Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

Molecular Markers Linked to Genes Important for Hard Winter Wheat Production and Marketing in the U.S. Great Plains

Shuyu Liu*, Jackie C. Rudd, Guihua Bai, Scott D. Haley, Amir M.H. Ibrahim, Qingwu Xue, Dirk B. Hays, Robert A. Graybosch, Ravindra N. Devkota, and Paul St Amand

Shuyu Liu, Jackie C. Rudd, Qingwu Xue, and Ravindra N. Devkota, Texas A&M AgriLife Research, Amarillo, TX 79106; Guihua Bai and Paul St Amand, USDA-ARS Central Small Grain Genotyping Laboratory and Hard Winter Wheat Genetics Research Unit, Manhattan, KS 66506; Scott D. Haley, Soil and Crop Sciences Dept., Colorado State University, Fort Collins, CO 80523; Amir M.H. Ibrahim and Dirk B. Hays, Soil and Crop Sciences, Texas A&M University, College Station, TX 77843; Robert A. Graybosch, USDA-ARS, University of Nebraska, Lincoln, NE, 68583. *Corresponding author (SLiu@ag.tamu.edu).

Abbreviations: APR, adult plant resistance; Cmc, curl mite colonization; EST, expressed sequence tag; GAI, gibberellic acid insensitive; GB, greenbug; GS, glutenin subunit; HMW, high molecular weight; Hf, hessian fly; KASPar, KBioscience competitive allele-specific polymerase chain reaction; LMW, low molecular weight; Pin, puroindoline; Ppd, photoperiod; PPO, polyphenol oxidase; QTL, quantitative trait loci; RAPD, randomly amplified polymorphic DNA; Rht, reduced height; RWA, Russian wheat aphid; SNP, single nucleotide polymorphic; SSR, simple sequence repeat; STS, sequence tagged site; SRPN, southern regional performance

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nursery; TriMV, triticum mosaic virus; WCM, wheat curl mite; WSMV, wheat streak mosaic virus.

ABSTRACT

Biotic stresses including diseases [leaf, stem and stripe rusts], arthropods [greenbug (GB), Hessian fly (Hf), Russian wheat aphid (RWA), and wheat curl mite (WCM)] and their transmitted viral diseases significantly affect grain yield and end-use quality of hard winter wheat (*Triticum aestivum* L.) in the U.S. Great Plains. Many genes or quantitative trait loci (QTL) have been identified for seedling or adult plant resistance to these stresses. Molecular markers for these genes or QTL have been identified using mapping or cloning. This study summarizes the markers associated with various effective genes including genes or QTL conferring resistances to arthropods, such as GB (7), RWA (4), Hf (9), and WCM (4) and diseases including leaf, stem and stripe rusts (26) and *Wheat streak mosaic virus* (WSMV) (2); genes or QTL for end-use quality traits such as high (3) and low (13) molecular weight glutenin subunits, gliadin (3), polyphenol oxidase (2), granule-bound starch synthase (3), puroindoline (2), and pre-harvesting sprouting (1); genes on wheat-rye (*Secale cereale* L.) chromosomal translocations of 1AL.1RS and 1BL.1RS; and genes controlling plant height (12), photoperiod sensitivity (1), and vernalization (2). A subset of the markers was validated using a set of diverse wheat lines developed by breeding programs in the Great Plains. These analyses showed that most markers are diagnostic in only limited genetic backgrounds. However, some markers developed from the gene sequences or alien fragments are highly diagnostic across various backgrounds, such as those marking or linked to *Rht-B1*, *Rht-D1*, *Ppd-D1*, *Glu-D1*, *Glu-A1*, and 1AL.1RS. Knowledge of both genotype and phenotype of advanced breeding lines could help

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

breeders to select the optimal parents to use to integrate various genes into new cultivars and increase the efficiency of wheat breeding.

Keywords: wheat, curl mite colonization, greenbug, Hf, hessian fly, quantitative trait loci, reduced height, Russian wheat aphid, single nucleotide polymorphic, wheat streak mosaic virus, end-use quality.

Winter wheat (*Triticum aestivum* L.) is one of the major crops in the U.S. Great Plains. About 40% of the total 20 million hectares U.S. harvested wheat and more than 50% of the total 48 million metric tones U.S. wheat production are hard red winter wheat produced in the Great Plains (http://www.nass.usda.gov/, accessed March 6, 2013). Many biotic stresses including fungal and bacterial diseases, and arthropods limit wheat production in the region. Many genes or quantitative trait loci (QTL) have been identified conditioning resistance or tolerance to these pests and molecular markers associated with these genes or QTL have been mapped and applied in breeding (Supplementary Table S1, Fig. 1).

Arthropod and Virus Resistance

Various arthropods can be very detrimental to wheat by themselves or through synergistic effects with their transmitted plant pathogens. The resistance genes to three major insects in wheat including greenbug [GB, *Schizaphis graminum* (Rondani)], Russian wheat aphid [RWA, *Diuraphis noxia* (Mordvilko)], and Hessian fly [Hf, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae)] in the Great Plains have been studied and deployed in some wheat germplasm lines and cultivars (Supplementary Table S1, Fig. 1). Seven resistance genes to GB, designated

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gb1 to *Gb7,* have been identified from different sources (Lu et al., 2010). *Gb3* from 'Largo' shows a wide spectrum resistance to GB and co-segregated with marker Xwmc634 on chromosome 7DL (Joppa and WIlliams, 1982; Weng et al., 2005). After the *Gb3* region was saturated with 30 molecular markers in a different population, *Gb3* was found to be 37.3 cM away from Xwmc634 while Xbarc111 was the closest simple sequence repeat (SSR) marker at 4.8 cM proximal to *Gb3* (Azhaguvel et al., 2012). 'TAM 112' (PI 643143, PVP 200600274) released by Texas A&M AgriLife Research has *Gb3* (http://apps.ams.usda.gov/CMS//AdobeImages/200600274.pdf, accessed on May 23, 2013). *Gb7* from the synthetic line W7984 is linked to *Gb3* (Weng et al., 2005). In addition, six other genes including *Gbx1* from KS89WGRC4, *Gbz* from KSU97-85-3, *Gba* from TA4152L94, *Gbb* from TA4152L24, *Gbc* from TA4063.1, and *Gbd* from TA4064.2 were also mapped on the same chromosome region as *Gb3* (Zhu et al., 2005). The SSR markers Xwmc671 and Xbarc53 or Xwmc157 flank all of these six genes, suggesting that these genes are either linked or allelic to *Gb3* (Zhu et al., 2004; Weng et al., 2005; Azhaguvel et al., 2012). However, *Gbz* in KSU97-85-3 is not allelic to *Gbd*, indicating at least one of them is not allelic to *Gb3*. In addition, three chromosomal translocation lines, CI 17882, CI 17884, and CI 17885, showed resistance to GB biotype E (GBE) (Wells et al., 1973, 1982; Tyler et al., 1985), which might come from *T. speltoides* or from mutation induced by irradiation (Tyler et al., 1985).

Among 10 genes that were mapped for RWA resistance, *Dn7*, which is the same as *Dn2414* from ST-ARS02RWA 2414-11, showed a wide spectrum of resistance (Collins et al., 2005; Peng et al., 2007). *Dn7* from rye (*Secale cereale* L.) 1RS located on the translocation of 1BL.1RS of 94M370 and *DnCI2401*, from CI 2401 on chromosome 7DS, are two genes resistant to all known U.S. RWA biotypes (Anderson et al., 2003; Haley et al., 2004; Weiland et al., 2008).

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Two rye-specific sequence tagged site (STS) markers, Xrems1303 and Xib267, flank *Dn7* at 6 cM interval on 1RS (Lapitan et al., 2007). Single nucleotide polymorphism (SNP) marker Owm701 was designed to detect *DnCI2401* (Stankova et al., 2013; http://olomouc.ueb.cas.cz/system/files/users/public/stoces_65/Poster/2011_G4G_Helca.pdf , accessed on April 10, 2013). *Dn6* from PI 243781 on chromosome 7DS is either allelic or linked to several other genes including *Dn1*, *Dn2*, *Dn5* and *Dnx* (Liu et al., 2001, 2002). Allelism tests indicated that these five genes might be allelic to RWA resistance genes in PI 47545, PI 222666, PI 222668, and PI 225245 (Liu et al., 2005a). Another single dominant gene, *Dn626580*, was mapped onto chromosome 7DS of an Iranian wheat landrace accession, PI 626580, which showed resistance to both RWA biotype 1 and 2 (Valdez et al., 2012).

At least 33 genes for resistance to Hessian fly have been identified. However, only a few, namely *H13*, *H25*, *H26*, and *Hdic*, are still utilized in wheat breeding (Supplementary Table S1, Fig. 1). *H13* in Molly (Liu et al., 2005b, 2005c), *H23* in KS89WGRC03 (Ma et al., 1993; Gill et al., 1991a), and H_{WGRC4} in KS89WGRC04 for biotype D (Gill et al., 1991b) were mapped on chromosome 6DS. *H26* in SW8 was on the distal end of chromosome 3DL and confers resistance to biotypes L, GP and vH13 (Wang et al., 2006). Saturation mapping in the *H26* region identified two flanking markers, Xrwgs10 and Xrwgs12, in a 4.2 cM interval (Yu et al., 2009, 2010a). *H32* from the synthetic line W7984 flanked by Xgwm3 and Xcfd223 on 3DL confers resistance to biotype B, C, D, E, L, O, vH9 and vH13, but is susceptible to the least virulent biotype GP (Sardesai et al., 2005). *H24* in KS89WGRC6 flanked by Xcdo482 and Xbcd451 was also mapped on 3DL (Ma et al., 1993). The order of the three genes on 3DL is *H26, H24*, and *H32* from proximal to distal. KS99WGRC42 carries a gene *Hdic* derived from PI 94641, an emmer wheat line [*Triticum turgidum ssp*. *dicoccum* (Schrank ex Schubler) Thell]

(Liu et al., 2005c), and showed a wide spectrum of resistance to Hf biotypes GP, L, vH9 and vH13. *Hdic* was mapped on the distal portion of 1AS and flanked by Xcfa2153 and Xgwm33 at 2 cM apart. A set of genes including *H3*, *H5*, *H6*, *H9*, *H10*, *H11, H12*, *H14*, *H15*, *H16, H17, H19*, *H28,* and *H29* were all mapped on the same 1AS chromosome region (Liu et al., 2005d; Kong et al., 2005, 2008). Among them, *H5* and *H11* are ineffective against biotype L while *H9* and *H10* are ineffective against biotype vH9. Better diagnostic markers for effective genes need to be developed, validated in diverse backgrounds, and applied in breeding programs.

Four curl mite colonization (*Cmc*) genes, *Cmc1*, *Cmc2*, *Cmc3* and *Cmc4,* are known to provide resistance to wheat curl mite (WCM, *Aceria tosichella* Keifer) (Malik et al., 2003), the vector of *Wheat streak mosaic virus* (WSMV). *Cmc1* from *Aegilops tauschii* (Coss.). Schmal. (syn. *Ae. squarrosa* L.; *Triticum tauschii*) was located on chromosome 6DS (Thomas and Conner, 1986; Whelan and Thomas, 1989). *Cmc2* was derived from *Agropyron elongatum* (Martin et al., 1976; Whelan and Hart, 1988). *Cmc3* is on the 1AL.1RS wheat-rye translocation from the germplasm line Amigo (PI 578213; Sebesta et al., 1995) while *Cmc4* is also on 6DS of wheat but at a different locus than *Cmc1* (Malik et al., 2003). The germplasm line KS96WGRC40 carries both *Cmc3* and *Cmc4* (Cox et al., 1999). All WCM collections in KS, MT, and NE are avirulent to *Cmc4* but the NE collection is virulent to *Cmc1* and the KS collection is virulent to *Cmc3* (Malik et al., 2003). *Cmc3* from Amigo can be tagged with the rye-specific marker Xscm9 (Malik et al., 2003). *Cmc4* is dominant and confers resistance to six known collections of WCM. *Cmc4* was mapped on the distal end of chromosome 6DS, and linked proximally to Xgdm141 (4.1 cM) and distally to XksuG8 (6.4 cM). With closely linked markers available, marker-assisted selection for *Cmc3* and *Cmc4* is possible to increase the efficiency of transferring these

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

resistance genes into new cultivars in the Great Plains where WCM and WSMV are endemic problems.

