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Deployment of molecular markers for the improvement of some important quality traits in bread wheat.

Construction of framework linkage map(s) using trait-specific, intervarietal RIL populations. Three framework linkage maps using three mapping populations have been prepared in our laboratory for QTL interval mapping of various agronomically important traits. These three mapping populations were originally developed for the following three traits by Dr. H.S. Dhaliwal and his coworkers at Punjab Agricultural University (PAU), Ludhiana, India: (i) grain protein content (GPC); (ii) preharvest sprouting tolerance (PHST), and (iii) grain weight (GW).

QTL analyses for 11 yield and yield-related traits. The GPC and ITMI populations were used to identify QTL for nine yield traits including plot yield and its components, plant height, and peduncle length. For this purpose, single-locus (using QTL Cartographer) and two-locus (using QTLNetwork) QTL analyses were conducted. For all 11 traits, a total of 80 putative M-QTL on 19 chromosomes in the GPC population and 140 putative M-QTL on 20 chromosomes in ITMI population were detected. QTLNetwork identified a total of 113 and 190 QTL that included QTL with significant main effect and/or significant interaction effect (epistatic QTL or QTL involved in interaction with the environment). An important genomic region harboring important major co-localized QTL for each of the six yield traits was identified on chromosome arm 2DS in both the GPC and ITMI populations. In the ITMI population, this QTL influenced plot yield, spike weight, spike length, spikelets/spike, seed weight, and 1,000-kernel weight (explaining from 13.00% to 37.85% PV for individual trait), whereas in the GPC population, the QTL influenced plot yield, tiller number, spike length, spike compactness, number of seeds, and 1,000-kernel weight (explaining from 8.93% to 19.81% PV for individual trait). The genomic region with the above QTL was physically located in the distal bin (2DS5-0.47-1.00) covering 53% region of 2DS. Comparative mapping revealed that the genomic region harboring the QTL in wheat spans a distance of 11.51 Mb on rice chromosome 7 (R7). This information may prove useful for high-resolution mapping leading to map-based cloning of the above major QTL.

Marker-assisted selection for GPC and leaf rust resistance. In bread wheat, high grain protein content (HGPC) determines nutritional value, processing properties, and quality of the end-product. In view of this, marker-assisted selection (MAS) was used to introgress a major gene for high GPC (*Gpc-B1*) into six wheat genotypes. These six wheat genotypes included (i) three elite Indian bread wheat cultivars and (ii) three advanced lines derived from the cultivar PBW343 (each containing the leaf rust resistant gene *Lr*24). During backcrossing, foreground selection was exercised using tightly linked markers. Background selection was performed using SSR markers evenly distributed throughout the genome. As a result, 14 BC_3F_4 lines carrying *Gpc-B1* were developed and evaluated for GPC and grain yield. Ten of

these lines, homozygous for *Gpc-B1*, had significantly higher GPC, the increment ranging from 0.42% to 2.50% of the GPC (increment on the original concentration was ~4% to 25%). One of the derived lines with enhanced GPC also had significantly higher grain yield (others were equal with their recipient genotypes). No negative correlation was observed between grain yield and GPC (%), suggesting no yield penalty with improved GPC. The results presented in this study suggest that introgression of *Gpc-B1* gene through MAS, in combination with phenotypic selection, is a useful strategy for development of wheat genotypes combining high GPC with higher grain yield.

Marker-assisted selection for preharvest sprouting tolerance and leaf rust resistance. Preharvest sprouting and susceptibility to leaf rust are two major problems in wheat that lead to the degradation of grain quality and significant losses in yield. Development of PHST and leaf rust resistant wheat genotypes was undertaken in our laboratory using MAS. A major QTL (*QPhs.ccsu-3A.1*) for PHST, which we had earlier identified, was introgressed into HD2329, an elite but PHS-susceptible cultivar that has two *Lr* genes (*Lr24* + *Lr28*) earlier introgressed at IARI by Dr. K.V. Prabhu and coworkers using MAS. In each backcross generation, foreground selection for the PHS QTL was exercised using flanking markers (*Xgwm155* and *Xwmc153*), and background selection was performed using 61 simple sequence repeat markers mapped at loci spread over the whole genome. During backcrossing, desirable alleles of *Lr24* and *Lr28*, also were tracked using linked SCAR markers. Seven BC_3F_3 progenies having both the desirable PHST QTL and *Lr* genes and showing up to 93.44% genetic similarity with the recipient parent were selected. These lines exhibited a high level of PHST (PHS score 2–4) and resistance against leaf rust under artificial conditions. The study demonstrated successful application of MAS for targeted pyramiding of QTL/genes for more than one trait into an improved wheat cultivar (Kumar et al. 2009).

