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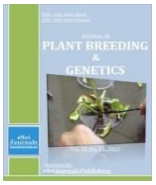

AGRONOMIC AND QUALITY QTL MAPPING IN SPRING WHEAT

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A B S T R A C T

Wheat (*Triticum aestivum* L.) flour represents one of the primary sources of calories and proteins for the human diet. The increase in the wheat yield without losing its baking and milling quality is an important breeding objective. The use of QTL analysis is an expedient methodology to help breeders to face this multifaceted challenge. Here, a population of 129 recombinant inbred lines (RILs) developed from a cross between 'Steele-ND' cultivar and 'ND 735' advanced line was used to evaluate several yield and quality traits and map the genomic regions controlling these traits. The phenotypic data were collected from field experiments conducted at four North Dakota (ND), USA environments. Transgressive segregation was observed for all traits, with RILs outperforming the most adapted parent and commercial cultivars. Using a linkage map of 392 markers, composite interval mapping identified a total of 13 environment-specific QTLs, all explaining large phenotypic variations (R^2=16-44%). The genotypic values of these "reserve" alleles were directly used as criteria of selection in breeding programs.

Keywords: Reserve alleles, quality; grain yield, grain hardness, baking traits, mixogram peak time.

INTRODUCTION

Wheat (*Triticum aestivum* L.), with a yearly production of over 650 million tons worldwide (FAO 2010), is among the most important source of plant calories and protein in the human diet. The United States contributes approximately 10% of world production (FAO 2010), of which 16.9 million tons are hard red spring wheat (HRSW) (USDA 2012). North Dakota (ND) is the leading state in the production of HRSW, accounting for over 7 million tons per year, followed by Minnesota, South Dakota, and Montana (Regional Quality Report 2011). The higher protein content and superior gluten quality of HRSW makes it an excellent source of flour for baked goods, which in turn guarantees lucrative returns to the farmers in domestic and international markets. The challenge before HRSW breeders is to release high yielding varieties, without losing their high value baking quality. Most agronomic and baking/milling traits are quantitative in nature with a complex array of genetic interactions, making selections for these traits far from simple. Nearly 85 years ago, Sax (1923) developed the basic concepts of detecting quantitative trait loci (QTL). Today, with the advent of molecular markers and the development of powerful statistical tools, QTL analysis has become a routine approach and is often applied for the identification of markers for molecular breeding (Salvi and Tuberosa 2005). Recombinant inbred lines (RILs) populations developed from genetically diverse parents (broad base) or elite lines (narrow base) have proven successful in mapping important agronomic and quality traits in wheat (Rousset et al. 2001; Börner et al. 2002; McCartney et al. 2005, 2006; Quarrie et al. 2005; Suenaga et al. 2005; Arbelbide and Bernardo 2006; Breseghello and Sorrells 2006; Kumar et al. 2007; Maccaferri et al. 2008). Zhang et al. (2010), after reviewing the distribution of 541 yield and yield related QTL, reached the conclusion that yield QTLs are distributed all over the wheat genome. Changes in almost any trait will inevitably always result in an effect on the final grain yield (Zhang et al. 2010). QTL analysis

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has also been used to study various wheat quality traits (Rousset et al. 2001; Arbelbide and Bernardo 2006; Breseghello and Sorrells 2006; McCartney et al. 2006; Nelson et al. 2006; Li et al. 2009; Kumar et al. 2009; Sun et al. 2010) and once again the wide distribution of QTLs suggest a large and complex interaction of many genes, each responding to small environmental and genotypic changes.

Regardless of the abundance and complexity of the QTLs identified for yield and quality traits, it is essential that conventional and molecular breeding work together to succeed in the daunting challenge of developing high yielding and high quality varieties (Phillips 2009; Carena 2009). The objectives of this study were to map QTLs for major agronomic and quality traits in a typical breeding population involving two elite genotypes adapted to the growing conditions of ND, and directly employ the detected QTL for selection within this population.

MATERIALS AND METHODS

Plant material and experimental design: The present study used a RIL mapping population comprising of 129 F_{2-8} lines developed from a cross between HRSW cultivar (cv.) 'Steele-ND' and HRSW breeding line 'ND 735' (S x N) as described by Mergoum et al. (2009a). The S x N RIL population, the parental genotypes 'Steele-ND' (Mergoum et al. 2005a) and 'ND 735' (Mergoum et al. 2006) and the checks were evaluated in a randomized complete block design with two replications for two consecutive years (2008 and 2009) at Prosper (PR; 47.002º, -97.115º; elevation 284 m) and Carrington (CR; 47.507º, -99.132º; elevation 475 m), ND. The four commercially grown HRSW cultivars. 'Faller' (Mergoum et al. 2008), 'Reeder' (PI200000211), 'Dapps' (Mergoum et al. 2005b), and 'Glenn' (Mergoum et al. 2006) were used as experimental checks. Each genotype was planted in a plot size of seven rows , with each row 2.44 m long and 15.20 cm apart. The CR location was irrigated and represents East Central region of ND, with soil type of Heimdal-Emrick series (loamy, mixed, superactive, and Calcic/Hapludolls). The PR location was rainfed and represents the Eastern region of ND with soil type of Beardon series (fine silty, mixed, superactive, frigid aeric Calciaquolls).

Agronomic and quality traits evaluation: In field, phenotypic data were collected for days to heading (DTH), plant height (PH) (cm), spike density per m^2, and spike length (cm). The DTH was recorded as number of days between sowing and inflorescence emersion in at least 50% of plants in each plot and the PH was recorded in cm for each plot by measuring the length of ten plants in each plot from soil surface to top of the spikes excluding the awns. Spike density (SD) per m^2 was calculated as the average number of spikes per 0.5 m in two individual rows and then converted to m^2. Spike length (SL) (cm) was calculated by averaging the length of ten individual spikes collected at random from each plot. The harvested grains from each plot were cleaned with clipper grain cleaner and all remaining agronomic traits evaluated. A sub-sample of 200 g of grain was further cleaned in the Cereal Quality Lab at North Dakota State University (NDSU) on a Carter dockage tester (Carter-day Co., Minneapolis, MN) to measure wheat grain quality data.