WCM is a vector for WSMV. 'Mace' and KS93WGRC27 are resistant to WSMV and contain *Wsm1* that was transferred from KS91H184, a derivative of a translocation line, CI 17884 (Gill et al., 1995; Graybosch et al., 2009). CI 17884 was derived from CI 15092, a disomic substitution line that carries a fragment from *Ag. intermedium* (syn. *Thinopyrum ponticum*) (Wells et al., 1982). *Wsm1* was located on chromosome translocation 4DL.4AgS. A marker STSJ15 with the target PCR fragment of 241 bp, is diagnostic for this gene (Talbert et al., 1996; Seifers et al., 2006). Several new markers based on expressed sequence tag (EST) sequences from wheat chromosome 4DS were reported (Qi et al., 2007) and the STS marker XBG263898 is also used to screen for *Wsm1*. A hard winter wheat breeding line, CO960293-2 (PI 615160), was also found to be resistant to WSMV (Haley et al., 2002). This line carries *Wsm2,* which is closely linked to Xbarc102 at 2.4 cM distance (Lu et al., 2011, 2012). *Wsm2* has been deployed in wheat cultivars, RonL and Snowmass (Seifers et al., 2007; Haley et al., 2011). *Wsm1* also confers resistance to Triticum mosaic virus (TriMV), but *Wsm2* does not (Lu et al., 2011). However, *Wsm2* is derived from wheat so it is easier to be utilized in the development of WSMV resistant cultivars than *Wsm1* from alien fragment. Both WSMV and TriMV can impact wheat production and their synergistic effects can be devastating (Tatineni et al., 2010; Byamukama et al., 2012), especially when they occur with drought conditions that are typical in many areas of the U.S. Great Plains.

To validate marker associations with some insect resistance genes, a collection of 55 lines with known pest resistance genes were screened with previously reported markers for these genes (Supplementary Table S2, Supplementary Fig. S1, http://www.ars-grin.gov/cgi-

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bin/npgs/html/csr.pl?WHEAT, accessed on August 1, 2012). The marker data were collected in the wheat breeding laboratory of Virginia Tech at Blacksburg, VA and USDA-ARS Eastern Regional Small Grains Genotyping Lab at Raleigh, NC using ABI3130xl. Marker screening procedures followed protocols from Liu et al. (2013b). Results showed that Xwmc671.120 linked to *Gbx1* and Xgwm397.170 linked to *H25* are diagnostic. Some markers may be diagnostic when donor lines are carefully chosen. They include Xwmc634.227 linked to *Gb3*; Xwmc157.150 linked to *Gbx1* and *Gbz*; Xgwm610.170 linked to *H25*; and Xrwgs10.837 and Xrwgs12.270 linked to *H26*. Most of the remaining markers are either only informative between the parents of original mapping populations or in a limited number of lines.

A set of 174 advanced winter wheat breeding lines from the USDA-ARS coordinated Southern Regional Performance Nursery (SRPN) from 2008 to 2012 were screened with markers linked to various genes at the USDA-ARS Central Small Grain Genotyping Laboratory, Manhattan, KS, following the protocol from Bernardo et al. (2013) (Supplementary Table S3, Supplementary Fig. S2). The SRPN contains the most advanced experimental lines from most Southern Great Plains hard winter wheat breeding programs. Results showed that only one line carries the marker allele associated with *H13*, ten have the marker allele associated with *H9*, and three have the marker allele associated with *Wsm1*. Markers linked to genes for resistance to RWA and GB were not screened on SRPN lines; however, evaluation of resistance of the lines was done with artificial infestation in standard greenhouse screening tests (http://www.ars.usda.gov/Research/docs.htm?docid=11932, accessed on December 10, 2012). Among the 174 SRPN lines tested over the five year period, only six lines have resistance to RWA, three lines are resistant to GB, and 13 lines are resistant to Hf. Three RWA resistant lines including CO03W139, CO50270, and 'Cowboy' (PI 668564; Haley et al., 2014) have *Dn4* while

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line OK03825-5403-6 (ST-ARS0601W) has *Dn7*. The sources of RWA resistance in lines, TX05A001398 and CO04393 were unknown. GB resistance was identified in TX06V7266 and two TAM 112-derived lines TX08A001128 and TX08A001249. The two TAM 112-derived lines have *Gb3,* but the source of resistance in TX06V7266 is unknown. Four lines from OK, including Gallagher (PI 667569, PVP 201300134), OK04315, OK08328, and OK08229, showed complete resistance to Hf biotype GP with the first three tracing back to the cultivar Duster or its ancestor (B. Carver, personal communication, 2013). Four lines, TX04M410164, LCH08-80 (LCS Wizard), NI08708, and BL11001 are resistant to Hf with line CO980829 as the source of resistance in the pedigree of the last two lines (http://www.ars.usda.gov/Research/docs.htm?docid=11932, accessed on May 1, 2013). In five lines, not all the tested plants showed complete resistance. Three Westbred lines HV9W04-1186W, HV9W04-1594R, and HV9W07-1028 , as well as in lines KS06HW46-3 and TX06V7266 had only about 90% to 95% of tested plants showing resistance to Hf. The line T150-1 from Trio is resistant to both GB and Hf. Overall, only a few adapted advanced hard winter wheaat breeding lines have insect resistance. A diagnostic SNP marker for *DnCI2401* and a rye specific marker for *Dn7* are available. Perfect SNP markers for *Gb3* are under development (S.Y. Liu, unpublished data, 2013). More effort is needed for the development of diagnostic markers for effective Hf-resistance genes.

Rust Resistance

Three wheat rusts, leaf rust (caused by *Puccinia triticina* Eriks), stem rust (caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn.) and stripe rust (caused by *Puccinia striiformis* West. f. sp. *tritic*i), can cause severe damage and yield loss when weather conditions

are optimal and inoculum is present, especially when changes of predominant races occur. Texas is the primary window through which rusts spread to the Great Plains in the U.S. and Canada. Depending on the spring climatic conditions, wind blows rust spores from Mexico into Texas. The resistance genes for the three rusts are designated as *Lr*, *Sr*, and *Yr*, respectively. Through a worldwide long-term breeding effort, many genes have been identified and deployed in new cultivars. To date, 71 *Lr*, 57 *Sr*, and 53 *Yr* genes have been named and many others have been identified (http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbolClassList.jsp, accessed on January 10, 2013). Many rust resistant sources containing these genes have been utilized in breeding programs. However, variations in rust race compositions over time make the management and the development of resistant wheat cultivars more challenging, thus requiring a continuous effort. For example, in 2010, dominant stripe rust races overcame some long-term *Yr* resistance genes such as *Yr17*. Only a few wheat cultivars, such as Hatcher, TAM 111, Snowmass, Doans, Fannin, and Winterhawk, showed resistance in yield trials of Texas A&M AgriLife Research (Haley et al., 2005, 2011; Lazar et al., 2004; http://varietytesting.tamu.edu/wheat/index.htm#VarietyTrials, accessed on December 1, 2012). In 2012, however, different predominant stripe rust races caused severe infections on TAM 111, Everest, Snowmass, and Armour while those cultivars heavily infected in 2010 showed low infection, including several of them carrying *Yr17*. Various races of Ug99, first observed in east Africa, are potential threats for global wheat production; however, only a few genes showing resistance to Ug99 and its derived new races are available in wheat (Bernardo et al., 2013; Lopez et al., 2014). High temperature adult-plant stripe rust resistance genes may not always be effective. Many of those named genes are only effective at the seedling stage, thus durable adult plant resistances to rusts would be preferred. This durable type of resistance is available in a few

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sources including *T. aestivum (ssp. spelta)*, *T. monococcum, T. turgidum (ssp. spelta, dicoccoides, dicoccom), Ae. taushii, T. ventricosum, T. timopheevi, Ae. speltoides, Ag. elongatum (Th. ponticum)* and rye cultivars such as Petkus, Imperial and Insave (Supplementary Table S1, Fig. 1).

Several adult plant *Lr* resistance genes from common wheat remain effective. Two durable gene complexes were reported in common wheat: the *Lr34*/*Yr18*/*Pm38*/*Ltn* complex on chromosome 7DS and the *Lr46*/*Yr29*/*Pm39*/*Ltn* complex on the distal region of 1BL (Rosewarne et al., 2006, 2008). Xcssfr1 and Xcssfr2 are two dominant gene markers representing presence (571 bp) and absence (523 bp) of the *Lr34* complex, thus have been used together as a co-dominant marker for *Lr34* (Lagudah et al., 2009). A TaqMan assay is available to identify the causal SNP in *Lr34*, but the SNP is associated with a false positive allele of *Lr34* in Jagger. Therefore, two sets of SNP markers were used to distiguish the *Lr34* complex from the false positive allele in the Jagger background (PI 593688, PVP 9500324, Sears et al., 1997; Lagudah et al., 2009; G. Brown-Guedira, unpublished data, 2013). Markers for the *Lr46* complex were reported by Rosewarne et al. (2006) but they are not widely used due to lack of diagnostic markers in many breeding populations. New marker for *Lr46* complex is under developing (Yan L., unpublished data, 2013).

A few leaf rust resistance genes were derived from *Ae. taushii*. *Lr21* has been cloned as a gene with nucleotide binding site – leucine rich repeat (NBS-LRR) (Huang et al., 2003) and a gel free diagnostic KBioscience competitive allele-specific polymerase chain reaction (KASPar) marker (LGC Genomics, Beverly, MA, USA), Lr21_GQ504819_1346_C/T, was developed for detection of the gene (Neelam et al., 2013). *Lr22a* is an adult plant resistance gene on chromosome 2DS. A SSR marker Xgwm296 is 2.9 cM distal to *Lr22a* (Hiebert et al., 2007).

Lr22a is also linked to *Lr41* at 21 cM (Raupp et al., 2001) but *Lr41* has been defeated by the leaf rust races in the Great Plains (Bernardo et al., 2013). Many genes and gene complexes have been transferred into wheat from wheat relatives through chromosome translocations. *Lr37*/*Sr38/Yr17* is a gene complex located on the translocation of *T. ventricosum,* 2AS/2NS. A PCR marker, Ventriup-LN2, for this gene cluster is frequently used as a diagnostic marker (Helguera et al., 2003). In addition, Xgwm1176.263 was located at 4.1 cM away from this gene complex (Blaszcyk et al., 2004), and a KASPar SNP marker was developed for the gene (G. Brown-Guedira, unpublished data, 2013).

The only durable, non-race specific, adult plant resistance gene to stem rust is *Sr2*, which originated from emmer wheat [*Triticum turgidum ssp*. *dicoccum* (Schrank ex Schubler) Thell] (Mago et al., 2011a). It was mapped on chromosome 3BS at 17 cM from Xgwm533 (Kota et al., 2006). Fine mapping using Chinese spring (CS) × CS (Hope 3B) showed that *Sr2* co-segregated with a marker, XcsSr2, a LR resistance gene, *Lr27*, a gene for pseudo-black chaff (PBC), and a resistance gene to powdery mildew (caused by *Blumeria graminis f. sp. tritici*), named as *Sr2/Lr27/PBC/Pm* (Mago et al., 2011b). The gene is in contig 11 of CS physical map (Choulet et al., 2010). Thus XcsSr2 has been widely used as a diagnostic marker to screen for *Sr2* in breeding. Two genes, *SrTA10171* and *SrTA10187*, from *Ae. tauschii* confer resistance to Ug99 and were mapped on chromosomes 7DS and 6DS, respectively (Olson et al., 2013).