Introgression of QTL for grain weight using MAS. Crosses involving 10 elite Indian bread wheat genotypes as recipient parents and the genotype Rye Selection111 as a donor parent were attempted during the off-season of 2005–06 in a Phytotron Facility at IARI, New Delhi, and the F_1 seed collected. These F_1s were raised during the rabi season 2006–07 and backcrossed with their respective recurrent parents to obtain the BC_1F_1 seed. A total of 470 BC_1F_1 seeds belonging to five crosses (RS111/HD2329, PBW343 (*Lr9*)/RS111, HI977/RS111, K9107/RS111, and RAJ3765/RS111) were obtained. Using this seed material, ~259 BC_1F_1 plants were raised during rabi 2007–08. Following foreground selection, 27 positive plants for markers *Xwmc24* and *Xwmc59* (associated with two separate QTL for grain weight on chromosome 1A), 127 positive plants for the marker *Xwmc24* and 57 positive plants for the marker *Xwmc59* were selected. The selected BC_1F_1 plants were backcrossed with their respective recurrent parents and BC_2F_1 seeds was obtained, which were used to raise BC_2F_1 progenies in the field during the rabi season 2008–09. Following foreground selection, three positive plants for markers *Xwmc24* and *Xwmc59* (associated with two separate QTL for grain weight on chromosome 1A) involving the recipient genotype PBW343 (*Lr9*); 142 positive plants for the marker *Xwmc24* only involving recipient genotypes PBW343 (*Lr9*), K9107, and Raj3765; and 18 positive plants for the marker *Xwmc59* involving recipient genotype PBW343 (*Lr9*) were selected. The selected plants were backcrossed with their respective recurrent parents to obtain BC_3F_1 seed, which was used to raise the BC_3F_1 progenies during the rabi season 2009–10. The selfed seed (BC_3F_2 seed) of the corresponding progenies was harvested and phenotypic data on 1,000-kernel weight is being recorded. The BC_3F_2 seed will be used to raise the BC_3F_2 progenies during the rabi season 2010–11, and both foreground and background selections (for progenies possessing the desired QTL) will be undertaken to identify desirable plants for raising the BC_3F_3 progenies.

Genetic dissection of grain weight in bread wheat through QTL analysis. For the genome-wide genetic dissection of GW in bread wheat, both QTL interval mapping and regional association mapping were undertaken. QTL interval mapping involved preparation of framework linkage map with 294 loci (194 SSRs, 86 AFLP, and 14 SAMPL) using a biparental RIL mapping population derived from the cross 'Rye Selection111/Chinese Spring'. Using the genotypic data and data on GW of RILs collected over six environments (3 locations × 2 years), genome-wide single-locus QTL analysis (using inclusive composite interval mapping, ICIM) and two-locus QTL analysis (using QTLNetwork) were conducted to identify main effect QTL (M-QTL) and epistatic QTL (E-QTL). Single-locus QTL analysis identified 10 QTL (including four major and three stable QTL), contributing >20% phenotypic variation for GW. Two-locus QTL analysis resolved a total of 24 QTL, which included three M-QTL (also detected by single-locus analysis) and 21 E-QTL, the later involved in 12 digenic Q × Q interactions; no Q × E and Q × Q × E interactions were detected. The total PV due to all the M-QTL was 28.11%, whereas the PV due to all the E-QTL was 43.36%, which suggested that nearly three quarters (71.47%) of PV for GW was fixable. This study was further supplemented with association mapping, which allowed validation of seven QTL (including above two QTL) and helped to identify two new markers in the genomic regions that were not reported to contain QTL for GW in earlier studies. The validated markers linked with QTL for high grain weight may prove useful in marker-assisted selection for the development of cultivars with high GW in bread wheat.