Grain yield (GY) (Kg ha^{-1}) was determined weighing the cleaned seeds from each plot. Grain volume weight (GVW) (Kg m^{-3}) was calculated according to AACC standard method 55-10 (AACC 2000). The number of kernels per spike (KPS) was measured on ten randomly collected spikes from each plot before harvest, hand threshed, and the seeds of each spike were counted on an electronic seed counter (Seedburo Equipment Co., Chicago, IL). Thousand-kernel weight (TKW) (g) was calculated by counting the number of kernels in 10 g of sample using an electronic seed counter and then converted it into the weight of 1,000 kernels. Kernel size distribution (KSD) (%) was determined on 100 g of seeds shaken for 2 minutes on a mechanical shaker. The kernels that remained on the top of the sieve (Taylor No.7, 2.92 mm) were classified as 'large', in the middle sieve (Taylor No.9, 2.24 mm) were considered as 'medium', and the ones which reached the bottom were classified as 'small'. Since the small size kernels are negligible (less than 1%), only large and medium size kernels are reported. A total of 100 g of seed was evaluated to determine the kernel size. Grain protein content (GPC) (%) was measured according to AACC standard method 46-30 (AACC 2000), using an Infratec 1226 Cold Grain Analyzer. Kernel hardness (KH) was measured using the Single Kernel Characterization System (SKCS) on 300 kernels, and the hardness is expressed as an index of 20 to 120, with 20 being very soft and 120 being very hard. Kernel diameter (KD) (mm) was measured as the average diameter of 300 kernels analyzed in SKCS system. Flour extraction (FE) was measured after sample cleaning using a Carter-Day dockage tester, before milling. Samples were tempered for 16 hrs to 15.5% moisture content, equilibrated to

150 g, and then milled on a Barbender Quadromat Junior Mill according to the standard procedures of Cereal Quality Laboratory, Department of Plant Sciences at North Dakota State University. The percentage of flour extraction was calculated by dividing the flour weight by total grain weight milled. The mixograph peak time (MPT) test (min) was determined using the National Manufacturing Mixogram with a ten grams mixing bowl (National Manufacturing, TMCO Division, Lincoln NE). Mixograph water absorption was based on GPC in each location following the formula of Finney (1945). Mixograph data was collected using Mixsmart software program.

Molecular Analysis: The linkage map as described previously by Singh et al. (2011) was used in present study. Briefly, 364 Diversity Array Technology markers (DArT; Akbari et al. 2006) and 28 simple sequence repeat (SSR) markers were assigned to 277 unique loci spanning 14 chromosomes (AABB) and none to the D genome (for more details about genetic map, see Mergoum et al. 2013). The total genetic length of the linkage map was 1,789.3 cM, with an average density of one marker per 4.57 cM.

Statistical Analysis: The analysis of variance (ANOVA) on the collected data was performed as general linear model (PROC GLM) (Statistical Analysis System version 8.2) (SAS Institute 1999). Error homogeneity was tested using factor of 10 fold test. Genotypes were considered as having fixed effects and the environments having random effects; the combined ANOVA across four environments are provided as supplementary data. Standard deviations were used to identify differences between parents, checks and RILs, for all traits across environments. For every trait, a difference between genotypes that is larger than one standard deviation unit in each environment was considered as significant. Broad sense heritability (H^2) was estimated using the formula:

$$1 - \frac{MSge}{MSg}$$

where MSg is the mean sum of squares (MS) of the genotype, MSge is the MS of genotype by environment (Falconer and Mackay 1996; Tsilo et al. 2011b).

The QTL analysis was conducted for individual experimental data with composite interval mapping (CIM) using Windows QTL Cartographer v2.0 software (Wang et al. 2004) employing a standard model Zmapqtl 6 with window size of 10 cM and automatic cofactor selection. The walking speed chosen for the CIM was 1 cM. The empirical LOD threshold at the 95% level of confidence was determined by a 1,000-permutation test.

RESULTS

Agronomic and quality traits segregation: Only five traits (PH, SL, FE, KH and MPT) of the 15 measured segregated significantly between the two parental genotypes 'ND 735' and 'Steel ND' (Table 1), with the former having harder kernels (KH) and shorter MPT. For all other traits, the performances of the parental lines were not significantly different. The experimental checks 'Faller', 'Dapps', 'Reeder', and 'Glenn' differed significantly from 'Steele-ND', but mainly in an environment specific manner, with only KH values more than one standard deviation away in most environments, and with only 'Faller' more than one standard deviation superior to 'Steele-ND' for GY and GPC across environments (Table 1).

Regardless of the phenotypic similarity between 'Steele-ND' and 'ND 735', the S x N RILs population had considerable variation, with several traits showing transgressive segregation (Table 1, Figure 1, and Supplementary Material). The combined analysis of data for all traits that were homogenous across the four environments showed significant differences ($P < 0.05$) between RILs for all traits, and also significant interaction between RIL and environment for all traits except DTH, SD, and KH.

The GY mean of RILs (4493.0 Kg ha^{-1}) was lower than the parental lines 'Steele-ND' (4510.8 Kg ha^{-1}), 'ND 735' (4507.2 Kg ha^{-1}), and the check cultivar 'Faller' (5111.6 Kg ha^{-1}), but higher than check cultivar 'Glenn' (4163.6 Kg ha^{-1}). The upper range of GY of RILs exceeded GY of parents and checks in all experiment, with four lines (S x N101, S x N033, S x N161, and S x N108) more than one standard deviation higher than their parental line 'Steele-ND' in two environments. The average RILs value for GPC was commercially appreciable at 15.1 %, with a maximum of 17.1% in CR09 for the low yielding line S x N095. The same GPC was achieved by 'Glenn' in the same environment, while the parental lines averaged 14.8%. The high yielding S x N lines (S x N101, S x N033, S x N161, and S x N108) had generally lower than average GPC, with a maximum of 15.8% in CR09 for line S x N161. KH, and MPT had very large range of variations with RILs averaging 76.4 and 6.4 min, respectively, with clear evidence of transgressive segregation.

Table 1. Transgressive segregation in traits for which no QTL was found in the 'Steele-ND' x 'ND 735' (SxN) RILs expressed as mean of four environments, their standard deviation (StD), minimum-maximum range, and broad sense heritability (H^2)

	Parents		Checks		SxN RILs			H^2
Trait	Steele-ND	ND 735	Glenn	Faller	Mean	Range	StD	(%)
DTH (days)	58.8	59.5	56.1	60.3	59.1	48.8-61.3	1.2	31.4
PH (cm)	86.4	93.6	86.3	86.6	90.3	80.0-102.6	3.3	75.3
SL (cm)	7.8	8.6	7.9	7.7	8.1	7.9-8.9	0.3	84.9
SD per m^{-2}	421.1	428.2	387.4	384.0	431.1	326.3-488.2	27.8	40.8
GVW ($Kg\ m^{-3}$)	776.4	786.8	810.6	774.8	782.6	701.5-801.1	11.6	38.6
LSK (%)	58.3	52.9	52.7	70.4	58.6	36.3-74.5	7.2	81.3
FE (%)	61.1	58.7	60.9	65.1	59.5	52.6-63.5	2.1	57.8
GP (%)	15.4	14.9	15.6	14.6	15.2	14.1-17.1	0.6	80.3

DTH, days to heading; PH, plant height; SL, spike length; SD, spike density; GVW, grain volume weight; LSK, large size kernels; FE, flour extraction; GP, grain protein.

