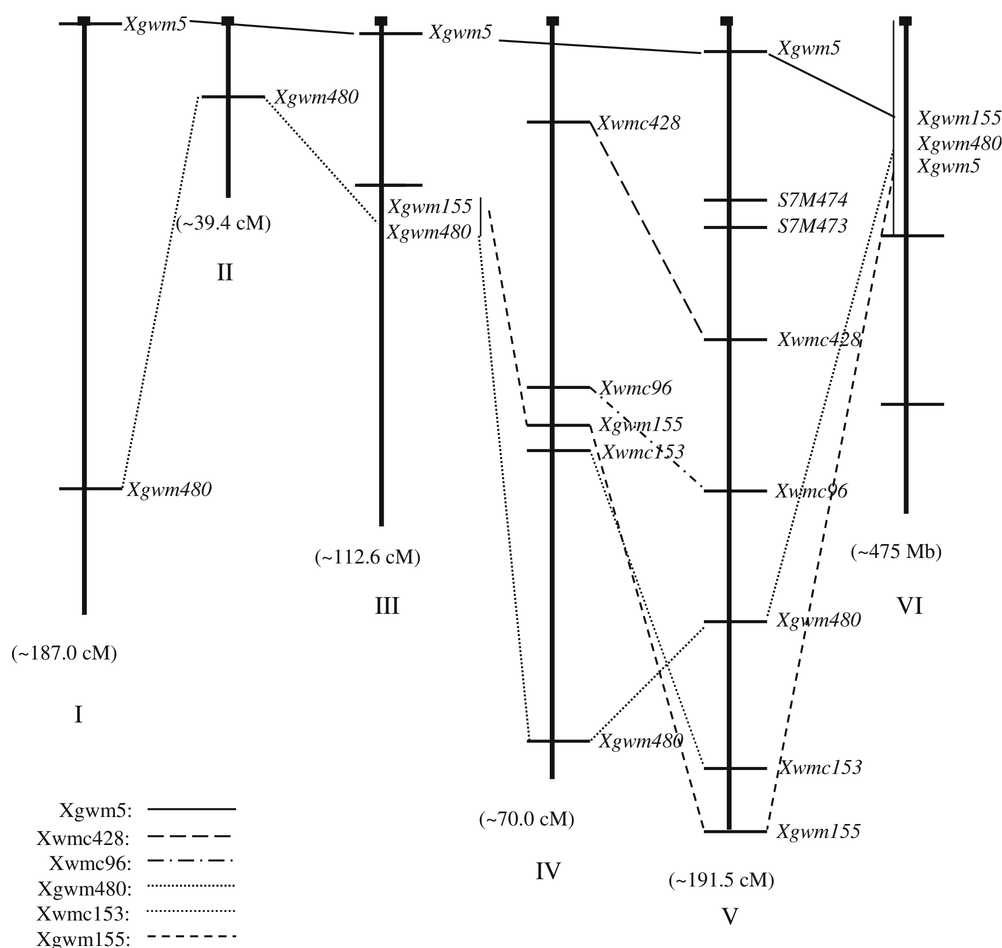

Fig. 2 Alignment of the 3AL framework map used in the present study (V) with four other genetic maps (I–IV) and one physical map (VI); these maps each carried at least one marker mapped in the present study. Markers in other maps that are common with map V (present study) are aligned through different types of lines, as detailed in index. The maps I–IV and VI were extracted from the following studies: I (Osa et al. 2003); II (Groos et al. 2002); III (Roder et al. 1998); IV (Somers et al. 2004); VI (Sourdille et al.2004).

maps also included maps used earlier in QTL analyses for PHST (Fig. 2). The order of the SSR markers in the present map for 3AL differed slightly from that in the maps published earlier (Röder et al. 1998; Groos et al. 2002; Osa et al. 2003; Somers et al. 2004; Sourdille et al. 2004), thus making a comparison of the results of the present study with those of earlier studies difficult.