In addition to those genes from emmer, *Ae. tauschii*, and common wheat, *Sr22* was transferred from *T. boeoticum* (AA) which confers resistance to Ug99 and its derivatives except race 316 and 317 (Olson et al., 2010a). Several mapping populations showed consistent marker orders with Xcfa2123 at 4.3 cM proximal and Xcfa2019 at 2.8 cM distal to *Sr22* based on the linkage map from the cross of Sr22TB/Lakin. A robust STS marker, Xcssu22, co-segregating

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with *Sr22*, was developed and used to confirm a short *Sr22* segment in Line RAC177 (Periyannan et al., 2011).

Sr24/*Lr24* conferring resistance in Amigo (PI 578213) was located on 1BL.1BS-3Ae translocation while *Sr24*/*Lr24* in Agent (CItr 13523) was located on 3DL-3Ae translocation (Smith et al., 1968; McIntosh et al., 1976; The et al., 1992). Sr24#12 was designed to screen for a 500 bp fragment associated with *Sr24* (Mago et al., 2005) from both sources. In addition, a co-dominant marker Xbarc71 can be used to identify the rust resistance gene in Agent. *Sr26* was located on a 6AL-6Ae translocation and marker Sr26#43 was designed to screen for the gene (Mago et al., 2005).

The *Sr39* gene, which confers resistance to Ug99, is from *Ae. speltoides* and is linked to *Lr35,* an adult plant resistance (APR) gene to leaf rust. It is located on a 2BS/2S translocation. A dominant marker, Sr39#22r for *Sr39* was developed (Mago et al., 2009). However, a larger portion of the chromosome in translocation lines is from chromosome 2S of RL6082. Through chromosome engineering, lines such as RWG1 and RWG3 with only 3-9 % of chromosome 2S, have recently been released (Niu et al., 2011). Two new co-dominant markers, Xrwgs27 and Xrwgs29, were developed to monitor the shorter version of the *Sr39* fragment. Several genes, such as *Sr36* and *Sr40*, were transferred to common wheat from *T. timopheevii* (AAGG). Xstm773 and Xsr39#22r, linked to *Sr36* and *Sr40*, respectively, are the markers for identification of the *T. timopheevii* fragments (Bariana et al., 2001; Bernardo et al., 2013). Two genes, *Sr33* and *Sr35*, conditioning resistance to Ug99 and its derivatives, were recently cloned and the sequence knowledge will facilitate the designing of allele specific SNP markers (Periyannan et al., 2013; Saintenac et al., 2013). Marker Xscm9, specific to 1RS, is used to tag $Sr1RS^{Amigo}$ on 1AL.1RS.

Effective resistance to stripe rust is conditioned by *Yr5* on chromosomes 2BL of common wheat and *Yr15* on 1BS of durum wheat (Murphy et al., 2009). *Yr5* is linked to Yr5STS-7/8 and Xbarc349; however, the markers are not very diagnostic across different genetic backgrounds. Markers Xbarc8 and Xgwm413 are diagnostic for *Yr15*. Several other *Yr* genes were reported on chromosome 2BL, including *Yr7*, and *YrQz* (Sui et al., 2009). *Yr5* and *Yr7* are allelic or tightly linked based on both phenotypic and genotypic assays (Zhang et al., 2009) while *Yr44* is about 42 cM away from *Yr5* (Sui et al., 2009). *Yr53* from durum wheat PI 480148 and *Yr43* from common wheat IDO377s were mapped at the similar chromosome region but linked to different markers (Xu et al., 2013; Cheng et al., 2010) (Fig. 1). Rosewarne et al. (2013) summarized 140 QTL for stripe rust resistance on 49 chromosome regions (meta-QTL) using a concensus map derived from more than 30 publications. Xgwm501 is linked to one meta-QTL on chromosome 2BS while Yr7 and Xgwm619 belong to another meta-QTL on chromosome 2BL. At least four independent genes, *Yr5* (*Yr7*), *Yr44*, *Yr53*, and *Yr43*, were located on chromosome 2BL in addition to the newly mapped stripe rust resistance QTL from TAM 111 (Basnet et al., 2013). However, the allelic relationships of these genes remain to be investigated.

Kuchel et al. (2007) used markers for two gene complexes, *Lr34*/*Yr18*/*Pm38*/*Ltn* and *Lr46*/*Yr29*/*Pm39*/*Ltn,* to select for the two genes and reported that selected lines were significantly improved in rust resistances and yield at some locations. Lillemo et al. (2008) also noticed large effects of these two genes on resistance to leaf rust, stripe rust, and powdery mildew. In another experiment, 776 U.S. wheat lines were screened for *Sr24*, *Sr36*, $Sr1R^{Amigo}$, and *Sr31* using their respectively linked markers Xbarc71, Sr26#43, Xwmc477, and Xscm9 (Olson et al., 2010b). The results showed that *Sr36* was present more frequently in eastern soft winter wheat (170/290 lines) while *Sr24* is more frequent in the Great Plains hard winter wheats

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(105/194). Haplotype analysis of linked markers to Ug99 resistance genes, *Sr2*, *Sr22*, *Sr24*, *Sr25*, *Sr26*, *Sr36*, *Sr40*, and *Sr1R*^{Amigo}, across 115 wheat breeding lines from the International Maize and Wheat Improvement Center (CIMMYT) showed that 83 lines may carry *Sr2*, a few have *Sr24*, *Sr25* and *Sr36* but none has *Sr26* or *Sr4*0 (Yu et al., 2010b).

A set of 55 diverse germplasm lines were screened with 23 markers for 11 genes for rust resistance (Supplementary Table S2, Supplementary Fig. S1). Three markers, Xgwm614.134 linked to *Lr17a*, XBF14593.198 linked to *Sr25*, and Xcfa2170.180 linked to *Sr35* were diagnostic among the tested lines. Several other markers linked to various rust resistance genes, such as Xwmc382.217, Xwmc667.164, and Xwmc407.149 linked to *Lr17a*, Xgwm271.171 and Xgwm501.107 linked to *Sr36*, STS7/8.478 linked to *Yr5* were diagnostic when a group of carefully chosen lines were screened.

Among 174 lines from the SRPN tested from 2008 to 2012, eight genes for rust resistance were tested with linked markers (Supplementary Table S3, Supplementary Fig. S2). The results showed that *Lr21* is in four, *Lr34/Yr18/Pm38* is in eight, *Lr39/Lr41* is in three, *Sr2* is in 15, *Lr24/Sr24* is in 18, and *Lr37/Sr38/Yr17* is in 80 lines, indicating that most of the resistance genes are present only in a few breeding lines. Recently, markers linked to *Sr2*, *Sr22*, *Sr26*, *Sr32*, *Sr35*, *Sr36*, and *Sr40* have been validated in diverse genetic backgrounds (Bernardo et al., 2013) and these markers may facilitate pyramiding of these *Sr* genes in new cultivars to enhance resistance durability of these cultivars.

End-Use Quality

Wheat end-use quality is a an important trait in breeding and is evaluated by different physical, functional, biochemical, and rheological assays. Major quality traits are discussed

including grain and flour protein and ash concentration, dough strength and extensibility, starch composition, grain hardness, and end-use product color. These traits are controlled by different genes, such as *Glu* and *Gli* loci, and genes encoding the granule-bound starch synthase (waxy protein), puroindolines, and polyphenol oxidase (PPO) (Supplementary Tables S1, S3, Fig. 1). Both biotic and abiotic stresses can affect wheat end-use quality (Graybosch et al., 1995).

Wheat gluten is composed of glutenin subunits and gliadins and is the major storage protein in the endosperm of common wheat (Lindsay and Skerritt, 1999). Glutenins are classified as low-molecular-weight (LMW) and high-molecular-weight (HMW) subunits (Payne et al., 1987a; Ciaffi et al., 1999). *Glu-A3*, *Glu-B3*, and *Glu-D3*, located on the short arm of group 1 homoeologous chromosomes, encode the LMW glutenin subunits while *Glu-A1*, *Glu-B1*, and *Glu-D1*, on the long arms of the same chromosome groups encode the HMW glutenin subunits (Payne et al., 1987b; Gupta and Shepherd, 1990). These loci have large influence over both dough strength and extensibility (Payne et al., 1987b; Luo et al., 2001).

LMW-glutenin subunits (GS) can be further divided into LMW-m, LMW-s and LMW-i depending on whether the first N-terminal amino acid is methionine, serine, and isoleucine, respectively (Cloutier et al., 2001). Gupta and Shepherd (1990) identified 20 different LMW glutenin alleles; subsequently, many studies have characterized the different alleles and developed allele specific markers. *Glu-A3*, *Glu-B3*, and *Glu-D3* encode an LMW-GS i-type proteins (Cloutier et al., 2001). Among different alleles of all loci for LMW glutenin subunits, *Glu-3* with composition of 'bbb' has the best extensibility in Australian wheats (Cornish et al., 1993). Allele specific markers linked to seven alleles of *Glu-A3* and 10 alleles of *Glu-B3* were developed (Wang et al., 2009, 2010; Zhao et al., 2006, 2007a). Although specific DNA marker for *Glu-A3b* is not available, it has a positive effect on wheat quality (Zhang et al., 2004). Other

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Glu-A3 alleles have been selected against in Australian wheat breeding programs (Eagles et al., 2001). For *Glu-D3* genes, it was found that the base sequences of six genes are significantly different (80 to 92%) but the differences in alleles and haplotypes are very small (99 to 100%) (Zhao et al., 2007a). A primer set S13F2/S13R1 designed by Zhao et al. (2007b) can be used to discriminate between *Glu-D3c* and *Glu-D3d*. *Gli-1* genes closely linked to the LMW glutenin loci on group 1 chromosomes encode for γ and ω gliadins while the *Gli-2* genes on group 6 chromosomes encode the α/β gliadins (Brown and Flavell, 1981; Zhang et al., 2003). The main and interaction effects of these genes influence wheat flour end-use quality. Allele specific SNP markers were designed for γ gliadin encoded by *Gli-D1*, which is linked to the *Glu-D3* locus (Zhang et al., 2003). These markers can be used to differentiate alleles of *Glu-3*, such as *Glu-A3d*, *Glu-B3c*, and *Glu-D3c*.

These designed markers have been applied in various studies. Markers linked to *Glu-B3* were validated using 170 wheat cultivars and elite lines from Australia, France, USA, and CIMMYT (Wang et al., 2009) and the results showed that *Glu-B3* alleles can be very accurately discriminated using markers compared with sodium-dodecyl-sulphate polyacrylamide gel electrophoresis (SDS-PAGE). *Glu-A3d* and *Glu-B3d* are better for dry white Chinese noodles (He et al., 2005).

Primers were also designed for different HMW-GS gene variants. Since the amino acid (aa) sequences of different HMW-GS gene variants have more than 80% similarity, design of gene and allele-specific markers has been a challenge (Zhao et al., 2006). There are two variants of *Glu-B1b* (Bx7+By8*)*, *Glu-B1u* (Bx7*+By8), and *Glu-B1al* (Bx7^{OE}+By8*), can be differentiated by the presence of an 18 bp indel at a repetitive domain of hexapeptide motif (Radovanovic and Cloutier, 2003; Butow et al., 2004). The *Glu-B1al* lines have higher dough strength than the

lines with other *Glu-B1*alleles and markers have been designed (Ragupathy et al., 2008). Three locus specific STS markers are very diagnostic for tagging target alleles of *Glu-A1* and *Glu-D1*. UMN19 was developed to differentiate *Glu-A1b* (Ax2*) from *Glu-A1a* (Ax1) on *Glu-A1* while UMN25 and UMN26 were designed for *Glu-D1a* (Dx2 + Dy12) and *Glu-D1d* (Dx5 + Dy10) on *Glu-D1* (Liu et al., 2008a). Wheat lines with *Glu-A1a* or *Glu-A1b* have higher dough strength than lines with the null allele, *Glu-A1c*. *Glu-D1a* is more common in most soft wheats while *Glu-D1d* is good for bread making and presents in most hard wheats. These markers are diagnostic and have been used in many U.S. wheat breeding programs.