The broad sense heritability for the majority of the traits studied was high. Among the agronomic traits, GY reached a heritability of 63.3%, while the other components were inherited at higher levels with PH, SL, TKW, KD, LSK, all above 75%. Particularly low was the heritability of DTH, SD, GVW, and KNS with values between 31% and 41%. Among the quality traits, GP, KH, and MPT had heritability values above 80.0%, while FE was 57.8% only.

Environment specific QTL mapping: QTL mapping was performed by CIM on ten agronomic and five quality traits, for each environment independently. The details of QTL mapping are provided in Table 3 and Figure 2. A total of 13 QTLs were identified for six traits: GY, TKW, KD, KH, KPN and MPT. All the QTLs were identified only in one of the four environments. Two potential pleiotropic QTLs for GY, TKW, and KPN were detected on chromosome 5A between markers *Xwpt-4131* and *X344239* and on chromosome 6B between markers *Xwpt-9881* and *Xwpt-9270*. Similarly, one potential pleiotropic QTL for KH and MPT was observed on chromosome 7B in the proximity of marker *Xwmc273*. Additional three QTLs were identified for KH, one each on chromosomes 1A (*Xwpt3698-Xwmc312*), 5A (*Xwmc475-X345412*), and 7A (*Xbarc222-Xwpt1076*). Two QTLs for MPT, one each on chromosome 2B (*Xwmc382-Xwpt8004*), and chromosome 3B (*X343926-Xwpt1081*), making the total to eight genomic regions with the QTLs. All QTLs had major effects, explaining large phenotypic variations (PV) with R^2 varying from 16% to 44%. In particular, the strongest QTL identified in this study was for MPT in CR09 on chromosome 7B which explained 44% of the PV. The GY QTL on chromosome 5A had LOD of 3.5 and explained 27% of the PV under PR08 conditions. The QTLs for TKW and KPN located on chromosome 6B explained 19% and 20% of the PV, respectively under the heavy rain conditions of PR09. All the remaining QTLs accounted for more than 20% of the PV, with the exclusion of GY on 6B that controlled only 16% of the total PV. The 'ND 735' allele (N) on the 5A and 6B chromosomes yield QTLs that increased the GY of 252.04 kg ha^{-1} and 243.14 kg ha^{-1} respectively, as compared to the 'Steele-ND' allele (S) (Table 2). The TKW was positively influenced by the presence of the N allele on chromosome 5A and 6B QTLs under the stressed PR09 conditions. Among the four QTLs detected for KH, the N allele on chromosome 5A and 1A reduced the KH, while the S allele on chromosome 7B and 7A increased the KH. The only QTL detected for KD mapped to chromosome 3B and explained 23% of PV at CR08. The S allele at this QTL has an additive effect that increased the kernel diameter. Two QTLs were mapped for MPT on chromosomes 2B, and 7B, where the N allele contributed to extend the MPT by about 2 minutes in grains from CR09 and PR08.

QTL analysis for the selection of the best S x N lines: Twelve S x N RILs were selected on the basis of having phenotypic performances similar or superior to their parents for GY, TKW, KD, KH, MPT, and GPC (Table 2). Thirteen environment-specific QTLs were identified for five of these traits (no QTL was identified for GPC). The

allele at each QTL was used as an additional element for selection among the best performing twelve S x N progenies. In general, the best performing genotypes had the N allele at all QTLs, with the exception of the QTLs for KH and KD, where the S allele is most advantageous. The best yielding line S x N101 has the N allele at the 5A and 6B QTLs, that provides superior yield and TKW in two of the four environments. Also, the N allele at MPT QTLs at 7B and 2B provides very long mixograph peak time across all environments. However, the presence of the N allele at the four KH QTLs cause a softening of the kernel as compared to lines harboring the S allele for hard kernels. Also, GPC for this line is below average in all environments. SN-0101 has a total of eight positive alleles for the 13 environment specific QTLs considered (62%). SN-0095 is the lowest yielding line and has practically the opposite alleles at all QTLs, except for KH where it shares the N allele with S x N101, but the lower GY provided high GP. S x N141 and S x N161 have nine positive alleles for the 13 QTLs considered (69%), which resulted in average yield across all environments, above average TKW for most environments, average KD but softer kernels, extended MPT, and average GPC levels. The remaining lines follow similar trends, with advantages determined largely by the specific alleles at each QTL. However, among the S x N RIL progenies we could not find any lines with all the desirable alleles at all QTL loci.

DISCUSSION

S x N Parental selection: The parental genotypes of the RIL population described here are the cultivar 'Steele-ND' (Mergoum et al. 2005a), a cultivar that was commercially grown on over 250 thousands hectares in North Dakota between 2006 and 2008 (Regional Quality Report 2011), and the advanced breeding line 'ND 735' (Mergoum et al. 2006; Mergoum et al. 2009a). 'Steele-ND' is a good yielding cultivar, with very good milling and baking qualities, moderate resistance to Fusarium head blight (FHB) (*Fusarium graminearum* Schwabe), good leaf rust (*Puccinia triticina* Eriks.) and stem rust (*P. graminis* Pers. f. sp. *tritici* Eriks. & E. Henn) resistance, but it is highly susceptible to major leaf spotting diseases and to all virulent races of tan spot fungi found in ND (Mergoum et al. 2007; Singh et al. 2011). 'ND 735' combines resistance to leaf rust, stem rust, and major leaf spotting diseases, with adequate yield and quality performances (Mergoum et al. 2006). The S x N population segregates for resistance responses to three major leaf spotting diseases that affect the Northern Great Plains: tan spot caused by *Pyrenophora tritici-repentis* Drechs (Singh et al. 2010), *Stagonospora nodorum* blotch caused by *Phaeosphaeria nodorum* (Singh et al. 2011), and *Septoria tritici* blotch caused by *Mycosphaerella graminicola* (Harilal et al. 2012). Three major QTLs have been previously identified as providing resistance to all three pathogens when harboring the N allele, two located in close proximity on chromosome 5B and a third on chromosome 2B (Singh et al. 2010, 2011; Harilal et al. 2012). Additionally, 'ND 735' is moderately resistant to FHB due to the presence of the 'Sumai 3' genotype in its pedigree. It is worth pointing out that the cross of 'Steele-ND' x 'ND 735' was specifically designed for breeding of superior HRSW cultivars adapted to the ND conditions. The progenies of S x N were aimed to combine good agronomic performances equal or superior to the best parent, while stacking disease resistance and quality traits.