Discussion

In bread wheat, QTL mapping for different traits has been an area of active research, which led to the identification of many QTLs for several important traits including PHST/dormancy (Gupta et al. 1999; Langridge et al. 2001; Jahoor et al. 2004; Li and Gill 2004; Tuberosa and Salvi 2004; Mori et al. 2005). The present study is an extension of our earlier study on PHST (Kulwal et al. 2004) and highlights the importance of group 3 chromosomes of wheat in controlling PHS/dormancy. In our earlier study, we detected 14 QTLs through two locus QTL analysis, which also included four of the five QTLs detected through single locus CIM. In this study, a major part of the phenotypic variation (78.80%) was explained by M-QTL/E-QTL; and QE and QQE explained only 3.24% of the variation, suggesting that the Q×E interactions were almost absent. The present study substantiates this earlier observation. In contrast to this, in a recent study, significant QTL×E interaction was reported, when germination tests were conducted at two different temperatures (15°C, 20°C). It is possible that this significant Q×E interaction is due to specific effect of temperature variation on germination in Petri-dishes.

The QTL (*QPhs.ccsu-3A.1*) identified in the present study represents a major QTL, which was detected at a LOD score of 9.58 and explained up to 78.03% of the phenotypic variation. The QTL was consistent across environments and was also detected when data were pooled over six environments. The significant rank correlations between the ranks of mean PHS values in different environments and the amount of variation explained by the identified QTL suggest a minor role of genotype × environment interactions, as also reported for this trait in our previous study (Kulwal et al. 2004). This receives further support from the analysis conducted across environments using MultiQTL Package, where QTL×E interaction was found to be absent.

The QTLs for PHST/dormancy earlier detected on the long arms of group 3 chromosomes have been

reported to be linked with *TaVp1* and/or *R* gene(s) in several earlier studies (Bailey et al. 1999; Flintham 2000; Warner et al. 2000; Watanabe and Ikebata 2000; Groos et al. 2002), with the exception of a solitary study (Osa et al. 2003), where no such association was reported. In the present study, the red kernel gene-*R* could not be mapped on 3A using the data on kernel colour of RILs. Further, the test of independence showed absence of association between the kernel colour and the marker (*gwm155*) associated with the major QTL *QPhs.ccsu-3A.1*, identified during the present study. These results suggested that the alleles contributing to red grain colour in this population might be located on the other two *R*-gene homoeoloci on chromosomes 3B and 3D of SPR8198. In our earlier study on PHST using ITMI*pop*, important QTLs for PHST were detected on chromosomes 3BL and 3DL, but no QTL was detected on chromosome 3AL (Kulwal et al. 2004). The results of the present study, therefore, also confirm the need for conducting QTL analysis for the same trait using more than one mapping populations.

The QTL identified in the present study falls in the 17 cM interval at the end of 3AL (~183 cM from centromere) between the two adjacent markers *Xwmc153* and *Xgwm155*. QTL for PHST/dormancy on 3AL were also reported in two earlier studies. In one of these two studies, a QTL was identified on 3AL at a distance of ~50 cM from the centromere, in the interval between *Xfbb293-1* and *Xgwm480* (Groos et al. 2002). In the other earlier study, QTLs for PHST were identified on both arms of 3A, a major QTL on 3AS *(QPhs.ocs-1)* explaining as much as 23–38% variation and a minor QTL *(QPhs.ocs-2)* on 3AL explaining as much as 13% of variation (Osa et al. 2003). In a more recent study, *QPhs.ocs-1* was shown to explain as much as 11.6–44.8% of the variation for seed dormancy under dormancy breaking condition of low temperatures (Mori et al. 2005). In the present study, the PV explained by the identified QTL ranged from 24.68% (environment V) to 35.21% (environment I) in individual environments, and 78.03% in pooled data. In another study in bread wheat using doubled haploid mapping population, Kato et al. (2001) detected a major QTL for dormancy on chromosome arm 4AL explaining up to 77% PV. However, in each of these studies, PVE is based on the variation released from a specific cross and in no case reflects the total diversity for PHST available in the germplasm. It is also important to note that the analyses in the above studies (Kato et al. 2001; Osa et al. 2003; Mori et al. 2005) were based on simple interval mapping, where PVE could be overestimated. Further, the parameters used to estimate the degree of dormancy in these above studies were different from those used for evaluation of PHS in several studies including the present study. While dormancy is often tested through germination tests using dry threshed seeds, PHST is tested using mature spikes, before threshing. Therefore, the QTLs for dormancy identified in these earlier studies and the one identified for PHST in the present study are not comparable, although some of the QTLs may affect both, PHST and dormancy.