Markers for *Glu-A1* and *Glu-D1* were used to screen wheat cultivars worldwide (Jin et al., 2011) and the results showed that about 50% of 718 cultivars from 20 countries carry *Glu-A1b* and *Glu-D1d* . A higher frequency of *Glu-A1b* was observed in wheat from U.S. and Canada than wheat from Austria and Japan. A survey of diploid, tetraploid, and hexaploid wheat using SDS-PAGE showed that the overexpressed phenotype of *Glu-B1a, Glu-B1al*, only occurred in *T. turgidum* and *T. aestivum* (Lei et al., 2006; Ragupathy et al., 2008). Among 300 common wheat lines screened, North and South American lines have the highest percentage of *Glu-B1al* while more Asian and European lines have *Glu-B1a* or *Glu-B1u*. An Argentinean landrace, Klein Universal II, is the source of *Glu-B1al*, which was distributed through CIMMYT breeding programs to other breeding programs worldwide (Butow et al., 2004).

Many markers for end-use quality traits are diagnostic because they were designed based on the sequences of respective genes. In the Great Plains of the U.S., markers UMN 19, UMN 25, and UMN26 are widely applied in screening for *Glu-A1b* and *Glu-D1d*. Among the 174 SRPN lines screened with UMN19, *Glu-A1b* is in about 66% of tested lines (Supplementary Table S3). The *Glu-D1d* is associated with bread making quality and present in 75% of tested

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lines while the *Glu-D1a* is present in only 20%. These percentages are very consistent with results of Shan et al. (2007) who reported the frequency of lines with *Glu-A1b* as 76%, lines with *Glu-D1d* as 81%, lines with *Glu-D1a* as 11% using 111 hard red winter wheat lines or cultivars released from 1991 to 2007 using SDS-PAGE. Doughs formed from wheats with *Glu-D1d* tend to be stronger than those from wheats with *Glu-D1a*.

In addition to the genes for glutenin subunits, several other genes also affect wheat end-use quality. Polyphenol oxidase (PPO) is related to browning and discoloration of pasta, bread, and Asian noodles, including white-salted Udon noodles, yellow alkaline (Ramen), and Chinese white salted noodles, which require low PPO activities for brightness (He et al., 2004); therefore, hard white wheat cultivars with low PPO are favorable. An STS marker, PPO18 on chromosome 2AL , was developed as a co-dominant marker to diferentiate high and low PPO (Sun et al., 2005). A set of STS markers, PPO16 and PPO29 for *PPO-A1* on chromosome 2A, PPO33 and PPO43 for *PPO-D1* on chromosome 2D, were designed (He et al., 2007) and PPO33/PPO16 can be multiplexed to differentiate the very high and very low PPO wheat lines at both loci. However, additional alleles conditioning low PPO were also reported in some wheat lines (Nilthong et al., 2012; Beecher et al., 2012).

Multiple genes control the starch biosynthetic pathway (Preiss, 1997). ADP-glucose pyrophosphorylase (AGP) large and small subunits (AGP-L and AGP-S), sucrose transporter (SUT), granule-bound starch synthase I (GBSSI, waxy), and soluble starch synthases I (SSI) are important enzymes involved with this process (Shure et al., 1983; Preiss 1998; Lemoine 2000). GBSSI is important for amylose synthesis in endosperm and affects noodle and other product quality. Genome specific markers were developed for these genes (Blake et al., 2004). Co-dominant markers for *Wx-A1*, *Wx-B1*, and *Wx-D1* on chromosome 7AS, 4AL, and 7DS were

designed to identify *Wx* null alleles, which is preferable for Asian noodles (Nakamura et al., 2002; Saito et al., 2009).

Puroindoline (Pin) is a LMW cysteine-rich protein. It may be involved in the plant defense mechanism and is tissue-specific and developmentally regulated. Genes for *Pina* and *Pinb* , are linked to the hardness gene *Ha*, and genes for the grain softness related protein (*Gsp-D1*), which were located on chromosome 5DS and all of them are associated with grain softness (Tranquilli et al., 1999). Markers were designed for *Pina* and *Pinb* (Gautier et al., 1994). In general, soft wheats have *Pina-D1a* and *Pinb-D1a* while hard wheats have a mutation at either *Pina* or *Pinb*. A point mutation on *Pinb-D1a* resulted in the *Pinb-D1b* allele which can increase flour yield, lower ash, loaf volume, and improve crumb grain score (Hogg et al., 2005). However, the mutation did not affect dough mixing time.

In our evaluations, the low PPO allele at *PPO-D1* (*D1a*) is in 75% of 174 SRPN lines but the low PPO allele at the *PPO-A1* locus (*A1a*) was present in only 7% of these lines (Supplementary Table S3). However, the *PPO-A1a* is more functional as these 9 lines have the actual low PPO measurement (0.11 to 0.47 change of 0.001 absorbance unit /min/mL) (Supplementary Table S3). *Pinb-D1b* mutants were in 60% of lines tested, whereas *Pina-D1b* mutants were only in 10% of tested lines. Three null mutants at *Wx* loci occurred in low percentage with the *Wx-B1* as the highest (21%). We can clearly see that most of the hard red winter wheat lines have *Glu-A1b*, *Glu-D1b*, *PPO-D1a*, *Pinb-D1b*, and wild type of *Wx alleles*.

Pre-harvest sprouting (PHS) results from prolonged wet weather close to harvest. With the advent of hard white wheat breeding in the Great Plains, developing lines with tolerance to PHS has become a priority; hard white wheats generally are less tolerant of PHS than hard red wheats (Morris and Paulsen, 1992), though hard red genotypes with lower sprouting tolerance are not

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uncommon. Among Great Plains hard white winter wheats, 'RioBlanco' (PI 531244) is reported to be among the most tolerant (Wu and Carver, 1999), and a major QTL (*QPhs.pseru-3AS*) conditioning tolerance to PHS has been identified in this cultivar (Liu et al., 2008b). More recently, the QTL has been cloned as a MOTHER OF FLOWERING TIME-like gene, designated as *TaPHS1* (Liu et al., 2013a). Two mutations in the coding region of the gene lead to mis-splicing and a truncated protein that switch wheat from resistance to susceptibility. A SNP marker from the gene was developed to facilitate marker assisted selection in breeding. Among 174 SRPN lines, about 10% of the lines have the sprouting tolerance allele at this QTL based on linked SSR markers (Supplementary Table S3).

The USDA-ARS Hard Winter Wheat Quality Laboratory at Manhattan, KS provides yearly testing of SRPN and other regional nursery lines. (http://www.ars.usda.gov/Main/docs.htm?docid=14298&page=3, accessed on May 1, 2013) and USDA-ARS Central Small Grain Genotyping Laboratory at Manhattan, KS conducted marker analysis for the same materials. Since end-use quality can be affected by environment, for example, soil water, soil nutrition, pests, temperature, and precipitation, combining both marker data and quality testing from these laboratories is necessary for researchers to make a better decision on parental selection.

Rye Chromosomal Translocations

Rye chromosomal translocations, 1AL.1RS and 1BL.1RS, have been used in wheat breeding for many decades as they carry several resistance or tolerance genes or QTL to arthropods (RWA, GB, WCM), diseases (rusts including Ug99 and powdery mildew), and abiotic stress. The 1AL.1RS translocation from ‘Insave’ rye conditions resistances to greenbug

(*Gb2* and *Gb6*), wheat curl mite (*Cmc3*), rust ($Sr1R^{Amigo}$) and powdery mildew (*Pm17*) (Lu et al., 2010; Malik et al., 2003) while 1BL.1RS from Imperial and Petkus provides resistances to rust (*Lr26/Sr31/Yr9*), powdery mildew (*Pm8*), and RWA (*Dn7*) (Weng et al., 2007; Peng et al., 2007; Lapitan et al., 2007). In some genetic backgrounds, the 1RS translocation can be more adapted to drought conditions and increase yield due to increased root biomass (Villareal et al., 1998; Ehdaie et al., 2003). Unfortunately, the 1RS translocations also have negative effects on end-use quality most likely due to the loss of LMW glutenin and gliadin encoding genes and the addition of the rye secalin proteins (Graybosch, 2001). In addition to Xscm9 linked to rye 1RS (Saal and Wricke, 1999), another marker used for 1RS translocation is Xtsm120, developed by Kofler et al. (2008). With this marker, a PCR product of 228 bp was found in all of the lines with 1AL.1RS from Insave rye and 1BL.1RS from Salmon, while the 207 bp band was found in all 1BL.1RS of wheat lines derived from Petkus rye including Kavkaz wheat (Weng et al., 2007). The Salmon 1BL.1RS translocation has rarely been used in wheat breeding programs, while the Kavkaz translocation is distributed worldwide (Graybosch, 2001; Lukaszewski, 2006). Another rye specific marker, PAWS5/S6 can be used to differentiate the 1AL.1RS between Amigo (220+320 bp) and GRS1201 (220 bp) but it could not distinguish 1BL.1RS from non-1RS lines (Weng et al., 2007). Two other markers, Xiag95 for *Sr31* from Petkus rye (1BL.1RS) and Xib-159 for *SrR* from Imperial rye (1BL.1RS) (Mago et al., 2002, 2004), were used to stack four genes including *Sr24* and *Sr26* for improved Ug99 resistance (Mago et al., 2011c).

Marker Xscm9 was used to screen 24 out of those 55 collected germplasm lines from the U.S. Great Plains and three lines were found to have 1AL.1RS (Supplementary Table S2). Among 174 SRPN lines screened, 20 (11%) carried 1AL.1RS while 17 (10%) carried 1BL.1RS (Supplemantary Table S3). A breeding effort at Colorado State Univ. is being made to

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recombine the 1BL.1RS translocation to carry both the *Dn7* for RWA resistance and *Glu-B3/Gli-1*, without the *Sec-1* locus to improve end-use quality (S. Haley, unpublished data, 2013).

Plant Height, Photoperiod Insensitivity, and Vernalization

Since the Green Revolution, semi-dwarfing genes have been used in many wheat breeding programs. About 90% of the worldwide wheat cultivars are semi-dwarfs having genes *Rht-B1b (Rht1)* or *Rht-D1b (Rht2)* (Worland et al., 1998). Gene *Rht8c* is linked to the *Ppd-D1* gene whose *Ppd-D1a* allele confers photoperiod insensitivity and early flowering in wheat (Welsh et al., 1973). The semi-dwarf genes, *Rht-B1b* and *Rht-D1b*, are insensitive to gibberellin and are advantageous in high yielding environments, while other genes, such as, *Rht4*, *Rht5*, *Rht8*, *Rht12*, and *Rht13* are responsive to gibberellin and may be more advantageous in rain-fed environments because they do not reduce the coleoptile length (Flintham et al., 1997; Worland et al., 1998; Ellis et al., 2005). Tall wheats, however, are still favored in many dryland environments, particularly in the north-western portion of the northern Great Plains.