Transgressive segregation in a narrow base population suitable for breeding: Four commercially grown cultivars were used in our experiment as checks. These four checks are currently being planted on over a million hectares in ND and the surrounding regions (Regional Quality Report 2011). The two parental genotypes behaved similarly to the checks in all four environments, with the exclusion of 'Faller' which out yielded all other lines. The cultivar 'Dapps' produced higher GPC, 'while the cultivars Steele-ND' and 'Glenn' both had the hardest kernels and the longest MPT. Transgressive segregation was observed for all traits in this narrow base population, with some S x N lines outperforming the best checks. It is not surprising that a population developed from the cross between two elite genotypes outperforms commercially grown lines, since this is in perfect accordance with the basic principle of wheat breeding (Mergoum et al. 2009b). The heritability for traits was consistent with what was previously reported for PH, SL (Wu et al. 2012); SD (Marza et al. 2006); GY, GVW (Kilic and Yagbasanlar 2010); LSK (Toklu and Yagbasanlar 2007); TKW (Aydin et al. 2010) and KD (Tsilo et al. 2010). Also, the quality components GPC (Kilic and Yagbasanlar 2010); KH (Zhang et al. 2009) and MPT (Simons et al. 2012)

Table 2. Top 12 'Steele-ND' x 'ND 735' (S x N) RILs as compared to their parental lines and checks for traits identified by QTL analysis across four environments in North Dakota, USA.

Plant ID	Grain yield (Kg ha^{-1}) [1]					QTL [2]		Thousand kernels weight (gr) [1]					QTL [2]	
	CR08	CR09	PR08	PR09	StD	5A	6B	CR08	CR09	PR08	PR09	StD	5A	6B
Steele-ND	4281	4106	4609	4145	340	S	S	29.7	35.5	28.6	32.1	3.2	S	S
ND735	4139	4007	4638	4195	287	N	N	30.4	32.0	29.3	32.2	2.1	N	N
Faller	4440	5298	5400	4233	800			33.6	37.6	28.3	38.5	4.7		
Reeder	4106	4428	3833	4351	633			29.6	31.2	27.0	33.8	2.8		
Dapps	3751	4786	4415	3752	555			30.9	35.0	29.8	33.8	2.6		
Glenn	3471	4485	4475	3444	753			29.7	33.0	30.0	31.7	1.9		
SxN101	5237	5743	5202	4008	899	N	N	32.2	37.5	32.4	33.5	2.6	N	N
SxN141	5249	5062	5441	3039	1245	N	N	33.7	35.4	32.7	32.1	1.9	N	N
SxN033	3956	4695	5011	4620	519	N	N	29.2	32.7	28.4	29.9	2.6	S	N
SxN161	4395	5463	5719	4087	803	N	N	31.7	37.7	30.9	36.0	3.1	N	N
SxN095	3959	4360	3767	2932	707	S	S	35.1	35.5	31.0	32.8	2.4	S	N
SxN001	4046	4015	3999	3465	529	N	S	32.9	31.1	26.8	30.7	2.9	N	S
SxN159	4403	5227	5549	3189	1080	N	N	32.3	36.8	32.8	34.7	2.0	N	N
SxN009	3693	5163	4582	3444	755	-	S	34.4	38.6	31.1	36.2	3.2	-	N
SxN060	3896	5296	3879	3755	745	S	S	29.3	33.5	25.2	30.5	3.4	S	S
SxN097	4702	4143	4225	3439	676	N	S	30.8	36.3	27.1	32.6	3.8	N	S
SxN104	4866	5318	3942	3353	919	S	N	33.3	34.2	30.6	33.8	1.7	N	N
SxN108	4921	5515	4911	4088	627	N	N	28.5	33.3	26.2	28.8	2.9	N	-

Table 2 (continued)

Plant ID	Kernel diameter (mm) [1]					QTL [2]	Kernel hardness (index) [1]					QTL [2]			
	CR08	CR09	PR08	PR09	StD	3B	CR08	CR09	PR08	PR09	StD	5A	7B	1A	7A
Steele-ND	2.7	3.0	2.8	2.9	0.1	S	81.0	76.3	86.8	83.5	4.8	S	S	S	S
ND735	2.7	2.8	2.7	2.8	0.1	N	73.5	69.9	78.9	76.6	3.8	N	N	N	N
Faller	2.8	3.0	2.8	3.1	0.1		73.1	74.0	82.2	74.1	4.3				
Reeder	2.6	2.8	2.6	2.8	0.1		74.4	75.2	79.6	73.2	3.8				
Dapps	2.7	2.9	2.7	2.9	0.1		77.5	70.2	79.6	75.7	4.6				
Glenn	2.7	2.9	2.7	2.9	0.1		81.6	77.9	77.6	82.7	4.2				
SxN101	2.8	3.0	2.7	2.9	0.1	N	73.5	68.8	83.4	72.9	7.9	N	N	N	N
SxN141	2.8	2.9	2.7	2.8	0.1	S	69.3	67.8	77.8	72.4	5.0	N	S	N	N
SxN033	2.7	2.9	2.8	2.8	0.1	N	80.9	75.8	80.7	80.7	4.5	N	S	S	N
SxN161	2.7	3.0	2.8	3.0	0.1	S	73.6	69.0	77.5	70.2	4.0	N	S	N	N
SxN095	2.8	3.0	2.7	2.9	0.1	S	69.3	70.7	81.0	74.4	5.6	S	N	N	N
SxN001	2.7	2.8	2.7	2.8	0.1	N	84.1	83.7	88.3	85.7	3.3	N	S	N	N
SxN159	2.7	3.0	2.8	2.9	0.1	S	71.3	69.7	76.6	71.8	3.5	N	N	N	N
SxN009	2.8	3.0	2.8	3.0	0.1	N	75.7	70.2	82.6	74.8	5.0	N	N	N	N
SxN060	2.6	2.9	2.7	2.8	0.1	S	88.2	78.8	92.3	83.1	6.2	S	N	S	S
SxN097	2.6	3.0	2.7	2.8	0.2	S	74.9	70.2	81.6	78.2	4.7	N	N	N	N
SxN104	2.8	2.9	2.8	2.9	0.1	N	71.7	66.6	71.7	72.7	3.2	N	N	N	N
SxN108	2.8	2.9	2.7	2.8	0.1	N	86.5	78.1	82.4	78.3	7.8	S	N	S	.