Genetic diversity and population structure analysis among Indian bread wheat cultivars. As a first step towards association mapping in wheat, we analyzed genetic diversity and structure in a collection of 263 Indian bread wheat cultivars (45 developed during pre-Green Revolution period and 218 developed during post-Green Revolution period) that were released over a period of ~100 years (1910 to 2006). For this purpose, we used a set of 42 unlinked neutral SSRs and 48 SSRs (60 loci) from the genomic regions reported to have QTL for GW. The 42 SSRs detected a total of 295 alleles (mean 7.02; range 2-14/SSR), which is more than a total of 273 alleles (mean 4.55; range 2–9 alleles/SSR) detected by 60 SSR loci subjected to selection. The average number of alleles/locus (5.91 vs. 5.74) and the estimates of genetic diversity (0.65 vs. 0.61) in the pre- and post-Green Revolution period cultivars did not differ significantly indicating that the Green Revolution did not lead to any loss of genetic diversity. However, to better understand the scenario, decadal diversity also was studied, which indicated gradual loss in diversity during three decades (1970s-2000s). This loss in diversity is alarming and, therefore, needs attention of breeders. The model-based *Structure* analysis identified a total of 14 subpopulations including two subpopulations largely comprising cultivars from pre-Green Revolution period and the 12 subpopulations mostly comprising cultivars from post-Green Revolution period. These results suggest that modern wheat-breeding practices in India are slowly decreasing genetic diversity and, therefore, this issue need to be addressed by involving diverse/synthetic wheat germ plasm in Indian wheat-breeding programs.

Association analysis for grain weight, grain protein content, and preharvest sprouting tolerance. We attempted association analyses for the grain-quality traits GW, PHST, and GPC. For this purpose, only 230/263 of the above cultivars were used, because for the remaining 33 cultivars, either phenotypic data was not available, they had similar pedigrees, or they flowered/matured too early or very late making them unsuitable for study. The model-based *Structure* analysis identified a total of 13 subpopulations. These included two subpopulations largely containing pre-Green Revolution cultivars and the remaining 11 subpopulations containing post-Green Revolution cultivars.

The *Structure* analysis was used to make marker-trait associations for GW and GPC using a set of 48 SSR markers mapped in the genomic regions harboring QTL for GW. The association mapping allowed identification of nine and four markers ($P < 0.05$) having significant association for GW and GPC, respectively. The study validated two markers on chromosome 1A that earlier were reported to be associated with QTL for GW (through QTL analysis), and also helped in identification of two new markers for GW in the genomic regions that were not reported to contain QTL for GW in earlier studies. Five new markers also were identified in the genomic regions previously reported to have QTL for GW, so that relatively more closely linked markers with the QTL were identified in these cases.

Marker-assisted pyramiding of quality traits and leaf rust resistance in the background of PBW343. Pyramiding the QTL/genes for quality traits and leaf rust resistance in the background of PBW343 also was undertaken using the genetic stocks developed through MAS by us at our research farm and Punjab Agricultural University (PAU), Ludhiana, India. We decided to develop the following two single cross hybrids (i) PBW343 (*Lr24+GPC-B1*) / PBW343 (PHST) developed by us and (ii) PBW343 (*Lr24+Lr28*+GW) / PBW343 (*GluAx-Ay*) developed by PAU. F_1 seeds of these two hybrids were distributed between each institute (CCSU and PAU) for producing double cross hybrids for carrying out MAS for pyramiding the genes/QTL for leaf rust resistance, PHST, GW, and *GluAx-Ay*.

The above two hybrids were raised at CCSU and PAU in an off-season (2009) nursery at Keylong (a research station for raising off-season nurseries) for preparing the double cross hybrid seed. The two hybrids were intercrossed, and double cross hybrid seed (F_1 seed) was obtained. The double cross population comprising a set of ~192 plants were grown at CCSU during 2009–10 and foreground selection was undertaken using a set of six SSR/SCAR markers linked to corresponding gene/QTL for GPC, PHST, GW, and leaf rust resistance. Following foreground selection, four plants containing all the above genes/QTL in homozygous condition were selected and bagged to allow them self pollinate. An additional two plants containing all the above genes but showing heterozygosity for markers associated with GW or GPC loci also were selected and allowed to self pollinate. To increase the frequency of plants possessing all the important genes, we selected ~15 plants possessing either four or more than four genes and intercrossed them in different combinations and F_1 seeds were obtained.