Molecular markers were developed based on single nucleotide differences between mutant and wild alleles of *Rht-B1* and *Rht-D1,* respectively (Ellis et al., 2002) (Supplementary Table S1, Fig. 1). A KASPar SNP assay is now used for routine screening of the both genes in USDA Genotyping Labs (G. Brown-Guedira, unpublished, 2013). Marker Xgwm261 has a 192 bp allele linked to *Rht8c* (Ellis et al., 2007). Through genetic mapping, markers linked to gibberellic acid (GA) responsive genes including *Rht4*, *Rht5*, *Rht8c*, *Rht9*, *Rht12*, and *Rht13* were validated (Ellis et al., 2005). The effects of most genes on leaf elongation rate (LER), coleoptile length (CL) and GA responsiveness were tested and classified into three groups (Ellis et al., 2004). The first group contained those GA responsive genes, and no significant

differences on LER and CL were found, especially for *Rht8c* and *Rht12*. They are mainly associated with later growth and increased harvest index. The second group was composed of the GA-insensitive genes including *Rht-B1b*, *Rht-D1b*, *Rht-B1e* (*Rht11)*, and *Rht17*; they have significantly low LER and CL. The third group with *Rht16* and *Rht18* showed reduced LER and CL when GA was not present. Based on these results, the GA-responsive genes without effects on LER and CL, *Rht8c* and *Rht12*, may be desired in dryland wheat in the High Plains.

A set of 115 hard winter wheat cultivars and 247 soft winter wheat cultivars or breeding lines developed from 1808 to 2008 in North America were screened using the markers linked to *Rht-B1b*, *Rht-D1b,* and *Rht8c* (Guedira et al., 2010). They found that 90% of the tested lines developed after 1964 carried either *Rht-B1b* or *Rht-D1b*. In soft winter wheat, 28% of the tested lines had *Rht-B1b* and 45% had *Rht-D1b*, while 77% of the hard winter lines had *Rht-B1b* and only 8% had *Rht-D1b*. A very low percentage of lines (8% of soft wheat lines and 3% of hard wheat lines) were postulated to have *Rht8c*. Similar trends were found among the 174 SRPN hard wheat lines tested from 2008 to 2012. The majority have *Rht-B1b* (90%) while only 3% have *Rht2*. Only 5% of lines have *Rht8c*. *Rht8c* may confer better adaptation to the High Plains where drought is a persistent problem but we have a very low proportion of *Rht8c* lines and cultivars available in adapted genetic backgrounds in the U.S. Great Plains hard red winter wheat.

Markers were designed to differentiate the photoperiod insensitive allele (*Ppd-D1a*) from the sensitive allele (*Ppd-D1b*) for *Ppd-D1* on chromosome 2DS (Yang et al., 2009). About 32% of 174 lines tested after 2008 have *Ppd-D1a*. The percentage of lines with *Ppd-D1a* is still low but increased compared with the 5% of soft red winter wheat lines tested before 2008 (Guedira et al., 2010). On the other hand, wheat cultivars, germplasm lines, and landraces from China, Czech Republic, and Slovakia have higher percentage of *Rht8c* (20% to 72%) and *Ppd-D1a*

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

(56% to 95%) (Liu et al., 2005; Zhang et al., 2006; Yang et al., 2009; Sip et al., 2010). Therefore, it is possible to increase percentage of lines with *Ppd-D1a* by introducing more germplasm lines from those areas or utilizing more lines with *Rht8c* and *Ppd-D1a*.

Vernalization requirement also affect plant growth and development. The major vernalizarion genes, *Vrn-A1* and *Vrn-D3* on chromosomes 5A and 7D, whose dominance determine the spring (*Vrn-A1vrn-D3*) and winter (*vrn-A1Vrn-D3*) wheat types (Yan et al., 2003, 2006). Markers CDO708 and Vrn-D3F6/R8 were used to screen for *Vrn-A1* and *Vrn-D3* and were used to study their genetic effects (Wang et al., 2009; Chen et al., 2010). These two markers were used to screen 174 SRPN lines, 74% of them showed weak winter type (*Vrn-A1a*) and 55% of them showed early (*Vrn-D3a*).

Since wheat microsatellite markers were first publicly available in 1998 (Roder et al., 1998), many different types of molecular markers have been used to locate genes or QTL on chromosomes. Some tightly linked markers have been utilized at various degrees in wheat breeding. This review summarized those currently effective genes and their utilization to mitigate those stresses in the U.S. Great Plains. Through this review, linked markers for some effective genes and their target PCR fragment sizes were summarized (Supplementary Table S1, S2, S3, Fig. 1). Based on a collection of germplasm lines with wide genetic backgrounds and a set of 174 lines from the regional nursery program (SRPN), some diagnostic markers for certain genes were validated (Supplementary Table S2, S3, and Fig. S2). The gene frequencies were estimated based on associated markers among 174 advanced lines tested in the SRPN (Supplementary Table S3). The application of diagnostic markers and the dendrogram based on estimated genetic similarity (Supplementary Fig. S2) can help breeders to utilize these advanced breeding lines more efficiently to develop breeding populations with the consideration of their

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performance in yield, resistances to rust and viral diseases, and arthropod pests. As more genotyping-by-sequencing (GBS) data and SNP markers become available, we hope to design more gene- or allele-specific 'perfect' SNP markers and apply them in wheat breeding using high-throughput genotyping.

ACKNOWLEDGEMENTS

The authors thank Carl Griffey, Virginia Tech University and Gina Brown-Guedira and Jared Smith, USDA-ARS Eastern Regional Small Grains Genotyping Lab at Raleigh, NC, for their generous help for providing equipment and reagents for marker screening of the 55 lines at their laboratories. Yue Jin, USDA-ARS at St. Paul, MN, provided the lines with stem rust resistance genes.

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

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Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

Fig. 1. Molecular markers and their allele base pair size linked to target genes for various traits on chromosome maps. The traits are iarthropod resistance genes for greenbug (Gb), Russian wheat aphid (Dn) and Hessian fly (H), curl mite colonization (Cmc), wheat streak mosaic virus (Wsm), leaf, stem and yellow rusts (Lr, Sr, Yr), and end-use quality including low molecular weight glutenin subunit genes (Glu-A3/B3/D3), gliadin genes (Gli-A1/B1/D1), high molecular weight glutenin subunit genes (Glu-A1/B1/D1), polyphenol oxidase (PPO-A1/D1), starch biosynthesis (Wx-A1/B1/D1), puroindolines (Pina/b), pre-harvesting sprouting QTL, rye translocation (1AL.1RS/1BL.1RS), reduced height (Rht), photoperiod insensitive (Ppd), and vernalization genes (Vrn). The integrated map is based on the core frame map from the consensus map of Somers et al. (2004) and the International Trticeae Mapping Initiative (ITMI, http://wheat.pw.usda.gov/ggpages/maps.html) map developed by Song et al. (2005). Data from Graingenes 2.0 (http://wheat.pw.usda.gov/cgi-bin/graingenes/browse.cgi?class=marker, accessed on November 18, 2012) and the physical map by Sourdille (2004) were referenced as necessary. More information about genes and markers are in Supplementary Table S1. The information about the marker distances of target genes or QTL from the respective references was aligned onto chromosomes based on the integrated information. The maps were drawn using MapChart 2.0 (Voorrips et al., 2002).

Supplementary Table S1. Molecular markers, their target band base pair size, linked genes, chromosome locations, effects and sources of genes, associated with important traits in hard winter wheat in the U.S. Great Plains.

Supplementary Table S2. Molecular markers linked to various genes screened on diverse germplasm lines collected in the U.S. Great Plains.

Supplementary Table S3. Molecular markers linked to various genes screened on winter wheat lines in the Southern Regional Performance Nursery (SRPN) from 2008 to 2012 in the U.S. Great Plains.

Supplementary Fig. S1. Dendrogram of a collection of 55 germplasm lines and cultivars in the U.S. Great Plains with various genes based on 289 loci of 44 markers linked 22 genes. Wheat lines include nine for RWA, seven for Hf, 15 for GB, 21 for rusts, and three for wheat streak mosaic (WSM). Marker screening procedures were followed protocols from Liu et al. (2013b). The marker data were collected in the wheat breeding laboratory of Virginia Tech at Blacksburg, VA and USDA-ARS Eastern Regional Small Grains Genotyping Lab at Raleigh, NC using ABI3130xl. The Dendrograms of wheat lines were analyzed using TASSEL with unweighted pair-group method using the arithmetic average (UPGMA) (http://www.maizegenetics.net/index.php?option=com_content&task=view&id=89&Itemid=119, accessed on January 7, 2013). The tree text file from TASSEL was imported into Interactive Tree of Life (ITOL, http://itol.embl.de/, accessed on April 17, 2013) and a standard tree was output as png image. Genes are inside the parentheses.

Supplementary Fig. S2. A circular tree of 174 unique wheat advanced breeding lines from southern regional uniform nursery (SRPN) test from 2008 to 2012 (http://www.ars.usda.gov/Research/docs.htm?docid=11932) based on 104 marker loci linked to

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

various genes across the whole genomes. The 104 markers ranged from 42 to 76 were screened on SRPN lines from 2008 to 2012 by USDA-ARS Central Small Grain Genotyping Laboratory at Manhattan, KS following protocols from Bernardo et al. (2013). These markers linked to 43 genes associated with disease and insect resistance, aluminum tolerance, post-harvesting germination, height, photoperiod sensitivity and vernalization. Data analysis procedures using TASSEL and ITOL were same as those described in Supplementary Fig. S1.

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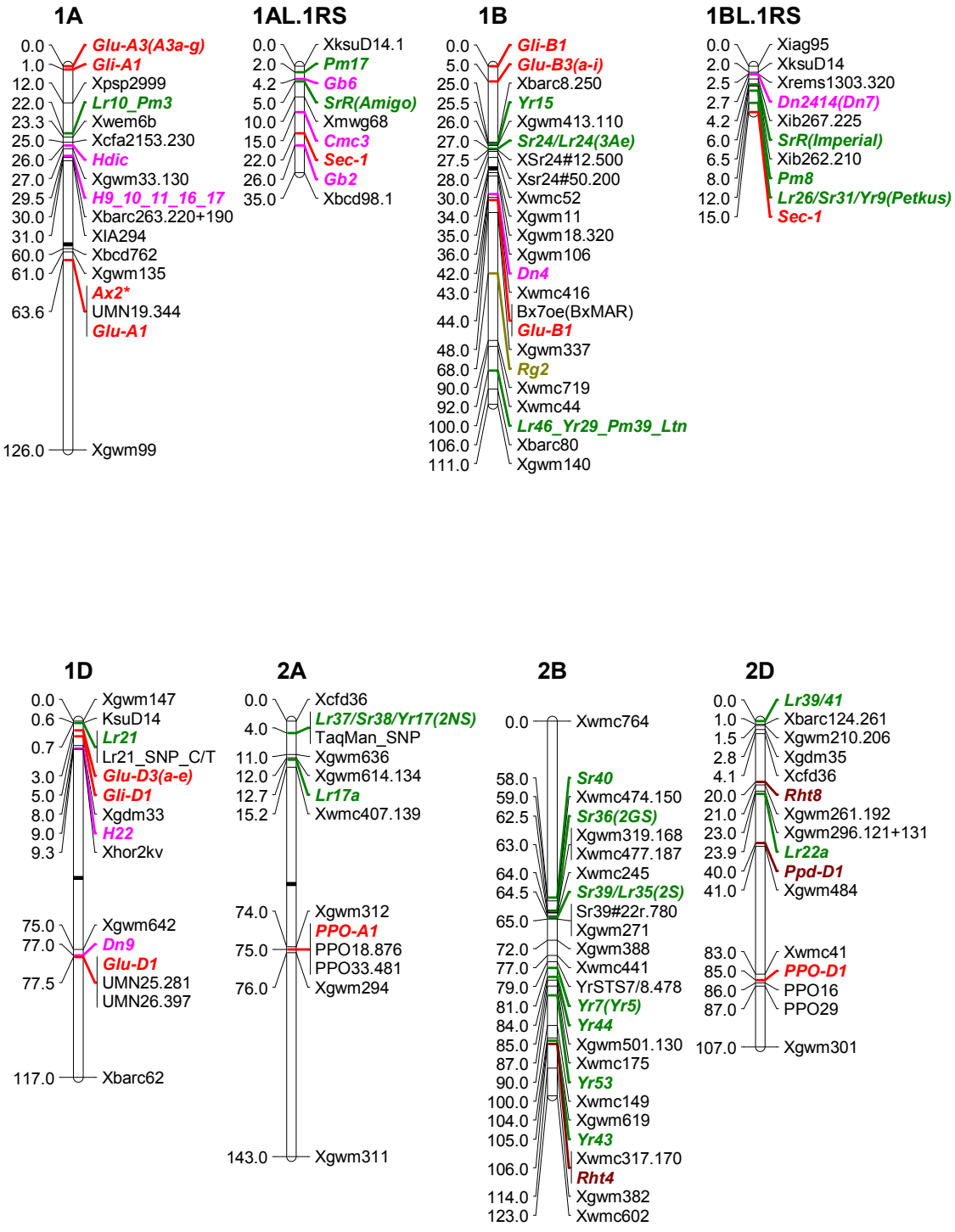
Fig. 1