Table 2 (continued)

Plant ID	Mixograph peak time (min) [1]					QTL [2]		Grain protein content (%) [1]					Disease response [3]			
	CR08	**CR09**	PR08	PR09	StD	7B	2B	CR08	CR09	PR08	PR09	StD	5B.1	5B.2	2B	Phen
Steele-ND	5.8	4.1	5.5	5.0	1.1	S	S	15.9	15.6	15.3	15.1	0.4	S	S	S	R
ND735	6.8	7.7	8.1	10.1	2.2	N	N	15.7	14.4	15.0	14.6	0.7	N	N	N	r
Faller	6.5	4.3	5.2	5.7	0.9			14.8	14.7	14.7	14.3	0.2				
Reeder	5.1	4.3	5.0	5.4	0.5			15.8	14.2	14.7	14.7	0.6				
Dapps	5.6	3.4	5.0	5.7	1.1			16.7	17.1	16.2	15.2	0.8				
Glenn	6.8	5.1	7.4	9.3	1.7			15.9	15.9	15.8	14.7	0.6				
SxN101	9.2	7.6	8.4	11.1	1.4	N	N	14.9	15.0	14.1	14.2	0.4	S	S	N	r/R
SxN141	7.4	6.2	8.0	9.5	2.0	S	N	15.2	15.8	14.9	15.0	0.4	S	S	S	r
SxN033	7.1	5.3	7.7	6.7	1.4	S	N	15.3	14.7	15.3	14.8	0.4	N	N	N	R
SxN161	6.1	3.8	5.3	6.2	1.2	S	S	15.3	15.8	14.6	14.8	0.5	S	S	S	r
SxN095	5.9	4.9	9.3	7.7	2.1	S	S	16.3	17.1	15.6	15.3	0.8	S	S	S	r
SxN001	6.8	5.8	5.7	8.5	1.5	S	N	15.3	14.9	14.9	14.9	0.4	N	N	N	R
SxN159	7.4	4.7	5.4	7.5	1.4	S	N	14.9	15.0	14.4	14.4	0.3	S	S	N	r/R
SxN009	7.5	5.0	7.0	6.5	1.5	N	N	15.6	15.7	14.9	15.0	0.4	N	N	N	R
SxN060	5.1	3.7	5.8	5.1	0.9	N	S	15.9	16.8	15.9	15.0	0.7	N	N	N	R
SxN097	10.7	7.0	10.7	11.5	1.9	N	N	15.1	15.6	14.8	14.0	0.7	S	S	N	r/R
SxN104	4.7	3.0	4.5	5.1	0.9	N	S	16.4	16.6	15.7	15.8	0.4	N	N	S	R/r
SxN108	7.3	4.7	7.0	6.4	1.2	N	S	15.3	15.3	14.5	14.4	0.5	N	N	S	R/r

1 In each environment (CR, Carrington; PR, Prosper; 08, 2008; 09, 2009) data are presented as average between two replications.
2 QTL, the chromosome of appurtenance is indicated and for each genotype the corresponding allele is provided (S for 'Steele ND'-like allele, N for 'ND 735'-like allele).
3 As measured in Singh et al. 2010, 2011 and Harilal et al. 2012 for *Pyrenophora tritici-repentis, Phaeospheria nodorum*, and *Mycosphaerella graminicola*; Phen, phenotype; R, resistance; r, susceptibile.

Table 3. Chromosomal location of 13 QTLs identified for 6 traits in a 'Steele-ND' x 'ND 735' RIL populations across four environments in North Dakota, USA.

Trait.	Chr.	Peak (cM)	Flanking markers	LOD	R^2 (%)	Add.	H^2 (%)	Env.
GY	5A	58.5	*Xwpt4131 - X344239*	3.53	27	-252.0	63.5	PR08
	6B	0.0	*Xwpt9881 - Xwpt9270*	2.79	22	-243.1	63.5	PR08
TKW	5A	58.4	*Xwpt4131 - X344239*	2.53	16	-3.1	82.8	PR09
	6B	2.1	*Xwpt9881 - Xwpt9270*	3.35	19	-3.4	82.8	PR09
KNS	5A	58.1	*Xwpt4131 - X344239*	2.81	27	-3.6	33.7	PR09
	6B	2.7	*Xwpt9881 - Xwpt9270*	4.04	20	-3.2	33.7	PR09
KD	3B	17.5	*X343926 - Xwpt1081*	2.50	23	0.1	80.0	CR08
KH	5A	131.8	*Xwmc475 - X345412*	2.67	23	3.5	89.0	CR08
	7B	5.9	*Xwmc723 - Xwpt5463*	2.57	23	-3.3	89.0	CR09
	1A	136.5	*Xwpt3698 - Xwmc312*	2.79	25	3.3	89.0	PR09
	7A	44.5	*Xbarc222 - Xwpt1076*	2.56	26	-3.2	89.0	PR09
MPT	7B	15.6	*Xwmc723 - Xwpt8106*	3.40	44	1.3	85.2	CR09
	2B	23.3	*Xwmc382 - Xwpt8004*	2.80	26	0.9	85.2	PR08

GY, grain yield; TKW, thousand kernels weight; KNS, kernel number per spike; KD, kernel diameter; KH, kernel hardness; MPT, mixograph peak time; CR, Carrington; PR, Prosper; 08, 2008; 09, 2009; Chr., chromosome; Add., additive effect; H^2, broad sense heritability; Env., significant environments.

had heritability values similar but higher than what was previously reported Thus, suggesting a good response to selection for these traits. This is consistent with the breeding purpose of this population that aimed to generate novel lines with improved disease resistances (Singh et al. 2011), maintaining the agronomic performance of the parents, while improving the quality traits. On the other hand, DTH, FE (Smith et al. 2011) and KNS (Marza et al. 2006) had heritability values lower than what were previously reported, indicating that this population would not respond well to selection for these traits. The transgressive segregation and high heritability traits were used to identify the twelve best performing RILs on the basis of disease resistance, GY, GP, TKW, MPY, KH, LSK, KD, SL and PH (Table 2).