Molecular marker-assisted transfer and pyramiding of one or more of the QTL/genes for quality traits.
To mobilize or pyramid one or more QTL/genes for grain quality into high-yielding wheat cultivars to develop genotypes/cultivars combining improved, five institutions from India, including CCSU, will focus on developing wheat cultivars combining grain quality traits (high GW, high PC, PHST, grain hardness, and flour quality) with leaf rust resistance and high grain yield using molecular MAS.

Analysis of host-pathogen interaction in leaf rust-infected bread wheat: wet-lab approach. To understand the host-pathogen interaction in detail, it is essential not only to study temporal and spatial expression of a particular gene, but also those of other genes that may be similarly co-regulated, at both seedling and adult-plant stage. The well known, classical method cDNA–AFLP analysis is most suitable for the above purposes, because it covers the whole transcriptome. For the study of seedling resistance provided by the gene *Lr28*, total RNA was isolated from seven-day-old seedlings of each of the resistant (HD2329 + *Lr28*) and susceptible (HD2329) wheat stocks (a) before inoculation, i.e., at 0 h; (b) at 48 h, 96 h, and 168 h after inoculation with leaf rust pathogen race 77-5; and (c) at 168 h after mock inoculation. Using the above RNA samples, high-quality cDNA samples were obtained. These cDNA samples were utilized to study the transcript derived fragments (TDFs) following cDNA–AFLP analysis using 17 *Eco*RI+3/*Mse*I+3 γP32 labeled primer combinations. Highly reproducible, single banded, and over-expressed, 37 TDFs in the resistant and susceptible hosts following pathogen inoculation were isolated, cloned, and sequenced. Analysis of the sequences showed that 29 TDFs had significant similarity with known nucleotide or protein sequences in the database, including a number of wheat BAC clones and known proteins. To gain more information regarding expression of the above TDFs across different treatments, quantitative RT-PCR analysis is being conducted.

For the study of adult-plant resistance provided by the gene *Lr48*, total RNA was isolated from leaves of a 120-day-old, leaf rust inoculated and mock inoculated APR resistant wheat stock CSP44 + *Lr48* at (a) 0 h, (b) 24 h, (c) 48 h, (d) 72 h, and (e) 168 h. Using the above derived 10 purified RNA samples, 10 high quality cDNA samples were synthesized followed by cDNA-AFLP analysis using 16 *Eco*RI+3/*Mse*I+3 γP32 labeled primer combinations. A total of 483 differentially expressed TDFs were identified, and 52 TDFs (out of 483) were eluted from the gels. A total of 48 TDFs were cloned and sequenced successfully. Some of these TDFs showed similarity with known genes which include genes expressed in leaf rust and stripe rust infected bread wheat plants and other stress responsive genes. A few TDFs did not match with nucleotide or protein sequences in the database and were considered new. One TDF showed similarity with a genomic sequence of *P. triticina* and was considered to be of pathogen origin. Primers for quantitative RT-PCR were designed using software primer express.

Analysis of host–pathogen interaction in leaf rust-infected bread wheat: *in-silico* approach. The availability of wheat UniGenes and ESTs from cDNA libraries of leaf rust infected susceptible and resistant wheat plant stocks in UniGene and the dbEST database of the NCBI are powerful resources to identify differentially expressed wheat genes expressed during resistance reaction . Using these transcriptomic resources, and with the help of the data-mining tool Digital Differential Display (DDD), three pair-wise comparisons were performed on three cDNA libraries, each derived from leaf rust inoculated susceptible wheat stock (i) Thatcher, leaf rust inoculated resistant wheat stock, (ii) Thatcher + *Lr10* and leaf rust inoculated resistant wheat stock, and (iii) Thatcher + *Lr1* . A total of 68 differentially expressed UniGenes were identified. Using the Cluster 3.0 program, the differentially expressed UniGenes were clustered in five major clusters based on correlated expression pattern . In this exercise, resistance specific up- and down-regulated genes were identified for both genes *Lr10* and *Lr1* in the cultivar Thatcher. Some of the differentially expressed UniGenes encode for proteins similar to DNAJ heat shock family protein, thiol-disulfide exchange intermediate (*A. thaliana*), Triticain gamma (CTSH), membrane-binding proteins, and many known and unknown but novel gene sequences. Further tissue-based cluster analysis of the differentially expressed UniGenes was performed and revealed that all the identified UniGenes are highly expressed in leaves, have moderate expression in the sheath, stem, and inflorescence, and have low expression in the seed, root, flower, crown, callus, and cell culture. The present study will be followed by wet-lab experiments to identify differentially expressed genes in leaf rust infected wheat.