A barley QTL explaining more than 70% PV for PHST was also reported by Li et al. (2004) on chromosome 5H (syntenic to wheat chromosome 4A) suggesting that in addition to 3A, 4A is also important for PHST in bread wheat. Possibility of the interaction of the product from gene(s) on 4A with products from genes on group 3 chromosomes has also been suggested (Appels et al. 2003). However, there is no earlier report of a major QTL on 3AL explaining as much as 78% PV. Thus, the present report of a QTL on 3AL is the first report of its kind. However, further studies are needed to narrow down the interval of the identified QTL by saturating the map using more polymorphic markers.

In order to find out, whether the QTL identified in the present study corresponds to any of the QTL earlier reported to be located on 3AL (Groos et al. 2002; Osa et al. 2003), framework map used in the present study was aligned with other available maps, including those used in earlier PHST QTL mapping studies (Fig. 2). The QTL identified in the present study is located in the interval *Xwmc153-Xgwm155* with *Xgwm480* as the next adjoining marker locus. One or more of these three markers *(Xgwm480, Xwmc153, and Xgwm155)*, are available in some other maps also, although not at the same position and not in the same linear order. For instance, the above three markers in the consensus map constructed by Somers et al. (2004) have an order, which is reverse to that in the map used in the present study. It is, therefore, possible that 3AL of our mapping population differs from that in some earlier maps by a small inversion. If it is so, the possibility of the QTL identified in the present study being the same as identified in two earlier studies cannot be ruled out, although the quantum of variation explained by the present QTL is several fold larger relative to that explained by a single 3AL QTL in any earlier study. Furthermore, the QTL detected in the present study is not at all associated with red grain colour, nor does it represent the pleiotropic effect of a R gene, as in the case with a QTL identified earlier (Groos et al. 2002)

In the past, it has been suggested that the QTL identified in more than one environment or those identified using data pooled over environments are useful from the point of view of MAS (Veldboom and Lee 1996; Fulton et al. 1997; Moncada et al. 2001). Furthermore, for use in MAS, it is desirable to have one or few QTLs, each with a major effect on the trait. In the light of this observation, the QTL detected in the present study will prove valuable in MAS aimed at improving the grain quality of wheat in terms of increased resistance to PHS. Positive QTL effect in the present study suggests that a superior allele of the QTL is available in the superior parent (SPR8198). The marker allele associated with this superior QTL allele

should be used for MAS for the transfer of this QTL allele to obtain superior progeny. Furthermore, wheats with white grains are more often susceptible to PHS, relative to wheats with red grain. However, in Asia, wheats with white grains are preferred over the red grains due to customers' preference for amber colour. Keeping this in view, efforts are underway in our laboratory to transfer PHS tolerance from SPR8198 (a PHS tolerant genotype with red grains) to HD2329 (a susceptible cultivar with white grains). Since in the present study, red grain was not found to be associated with the marker linked with the QTL for PHST, it is apparent that development of PHS tolerant white-grained cultivars should be possible.

Acknowledgements Financial assistance for this work was received from NATP-ICAR, New Delhi and the Department of Biotechnology, Government of India. PLK and NK both received Senior Research Fellowship of the Council of Scientific and Industrial Research (CSIR); PKG held the position of a Senior Scientist of the Indian National Science Academy (INSA). G.B.P.U.A. & T., Pantnagar and P.A.U., Ludhiana, India provided field facilities and helped in conducting field trials. Thanks are also due to Professor H. S. Dhaliwal, IIT Roorkee, India, for providing aliquots of gwm primers, and to Professor A. Korol University of Haifa, Israel, for conducting analysis on MultiQTL and for critical advice. Useful comments by an anonymous reviewer helped in the improvement of the manuscript.

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