Identification of QTL for economic traits using elite by elite population: The progenies of the S x N cross proved to be an excellent material for breeding purposes. However, the narrow genetic diversity between the two elite parents weakened the power of the QTL analysis. In fact, the two parents segregate for a limited number of traits, making QTL discovery challenging. While QTL discovery in broad based populations often provides good statistical significance with QTLs showing high LOD values and their effectiveness across environments (Collard and Mackill 2008). In elite by elite populations, the parents segregate minimally for most of the valuable traits (i.e. yield and quality traits), still progenies that outperform the parents are usually identified and selected for breeding purposes. This type of segregation is transgressive in nature, since its origin cannot be easily attributed to one of the two elite parents. Hence, the search for QTLs governing this phenotypic transgressive segregation is then a search for QTLs harboring those alleles with minor effects that additively contribute to the genetic gain sought by breeders through selection. In this study, thirteen QTLs were identified for six traits, four of which (GY, TKW, KNS, and KD) did not show any significant PV between the two parents (Table 2). Although all QTLs were environment-specific and explained more than 16% of PV. The four traits for which no phenotypic segregation was observed among the parents were associated to just three chromosomal regions. In particular, grain yield (GY) and its components (TKW and KNS) were associated to only two QTLs on chromosomes 5A and 6B and in only one location (PR) in both years. This location is the highest yielding of the two tested environments. All the S x N lines that carry the N allele at these two QTLs yielded more than both the parents.

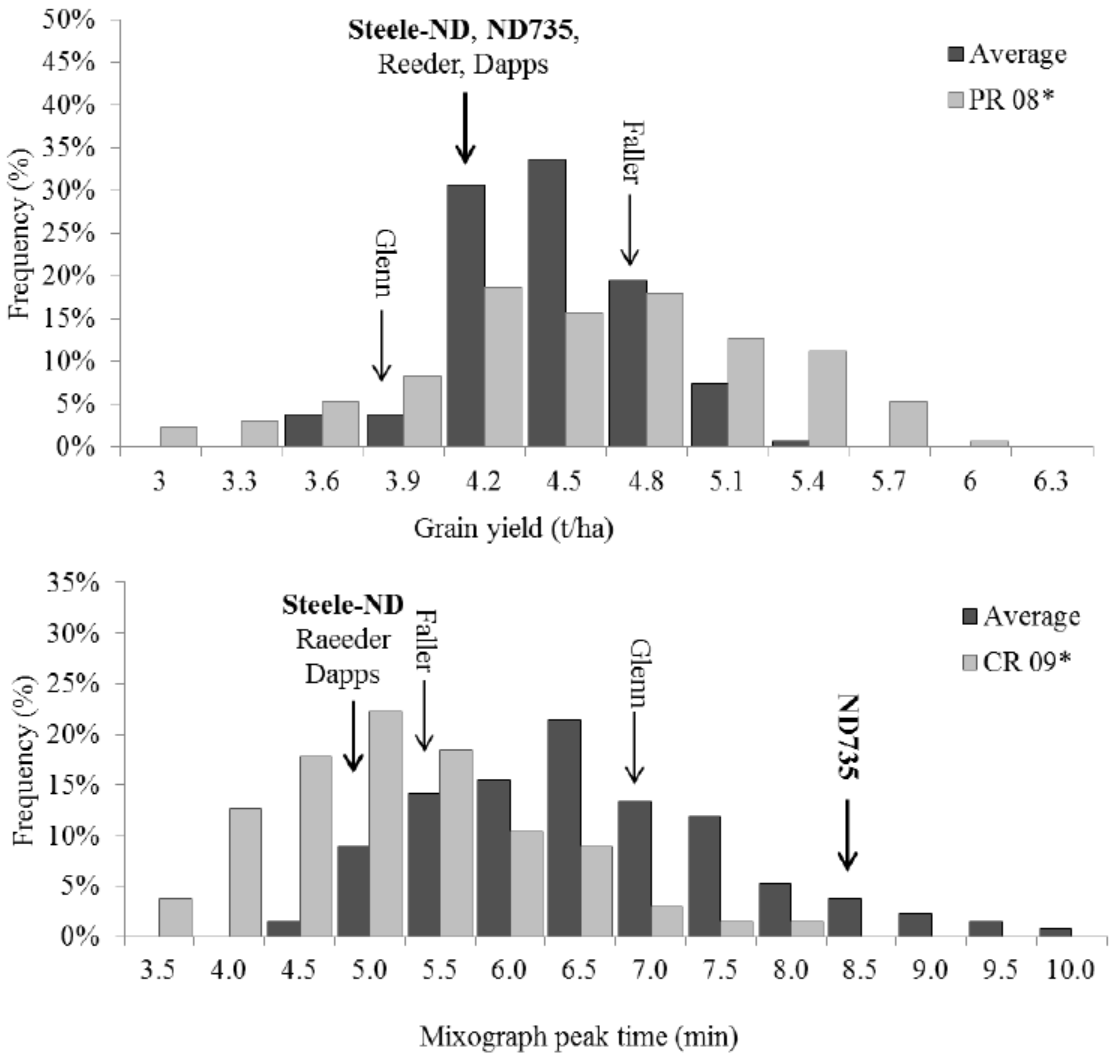

Figure 1. Frequency distribution of grain yield (top) and mixograph peak time (bottom) in the 'Steele-ND' x 'ND 735' population, across four environments in North Dakota, USA (dark grey) and for the environment for which a major QTL was found (light grey; PR08, Prosper 2008; CR09, Carrington 2008). The average values of the checks and the parents (bold) are indicated on the figure.

The chromosome locations of both QTLs (distal of *Xgwm433* on 5A, and close to the telomere of 6B) have been identified previously for association with yield-related traits (Huang et al. 2006; Marza et al. 2006; Wu et al. 2012), employing both narrow and broad base mapping populations. TKW and KNS appear as the primary traits controlled by these loci. Thus, making these regions as ideal targets for molecular breeding and fine mapping.

The present study also identified a QTL on chromosome 3B for KD that mapped in close proximity of a major QTL for test weight in durum (Qtgw.ics-3BS; Elouafi and Nachit, 2004). However, to the best of our knowledge, this is the first time that a QTL for KD *per se* has been identified on chromosome 3B, and thus, may represent a novel QTL. Following the wheat standard nomenclature (McIntosh et al. 2011) we propose to designate this QTL as QKD.ndsu-3B. This QTL was identified only in CR08, but the presence of the S allele increased kernel diameter by 23%, making it a potentially valuable allele for molecular breeding, especially when aimed at developing cultivars for the targeted environment. The KH is an important quality trait that positively affects flour yield (Bassett et al. 1989). This study found four QTLs for KH on chromosomes 7A, 5A, 7B, and 1A.