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Behavior of spring wheat genotypes under late and very late situations in northwestern India.

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Summary. A field experiment conducted during the winter seasons in 2000–01 to 2001–02 at the Directorate of Wheat Research, Karnal, evaluated new, promising genotypes under late and very late sowing situations. The mean of 2 years data revealed reductions of 16.96% and 17.15% in biomass and yield, respectively, when sowing was delayed from late to very late. This decline was due to 8.38% and 11.77% reductions in 1,000-kernel weight and grains/spike, respectively, and a more than 10 days less grain-filling period between late to very late sowings. Cultivar differences were observed for yield and yield-attributing parameters. For mean basis, cultivar HD 2643 produced the maximum biomass (106.95 q/ha) followed by Raj 3765 (106.77 q/ha); the lowest was by genotype WR 251 (94. 72 q/ha). Similarly, genotype PBW 435 recorded the maximum grain yield (42.86 q/ha) and lowest by UP 2425 (37.37 q/ha). Differential responses suggested different cultivars were suited for late sown conditions.

Wheat is the second most important crop after rice in India, occupying approximately 28 x 10^6 ha with a production of 78.4 x 10^6 metric tons during 2008–09, the highest level of production since the Green Revolution. Considering environmental and technological adaptation, India is broadly divided in to six wheat-growing regions, the Northern Hill Zone (NHZ; Jammu and Kashmir, Himachal Pradesh, and Uttarakhand), the North Western Plain Zone (NWPZ; Punjab, Haryana, Western Uttar Pradesh, and some parts of Rajasthan), the North Eastern Plain Zone (NEPZ; Eastern Uttar Pradesh, Bihar, West Bengal, Orissa, and Eastern states), the Central Zone (CZ; Madhya Pradesh, Gujrat, Southern Rajasthan, and the Bundel Khand region of Uttar Pradesh), the Peninsular Zone (PZ; Maharashtra and Karnataka), and the Southern Hill Zone (SHZ; Tamil Nadu). The growing period of wheat is variable from one agroclimatic zone to another, which affects vegetative growth and grain-filling duration leading to differences in attainable yield. The maximum wheat growing duration is in the Northern Hills Zone and the mininum is in the Peninsular Zone.

Farmers generally grow wheat in a cropping system that maximizes their total production. In this process, wheat is generally preceded by crops such as rice, cotton, sugarcane, maize, sorghum, potato, toria, and pigeon pea. In this plethora of cropping sequences, some crops, such as basmati rice, cotton, sugarcane, potato, toria, and pigeon pea, delay wheat sowing in different parts of the country. Due to late harvests of sugarcane, potato, and toria, wheat generally is sown in the first week of January. Under late and very late sowing conditions, low temperatures occur during seedling establishment and hot, dry spells prevail during grain-filling. Maturity is accelerated/forced because of high temperature and/or water stress, which reduces grain size and weight.

In India, wheat is sown from November to January, whereas the most appropriate time for sowing is the first two weeks of November. A delay in sowing to late mid-November to first two weeks of December resulted in decreases in yield of 15.5, 32.0, 27.6, 32.9, and 26.8 kg/ha/day in the NHZ, NWPZ, NEPZ, CZ, and PZ, respectively, for timely sown cultivars. Corresponding yield losses were 7.6, 18.5, 17.7, 17.0, and 15.5 %. For late-sown cultivars, a delay in sowing from late to very late, first two weeks of December to first two weeks of January, decreased grain yield by 42.7, 44.8, 51.6, and 44.2 kg/ha/day or 22.8, 27.1, 30.9, and 25.6 % in the NWPZ, NEPZ, CZ, and PZ, respectively (Tripathi et al. 2005). This huge reduction in yield due to delayed sowing prompted us to evaluate late and very late sown genotypes for maximum production. An effort was made to grow advance genotypes/cultivars under late (December sowing) and