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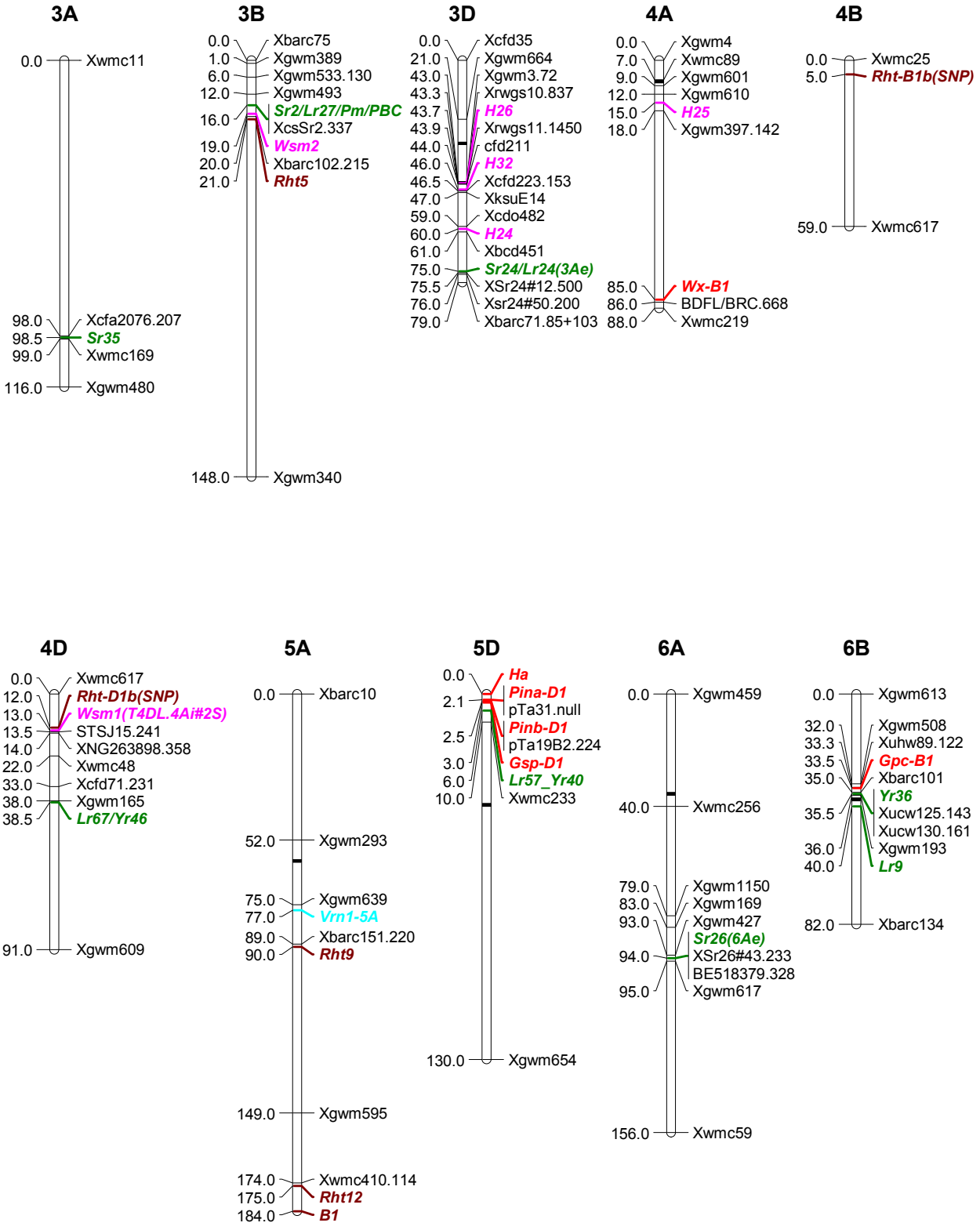
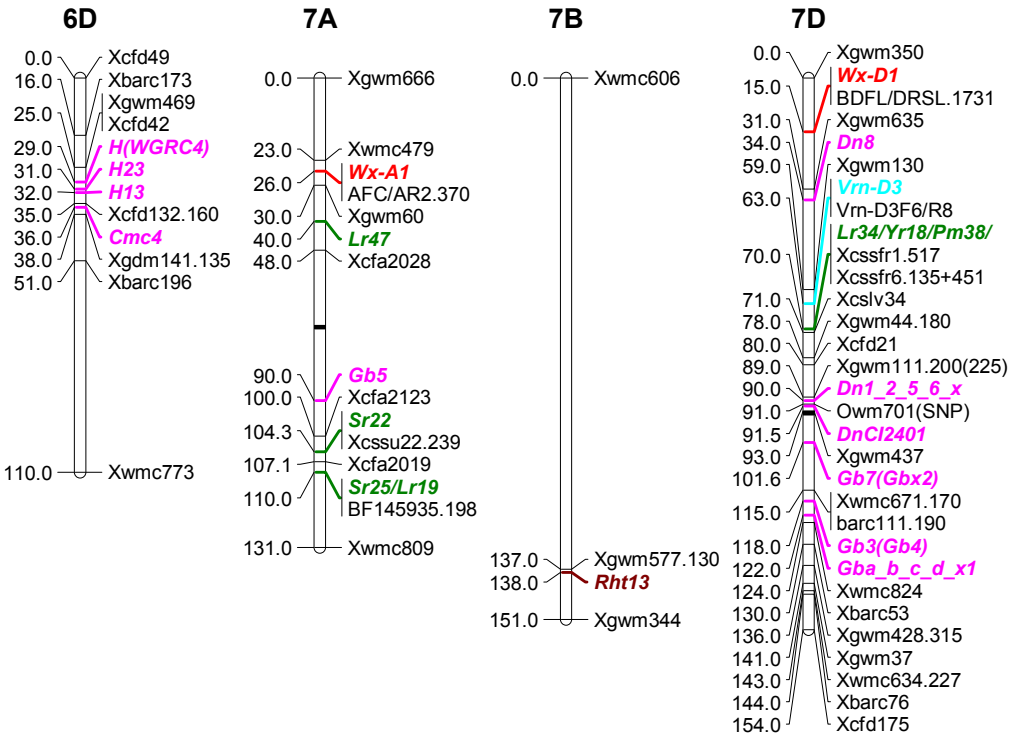


Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564



Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

Supplementary Table 1. Molecular markers, their target size, linked genes, chromosome locations, effects and sources of genes, associated with important traits in hard winter wheat in the U.S. Great Plains.

Traits	Genes	Chrom-osomes	Markers[‡]	Target bands (bp)[†]	References	Representative Germplasm lines	Resistances to races/biotypes or phenotypic effects[§]
Insect Resitance							
Greenbug	*Gb3*	7DL	**Xwmc634**, **Xbarc111**, Xgwm37, Xgwm428, Xbarc76; **Xwmc157**, **Xwmc671**, Xbarc53, Xgdm46, Xgwm428, Xgwm437	**227**, **190(M13)**; **150**/140, **170** or 120/140, 315/295, 135/150, 135/150, 120/90(Argrose)	Weng et al., 2005; Azhguvel et al., 2012; Zhu et al., 2004; Zhu et al., 2005	Largo, TAM 110, TAM 112; KSU97-85-3, TA1675 (TA4152L94, TA4152L24, TA4063.1, TA4064.2, and KS89WGRC4)	C,E,H,I,J,K; I, K
Russian wheat aphid	*Dn7* (*Dn2414*)	1BL.1RS	Xib267, **Xrems1303/Xgwm18**	225(M13), **320**/200,	Anderson et al., 2003, Laptian et al., 2007, Peng et al 2007; Liu et al., 2005a; Stankova et al., 2013	94M370 Stars02RWA2414	1,2,3,4,5,6,7,8
	DnCI2401	7DS	**Owm701(SNP)**			CI 2401	1,2
	Dn6265	7DS	Xbarc214, Xgwm473	237/239, 244/246+252	Valdez et al., 2012	PI626580	1,2
	Dn6	7DS	**Xgwm111**, Xgwm44;	**200**/220, 180	Liu et al., 2002	PI 243781, CO 960223	1,3,4,5,6,7,8
	Dnx	7DS	**Xgwm111**	**225**	Liu et al., 2001	PI 220127, KS94WGRC29	3,4,5,6,7,8
Hessian fly	*H13*	6DS	**Xcfd132**, Xgdm36	**160**/120, 170/130	Liu et al., 2005b	Molly, KU2076	GP, L

H24	3DL	Xcdo482, Xbcd451	-	Ma et al., 1993	KS89WGRC6	GP, L, vH9, vH13
H25	Ti4AS.4AL-6R1L-4AL	**Xgwm397, Xgwm610**	**142, 158**	Guttieri et al., 2003	KS92WGRC20, IDO586	GP, L, vH9, vH13
H26	3DL	**Rwgs10**, **Rwgs12**	**837**/856, **270**/247	Yu et al., 2009, 2010a	SW8, KS92WGRC26	GP, L, vH13
H32	3DL	Xgwm3, **Xcfd223**	72/84, **153**/183	Sardesai et al., 2005	W7984	B, C, D, E, O, L,vH9, vH13, but avirulent to GP
Hdic	1AS	**Xgwm33**, Xbarc263, **Cfa2153**	**130**/-, 220/200, **230**/190	Liu et al., 2005c	KS99WGRC42	GP, L, vH9, vH13
H9, H10, H11	1AS	**Xbarc263**; Cfa2153	**220+190**, 220+190, 210+180 (S);180, 180, 195	Liu et al., 2005d; Kong et al., 2005	Ella, Elva, Iris, Joy, Karen	Gp, L, vH13; GP, L, vH13; GP, vH9, vH13
Wheat curl mite						
Cmc1	6DS	-	-	Thomas and Conner, 1986; Whelan and Thomas, 1989	*Ae. tauschii*, Norstar, W304	MT, KS (NE virulent to W304)
Cmc2	6DS/6Ae	-	-	Martin et al., 1976; Whelan and Hart, 1988	*Ag. elongatum*, TAM 107, KS96WGRC40 (TA2397)	- MT, NE (KS virulent to TAM 107)
Cmc3	1AL.1RS	Xscm9	228	Malik et al., 2003		
Cmc4	6DS	**Xgdm141**, Xwms904	**135**/120, -/180	Malik et al., 2003	KS96WGRC40	KS, MT, NE
Wheat streak mosaic virus						
Wsm1	T4DL.4AgS, T4DL.4Ai#2S	**XSTSJ15**; XBG263898	**241**;358	Graybosch et al., 2009, Talbert et al., 1996, Seifers et al., 2006; Qi et al., 2007	CI 17884, KS93WGRC27, Mace	< 18 °C (Growth chamber)
Wsm2	3BS	Xbarc102	215	Lu et al., 2011,	CO 960293-2,	< 18 °C (Growth