Fig. 2.1

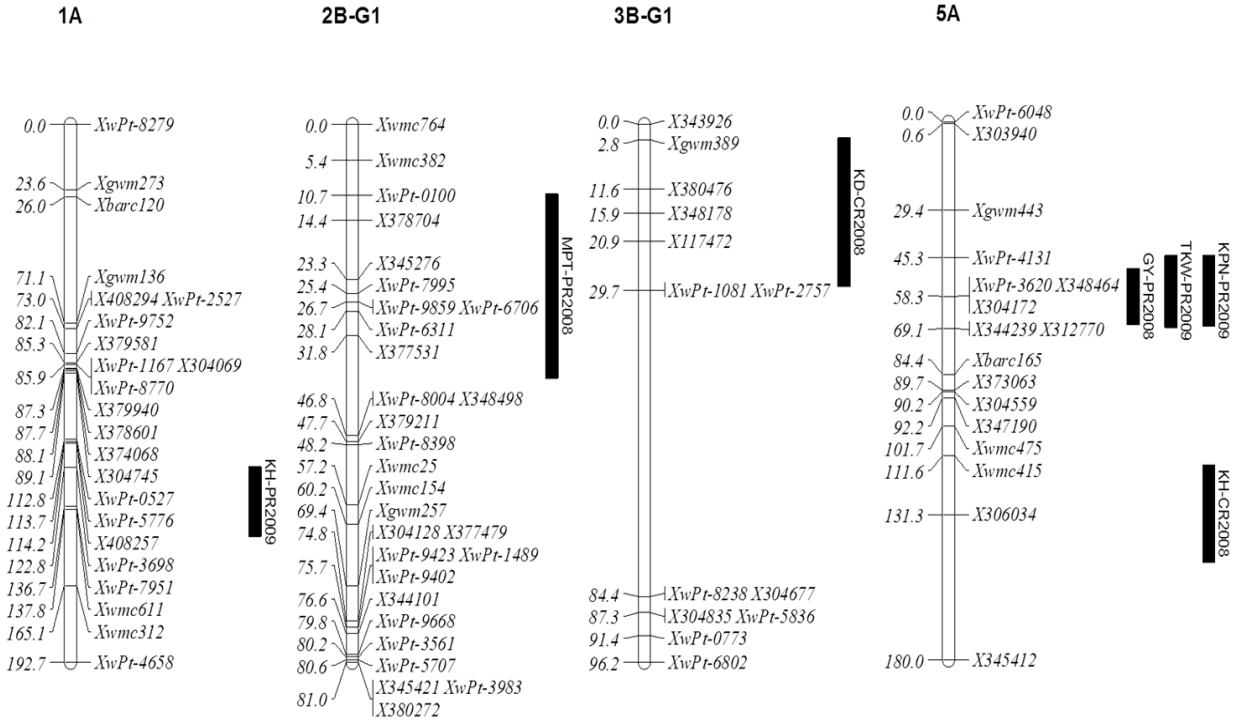

Fig. 2.1

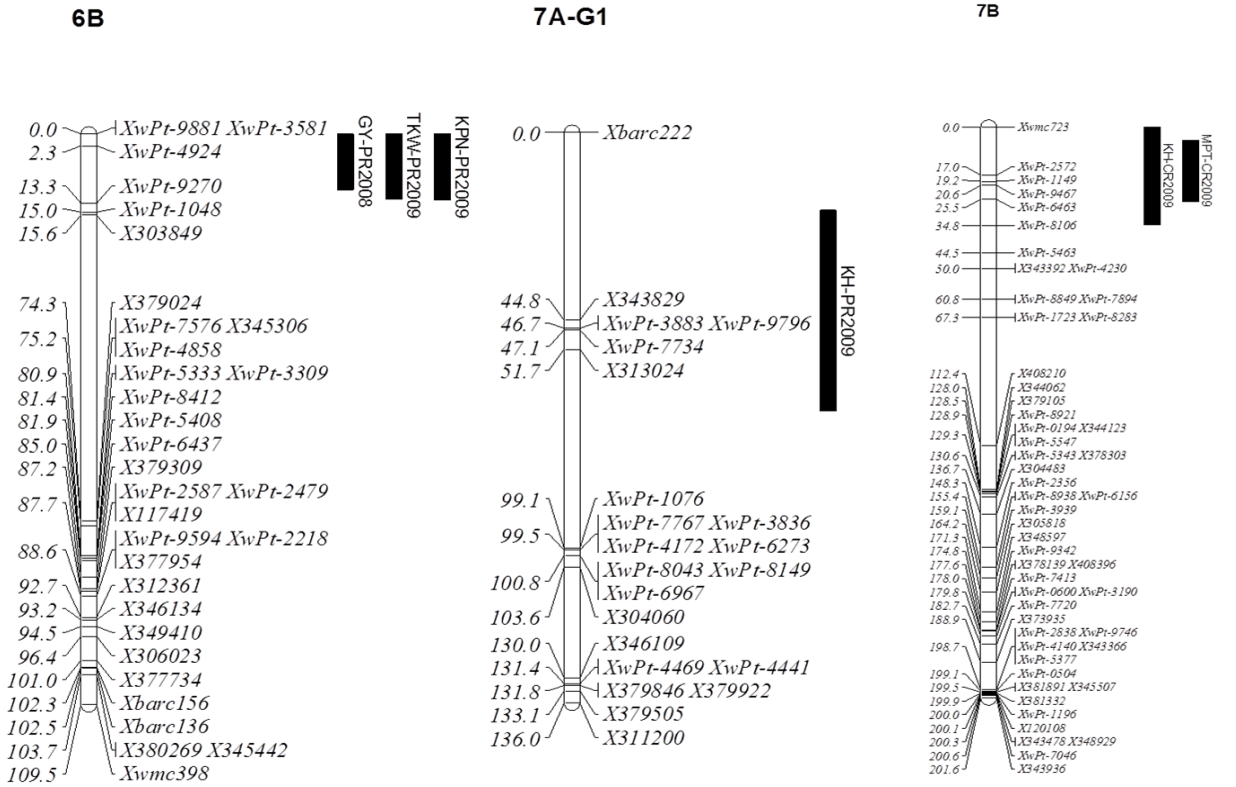

Figure 2. Map location of QTL identified for six traits evaluated in four environments in North Dakota, USA, using a RIL population derived from 'Steele-ND' × 'ND 735' cross. The black bars indicate regions of significant LOD. Abbreviations for traits are KD, kernel diameter; KH, kernel hardness; MPT, mixograph peak time; TKW, thousand-kernel weight; KPN, kernel per spike; GY, grain yield. Abbreviations for environment are CR, Carrington; PR, Prosper.