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					2012; Martin et al., 2006	RonL, Snowmass	chamber)
Rusts							
Leaf rust	*Lr21*	1DS	Lr21_GQ504819_1346_C/T		Neelam et al., 2012	WGRC2, WGRC7, TA1649	Broad resistance
	Lr22a	2DS	Xgwm296	121+131	Hiebert et al., 2007	RL5271, RL5404, RL6044, 98B34-74B	APR, low frequency in cultivars, undefeated gene, no virulent race found
	Lr34/Yr18/Bdv1/Pm38/Ltn1	7DS	Xcssfr1/Xcssfr2, Xcssfr6; TaqMan Assay	517/523, 135+451/589	Lagudah et al., 2009, Krattinger et al., 2009; Brwon-Guedira, unpublished, 2013	Anza, Jagger	Race non-specific Adult plant resistance (APR), multiple
	Lr37/Sr38/Yr17	2AS/2NS	Xgwm1176, SC-Y15, CslVrgal3, **Ventriup-LN2**, TaqMan SNP	263, 580, 383; **259**	Blaszczyk et al., 2004; Helguera et al., 2003; Brown-Guedira, unpublished, 2013	Kris, Renan; Anza, Thatcher Lr37, RL6081, UC1041, 28 -35 cM from *T. ventricosum* (*Ae. Ventricosa* Tausch)	APR, Multiple rust resistances
	Lr39/Lr41	2DS	**Xbarc124**, Xgwm210	**261**/271, 182+206/182+184	Sun et al., 2009	KS93U62, TA2460, TAM 112, Overley, Jackpot	-
	Lr46/Yr29/Pm39/Ltn	1BL	Xwmc719, Xwmc44	-	Rosewarne et al., 2006; Lillemo et al., 2008	Pavon76; Saar	APR to leaf and stripe rust
	Lr67/Yr46	4DL	**Xcfd71**, Xgwm192, Xgwm165	**231**/242, no 143 bp, no 234 bp	Herrera-Foessel et al., 2011	RL6077	APR to leaf and stripe rust
Stem rust	*Sr2/Lr27/PBC/Pm*	3BS	Xgwm533, XcsSr2 (CAPS), SNP	120, 337=172+112+53/225+112	Mago et al., 2011a, 2011b; Bernardo et al.,	CnS(Hope3B), Oasis, from emmer wheat (*T.*	APR, multiple resistance

			(BspHI),	2013	*turgidum* L.) Schomburgk, Sr22Tb, RAC177,	
Sr22	7AL	**Xcssu22**; Xwmc633	**239**; 135/178	Periyannan et al., 2011, Olson et al., 2010b, Bernardo et al., 2013	Translocation from *T. boeoticum* and *T. monococcum*	Resistance to Ug99 and its derivatives, but not race 316 and 317
Sr24/ Lr24	1BS.3Ae	**Sr24#12**, **Sr24#50**	**500**, **200**	Mago et al., 2005	*Agropyron Elongatum (=Thinopyrum. ponticum*), TX99A01531, BtSr24Agt Agent,	-
Sr24/Lr 24	3DL/3Ae	Xbarc71, red grain	85+103/107	Mago et al., 2005, Olson et al., 2010b, Jin et al., 2008	SwSR22TB, from *Ag. elongatum, 3DL.3Ae* #3 and 14 are white seeds	TTKST virulent, poor agronomic traits
Sr25/Lr 19	7AL(7Ae #1)	**BF145935**, GB	**198+180**/202+180, 130	Liu et al., 2010	LcSr25Ars, Wheatear, *Ag. elongatum*	Ug99
Sr26	6AL/6Ae #1	**Sr26#43**/**BE518379**	**233**/**328 (M13)**	Mago et al., 2005, Olson et al., 2010a, Liu et al., 2010, Bernardo et al, 2013	*Ag. elongatum,* Eagle, Sunelg	Ug99, yield penalty
Sr31	1BL.1RS	**Xscm9**, Iag95	**207**, 1.2 kb	Olson et al., 2010b, Mago et al., 2005, 2011c	rye Petkus	Ug99 avirulent, sticky dough
Sr33	1DS	AtM5F/R	-	Periyannan et al., 2013	*Ae. tauschii*	Ug99
Sr35	$3A^mL$	**Xcfa2170**, AK335187	~**180**/190, ~205/205+290	Zhang et al., 2010; Saintenac et al., 2013	Marquis Sr35, *T. monococcum*	Ug99 and its variants, TTKST and TTTSK
Sr36	2BS-2GS	**Xgwm271**, Xgwm319,	**171**, 168, **187**, **107**; 195;	Olson et al., 2010b, Yu et al.,	SD00W024, from *T. timopheevi*	TTTSK virulent

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			Xwmc477, **Xgwm501**; Xstm773; Xbarc51, Xcfa2076	236/327, 207/211	2010b, Bariana et al., 2001; Bernardo et al., 2013	wheat	
	Sr39/Lr 35	T2BS/2S	**Sr39#22r**; Xrwgs27, Xrwgs29	**780**, 740/710, 540/550	Niu et al., 2011, Mago et al., 2009	RL5711, *Ae. Speltoides*, T2BS/2S#2, RL6082, RWG1(2.87%) and RWG3 (3.6%)	Ug99 (TTKSK, TTKST, TTTSK) Lr35 for APR
	Sr40	T2BL/2G #2S	Xwmc474, Xwmc661, Xgwm344; **Sr39#22r**	150/135, 188/230, 264/132; **820**/818 (M13)	Yu et al., 2010b; Bernardo et al., 2013	RL6088, from *T. timopheevi* wheat	Ug99 all variants, seedling and APR
	SrTA10 171	7DS	Xgdm88, Xwmc827	118/116, 132/171	Olson et al., 2013	TA10171, *T. tauschii*	Ug99
	SrTA10 187	6DS	Xcfd49, Xbarc173	196/219, 275/237	Olson et al., 2013	TA10187, *T. tauschii*	Ug99
	Sr1R	1RS	Xib-262	210	Mago et al., 2002	Rye Imperial	Ug99 all variants, Sticky dough
	Sr1RS^{am} ^{igo}	1AL.1RS	Xscm9; TSM120	242 (M13); 377 (M13)	Saal and Wricke, 1999; Olson et al., 2010b; Kofler et al., 2008	Rye Insave, TAM 107, TAM 112	Ug99
Stripe rust	*Yr5*	2BL	**Yr5STS7/8**, Yr5STS9/10, Xbarc349, Xwmc175, Xbarc167, S19M93-100F/R, S23M41-275F/R	**478**/472, 439/433, 115, 270/280, 277/274, 100/null, 275/210	Chen et al., 2003; Murphy et al., 2009; Smith et al., 2007	*T. aestivum* L. ssp. *spelta*, UC1041, UC1107	Non race specific all stage
	Yr15	1BS	**Xbarc8**, Xgwm413	**250**/280, 110/120	Murphy et al., 2009	*T. turgidum* ssp. *dicoccoides*, UC1041, UC1107	Non race specific all stage
	Yr36	6BS	Xucw125, Xucw130	143, 161	Fu et al., 2009	*T. turgidum* ssp. *dicoccoides*,	Effect from 25 to 35 °C

	Yr43	2BL	Xgwm501, Yr5STS7/8	166/172, 480	Cheng et al., 2010	RSL65 IDO377s	PST-43, PST45 avirulent
	Yr44	2BL	Xgwm501, Yr5STS7/8	130/140, 482/476	Sui et al., 2009	Zak	PST-43, PST45 avirulent
	Yr53	2BL	Xwmc441, Xgwm501, Barc349, Yr5STS7/8	151/159, 130/(140, 150), 105, 478/472	Xu et al., 2013	PI 480148	Most races
Seed quality							
LMW-Glutenin	*Glu-A3 (1, 2, 3)*	1AS	*GluA3a, A3b, A3ac, A3d, A3e, A3f, A3g*	529, 894, 573, 967, 158, 552, 1345	Wang et al., 2010; Zhang et al., 2004	Glenlea NILs, Aroona NILs, Chinese spring (a), Sunco (b), Cheyenne (c), Sunlin (d), Halberd (e), Rescue (f), Glenlea (g)	Dough extensibility, Glu-A3-11 to 17; Glu-A3-21 to 24; Glu-A3-31 to 36, dough strength: b>d>e>c
	Glu-B3 (1, 2, 3, 4)	1BS	(*a, b, c, d, e, fg, g, h, i*) SB1F/R, SB2F/R, SB3F/R, SB4F/R, SB5F/R, SB6F/R, SB7F/R, SB8F/R, SB9F/R	1095, 1570, 472, 662, 669, 812, 853, 1022, 621	Wang et al., 2009; Zhao et al., 2007b; Sui et al., 2010	Cheyenne NILs, Chinese spring (a), Sunco (b), Halberd (c), Cranbrook (d/i), Matong (g), Silverstar (h), Norion 61 (i)	Significant than A3 and D3, Glu-B3-11 to 15, 21 to 23, 31 to 34, 41 to 45. Dough strength: i>b=a>e(f, g, h) > c
	Glu-D3 (1,2,3,4, 5,6)	1DS	(*a, b, c, d, e*) D3F3/D3R3, D3F63/D3F64, D3F22/D3R31,	941, 982, 974, 701, 880, 855	Gupta and Shepherd 1990; Zhao et al., 2006; Zhao et al., 2007a,	Chinese spring (a), Sunco (b), Halberd (c) Norin 61 (d); Hartog (e),	e>b>a>c>d; Glu-D3-11, 12, D3-21, 22, 23, D3-31, 32, D3-41, 42, 43; Glu-

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			S2F21/S2R21, S1F11/S1R11, S3F31/S3r33		b		D3-5, D3-6;
Gliadin	*Gli-A1*	1AS	GliA1.2 (*Glu-A3d*)	168	Zhang et al., 2003, Metakovsky et al., 1984	-	γ, ω
	Gli-B1	1BS	GliB1.1 (*Glu-B3b*), GliB1.2 (*Glu-B3a, B3h*)	369, 397	Zhang et al., 2003	-	γ, ω
	Gli-D1	1DS	GliD1.1 (*Glu-D3a, D3b*), GliD1.2 (*Glu-D3c)*	264, 270	Zhang et al., 2003	-	γ, ω: Dough tenacity, less extensibility
HMW glutenin	*Glu-A1*	1AL	UMN19	*A1b*=Ax2*=344/ *A1a*=Ax1=362 (No M13 label);	Liu et al., 2008a	-	*A1b* has better dough strength
	Glu-B1	1BL	BxMAR	*B1e*=**Bx20**+By20 =800, *B1b*=**Bx7**+Bx8=520, *B1al*=**Bx7^{OE}**+Bx 8*=563	Butow et al., 2004; Ragupathy et al., 2008; Shan et al., 2007; Lei et al., 2006	Prospur, Nordic, Red River 68, Glenlea	*B1al* has higher dough strength
	Glu-D1	1DL	UMN25, UMN26	*D1d*=Dx5+Dy10 =281+397/*D1a*= Dx2+Dy12=299+ 415 (No M13 label)	Liu et al., 2008a; Shan et al., 2007	TAM 111 (2+12); TAM 112 (5+10)	Dough strength, bread making
Polyphenol oxidase	*PPO-A1*	2AL	PPO18	*A1a*=876=low/*A1b*=685=high	Sun et al., 2005	TX07A001118, Anton,	AY596268, Low PPO is fvorable
	PPO-	2AL	PPO33	*A1a*=481=low/*A1*	He et al., 2007	-	-