The elite parents -used to generate the S x N populations are minimally polymorphic along their D chromosomes (Mergoum et al. 2009a), and likely do not segregate for the *Ha* locus on chromosome 5DS, known as the primary regulator of kernel hardness in wheat (Campell et al. 2001; Nelson et al. 2006; Souza et al. 2012). Sun et al (2010) also reported minor QTLs affecting the KH apart from the major *Ha* locus. Among those, a region of chromosome 7A was common with what is reported here. The QTL for KH identified in the S x N populations as distal of *Xwmc475* on chromosome 5AL was also recognized in a HRSW elite by elite RIL populations adapted to the environmental conditions of Northern Great Plains (QSkhard.mna-5A.2; Tsilo et al. 2011b). Chromosome 7B does not harbor any known KH QTLs *per se*. However, Tsilo et al. (2011a) identified a flour quality related QTL (QFash.mna-7B) in the same region proximal of *Xwpt8106*, in an elite by elite HRSW RIL population adapted to the same environmental conditions used in this study. The remaining QTL for KH on chromosome 1A has not so far been reported. This novel QTL has temporarily designated as QKh.ndsu-1A and it could be specific to the genetic background of the two HRSW parents.. The parental lines segregate largely for KH, with alleles for harder kernels on chromosomes 7B and 7A from 'Steele-ND' and alleles for soft kernels on 1A and 5A contributed by 'ND 735'. All of these QTLs are environment-specific and were expressed in three of the four test sites.

Two QTLs for MPT were mapped to the B genome (2B and 7B). The QTL on 2B covers the same chromosomal region identified as harboring an unlabeled QTL for bread making quality in a French elite by elite RIL populations (Gross et al. 2007). In the absence of a pre-established name, we temporarily designate this QTL as QMpt.ndsu-2B. The QTL for MPT on 7B overlapped with the QTL for KH (QFash.mna-7B). This is likely due to the inverse relationship that exists between KH and MPT, with harder kernels typically having shorter MT (Table 2) (Ohm and Chung 1999). Complex interactions exist between the loci controlling quality traits, probably not just at the genetic level *per se* but also because of the specific process of flour and dough handling (Ohm and Chung 1999). Similarly to the often observed negative correlation between yield and GPC (Table 2) (Mergoum et al. 2009b), KH and MPT also inversely interact to present an additional challenge to breeders. Harder kernels have a structural advantage against harvest and threshing damages, but simultaneously produce flours of lower quality, poorer gluten components, and shorter dough MT (Ohm et al. 2009). The 7B QTL was the most important for both traits, with up to 44% increase in MPT and 22% KH reduction when the N allele was present at the QTL interval. Specific combinations of soft/long peak and hard/short peak alleles (S or N) in the KH and MPT QTL could be tested. Ideal combinations could be identified by crossing the various S x N RILs and ultimately combined into a superior genotype with the desirable balance between hardness and baking quality.

The overall low number of QTLs identified in this study for the 14 traits analyzed is likely due to the narrow genetic variability of the parents used to create this population. However, the alleles at the QTL that have been identified are transgressive in nature and were detected under the unique environmental conditions of North Dakota, one of the most productive wheat regions in the world. Thus, the markers tagged to these QTLs provide an excellent selection tool for commercial molecular breeding within the S x N populations.

Selection for the "reserve" alleles within population: The QTL that were identified in the course of this work lack consistency across environments and we would not recommend the markers underlying them for marker assisted selection (MAS) in populations lacking 'Steele-ND' or 'ND 735' in their pedigrees (Collard and Mackill 2008). However, these QTLs are significant for the S x N progenies and can be directly employed for molecular selection within the population. To a lesser extent, this can be considered as an extrapolation of the concept of 'mapping as you go' (Podlich et al. 2004), with the mapping limited only to the selection generation.

Among the S x N lines, 12 RILs were considered as superior on the basis of their performances, including S x N101, S x N141, S x N033, S x N161, S x N159 and S x N108. All these lines carry the favorable N allele at two of the yield QTLs, but only three had the advantageous S allele for KD on chromosome 3B. The introduction of the S allele in the other three lines can help to further boost their yields. All lines had extended MPT, but only four had the advantageous N allele in 2B QTL. Only one line (S x N108) combined good KH and extended MPT. Similarly, only one line maintained GPC similar to 'Steele-ND'.

The alleles described above are not active under all environmental conditions, with QTLs identifiable only in determined locations by years combinations. From a breeding prospective, the alleles for agronomic or quality environment-specific QTLs are not less important than resistance loci against non-endemic pathogens, which become valuable only when the diseases occur. These genes become active and detectable only in specific environmental conditions, but at that time they provide additional yield, or better quality characteristics or resistance in the case of the disease. Given their ability to boost and help the genes controlling the trait only under determined ambient conditions, we defined these as "reserve" alleles.

Because of their eclectic nature, field selection is not likely to provide the finesse necessary to follow these "reserve" alleles. On the other hand, it is demonstrated that an environment-specific QTL analysis provide the statistical means to identify the advantageous "reserve" alleles in an elite by elite population. The allele values at the 13 environment-specific QTLs were included as criteria in the selection to identify five lines harboring the maximum number of advantageous "reserve" alleles (S x N001, S x N033, S x N101, S x N141, S x N161). Additionally, in Table 2 we reported the alleles carried by the S x N lines at the three major QTLs controlling resistance to leaf spotting diseases as established in Singh et al. (2010 and 2011) and Harilal et al. (2012). The presence of the resistance N allele at these QTLs was also added as criteria in the selection. The S x N001 and S x N033 are the only lines harboring the resistant N allele at all three loci. All five selected lines have been advanced and used in our HRSW breeding program. The particular attention is being given on lines S x N033 and S x N001, as they carry alleles for disease resistance, good yield, and good quality. Also, these five S x N lines represent a good starting point to design targeted new crosses for pyramiding the most useful loci into superior genotypes. Wheat growers and end-users are certain to appreciate cultivars combining disease resistance alleles together with these "reserve" alleles under the specific environmental conditions.

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