	A1			*b*=290			
	PPO-D1b	2DL	PPO29	*D1b*=high=490	He et al., 2007	TX07A001118, Anton, Mace	AY515506
	PPO-D1	2DL	PPO16	*D1a*=low=713/*D1b*=high=null	He et al., 2007	-	-
Starch synthase	*Wx-A1*	7AS	AFC/AR2	*A1a*=389/*A1b*=370 (null);	Nakamura et al., 2002	TX07A001118, TX06A001281 (null)	8 types including wild and mutant alleles at all three loci, null is favorable
	Wx-B1	4AL	BDFL/BRC1, BFC/BRC2; AFC/AR2	*B1a*=778, *B1b*=668=null; *B1a*=410/B1b=null; 441(M13)/null	Saito et al., 2009; Nakamura et al., 2002	RioBlanco, Yukon, TX1281, KS020638-5-1, OK08328	-
	Wx-D1	7DS	Waxy-D1, BDFL/DRSL	*D1a*=2307/*D1b*=1731=null	Nakamura et al., 2002	NX04Y2107 (Mattern)	-
Puroindoline	*Pina-D1*	5DS	pTa31	*D1a*=350 (soft)/*D1b*=null	Gautier et al., 1994	Gallagher, OK07231	-
	Pinb-D1	5DS	pTa19B2	*D1a*=337/*D1b*=241(M13) (hard)	Gautier et al., 1994	Most HRWW	Pinb-D1b: higher flour yield, lower ash, larger loaf volume, and better crumb grain score.
Pre-harvesting sprouting	*Qphs.pseru-3AS*	3AS	Xbarc12, Xbarc321	218 (M13), 187 (M13)	Liu et al., 2008b	KS06HW46-3, TX04M41021, Armour, T153, T154, T155, OK04111, TX03A0563, KS970187-1-10	-
Rye translocation							
1AL.1RS	*Gb2, Gb6,*	1RS	Xscm9, PAWS5/S6	228, 220+320 (Amigo)/220(GR	Saal and Wrick, 1999; Porter et al.,	Insave (Amigo, TAM 107, TAM	Gb2: GBC; Gb6: GBE, GBI, GBK;

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	cmc3, Sr1R(Amigo), Pm17			S1201)	1991; Lu et al., 2010	112, TAM 200; GRS1201, N96L9970)	GRS 1201-1205: GBB, C, E, G.
1BL.1RS	*Lr26/Sr31/Yr9, Pm8, Dn2414*	1RS	Xscm9	207	Schlegel and Meinel, 1994; Tsunewaki, 1964; Mago et al., 2002	Wheat line Kavkaz, from Petkus rye	-
Plant height							
	Rht1 (Rht-B1b)	4BS	BF/MR1, BF/WR1; KASPar SNP	237, 237 (complementary);	Ellis et al., 2002; Brown-Guedira et al., unpublished data, 2013	Most hard red winter wheat	Reduce leaf elongation, coleoptile length, GA insensitive (GAI)
	Rht2 (Rht-D1b)	4DS	DF-MR2, DF2-WR2; SNP	254, 264;	Ellis et al., 2002; Brown-Guedira et al., 2010	Most soft red winter	Reduce leaf elongation, coleoptile length, GAI
	Rht3 (B1c)	4BS	RAPD S1060, Xpsr584	1900/2000	McVittie et al., 1978; Wan et al., 2001	Tom Thumb	GAI
	Rht10 (D1c)	4DS	Maybe allelic with Rht2	-	Sasakuma and Izumi, 1983	Ai-Bian#1	GAI
	Rht11(Rht-B1e)	4BS	BF/WR3, BF/MR3	-	Ellis et al., 2004; Divashuk et al., 2012	Karlik	GAI

	Rht17	-	-	-	Ellis et al., 2004	Chris M	GAI
	Rht4	2BL (0.89-1.0)	Xwmc317	170/150	Ellis et al., 2005	Burt ert	GA responsive (GAR)
	Rht5	3BS (0.78 – 1.0)	Xbarc102	200/165	Ellis et al., 2005	Marfed M,	GAR
	Rht8c	2DS	Xgwm261	193	Ellis et al., 2007	Rare, ChuanMai 18	GAR, No effects on coleoptile length
	Rht9	5AL (0.35 – 0.57)	Xbarc151	220/230	Ellis et al., 2005	Maria	GAR
	Rht12	5AL 0.87-1.0)	Xwmc410	114/112	Ellis et al., 2005; Ellis et al., 2004	Mercia 12	GAR, No effects on coleoptile length
	Rht13	7BL (0.63-0.78)	Xwms577	130/120	Ellis et al., 2005	Magnif 41 ert1	GAR
Photoperiod sensitivity	*Ppd-D1*	2DS	Ppd-D1-F/R2+R1	*D1a*=288=insensitive/*D1b*=414	Yang et al., 2009	-	-
Vernalization genes	*Vrn-A1*	5A	CDO708	*A1a*=147=weak winter/*A1b*=132= Intermediate	Chen et al., 2010	Jagger	Affect stem elongation and maturity

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Vrn-D3	7D	Vrn-D3F6/R8	*D3a*=421=early/ *D3b*=420=late	Wang et al., 2009	Jagger/2174	Affect heading date and maturity

†‡ The underlined markers means that that marker is more diagnostic. The base pair size in front of "/" is the positive one showing genes. The band base pair size was from the respective published papers. It is the original base pair size if not tailed by M13 (extra 18 or 19 bp).

§The biotypes or races the gene showing resistance to or phenotypic effects from the genes on target traits.

Supplementary Table S2. Molecular markers linked to various genes screened on diverse germplasm lines of hard winter wheat collected from breeding programs in the U.S. Great Plains.

Genes	Markers	Total No. of alleles	Diagnostic†	No. of screened lines	Allele present‡	Target band size and present in lines§	Note¶
1AL.1RS	Xscm9	2	Yes	24	3	224 (3)	TX99A0153-1, KS98W0421-1-4, and KS98W0259-4-5
Dn6	Xgwm44	14	No	55	1-48	182 (6)	
Dn6	Xgwm111	3	No	8	3-7	225	
Gb3	Xgwm37	4	No	15	2-9	178 (4)	
Gb3, Gbz	Xgwm428	7	No	15	1-13	135	
Gb3, Gbz	Xbarc76	1	No	15	9	214 (9)	
Gb3	Xwmc634	12	Maybe	40	1-22	227 (2)	
Gb3	Xgwm428	7	No	15	1-13	Not sure	TA4063.2 (*Gbd*) has 132 bp, Amigo has 138 bp
Gbx1	Xwmc671	13	Yes	55	1-8	120 (1)	KS89WGRC4
Gbx1	Xgdm150	14	No	55	1-33	110 (1), 119 (1)	TX99A0153-1, CO960293-2
Gbz	Xgdm46	4	No	15	2-13	135 (7)	125 bp is unique in TA4152L94 and TA4152L24
Gbz,	Xwmc157	13	Maybe	55	1-16	150 (1)	KS82H1640GB has *Gb3* (*Gb4*) but TAM

Gbx1						112 has 140 bp
H13	Xcfd42	13	No	55	1-8	180 (6)	
H13	Xcfd213	4	No	55	41-43	229 (43)	
H13	Xcfd132	5	No	55	1-42	160 (5)	N96L9970 has 116 bp
H13	Xgdm36	2	No	8	1-4	170	128 bp only in KS09WGGRC51-J (*H21*) but not in Molly (*H13*)
H25	Xgwm610	12	Maybe	55	1-25	152 to 154 (1), 158 to 164 (1), 170 to 174 (2)	KS99WGRC42 (*Hdic*) has 152 to 154 bp and 158 to 164 bp but KS92WGRC20 (*H25*) has 170-174 bp (Dn6 source CO960223 also has)
H25	Xgwm397	7	Yes	8	1-5	170 (1), 194 to 198 (1)	only in KS92WGRC20 (H25)
H26	Xrwgs10	10	Maybe	55	1-18	837	
H26	Xrwgs12	5	Maybe	55	1-43	270	
Hdic	Xgwm33	2	No	8	6	130 (6)	
Lr17a	Xwmc382	11	Maybe	55	1-40	217 (1)	TAM 401 has 217 bp but Kelse has 219 +235, TAM 203 has 184 bp
Lr17a	Xgwm636	12	No	55	1-17	100 (2)	KS93WGRC26 and TAM 111 have 100 bp
Lr17a	Xwmc667	14	Maybe	55	1-20	164 (1)	Halt has 164 bp but TAM 203 does not. No bands shown in TAM 203
Lr17a	Xgwm614	7	Yes	27	1-10	134 (1)	TAM 304 has 134 and 162 bp
Lr17a	Xwmc407	3	Maybe	27	3-10	149	TAM 111, TAM 304, and Sr22TB have 135 bp
Lr19/Sr25	XBF1459 35	5	Yes	24	1-22	198+180 (1)	LcSr25Ars has 196+197 bp
Lr22a	Xgwm296	11	No	27	1-10	131 (7)	TX99A0153-1 has 147 bp, VA06W-49 has 151 bp, VA06HRW-108 has 155.7 bp
Lr24/Sr24	Lr24#12	2	No	55	1-22	500	112 bp is in Stars9302W but no lines show 500 bp
Lr41	Xbarc124	8	No	27	1-9	182+206 (-184)	RL6082 has 253 bp
Sr2	Xgwm533	4	No	24	1-14	120 (14)	LcSr25Ars (*Sr25*) has 100 bp, TAM 111 has 105 bp, KS09WGGRC51-C (*H21*) has 115 bp

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	XBE5183						only Triumph64 does not have 303 bp but
Sr26	79	1	No	55	53	303 (54)	Eagle has
Sr26	Sr26#43	4	No	55	1-10	211 (1)	only RL6082 has 211 bp band but not eagle
Sr35	Xcfa2170	8	Yes	27	1-15	181 (1)	only present in Mq(2)5_G2919, Agent has 187 bp
Sr36	Xgwm271	8	Maybe	27	1-20	171	TAM 400 has 106 + 161.6 bp, TAM 401 has 161.6 bp
Sr36	Xgwm501	7	Maybe	24	1-6	107 (1)	VA06W-49 has 107 bp and TAM 111 has 202 bp
Sr36	Xwmc477	3	Maybe	24	9-23	187	LcSr25Ars has 177 + 179 bp
Sr36	Xgwm319	4	No	24	1-24	168	
Sr40	Xwmc344	4	No	55	1-25	264	Only RL6082 (*Sr39*) has 231 bp
Sr40	Xwmc474	2	No	27	7-24	150	susceptible band (135 bp) present in R source, RL6088
Sr40	Xwmc661	3	No	27	3-17	188	RL6088 has 172 bp as well as Agent and KS93WGRC26 (*H26*)
Yr5	XSTS7/8	2	Maybe	27	1-2	478	TAM 304 has 286 bp, Eagle has 288 bp
Yr5	Xbarc349	7	No	55	1-32	115	104-108 bp showed in Stars9302W. Two bands 94 bp and 104 bp showed in UC1041 also appeared in other 19 and 32 lines.
Yr15	Xwgp34	5	No	55	1-13	Not sure	108 appear in Stars 9302W, 94.5 bp showed in UC1041 also appeared in other 5 lines.

† Markers showing unique band on certain lines which has the target gene; There are nine lines for RWA, seven for Hf, 15 for GB, 21 for rusts, and three for wheat streak mosaic (WSM).

‡ Various marker alleles present in screened lines among a total of 55 lines. '1-48' means that at least one allele of marker Xgwm44 was shown in one line and another alleles was showed in 48 lines among those 14 alleles from this marker.

§ Base pair size are based on labeled primers from corresponding cited papers (Supplementary Table S1). Most of them are not M13 labeled. The number inside the parentheses is the number of lines with the target bands. No parenthesis means no line has the target band. The marker data were collected in the wheat breeding laboratory of Virginia Tech at Blacksburg, VA and USDA-ARS Eastern Regional Small Grains Genotyping Lab at Raleigh, NC using ABI3130xl. Marker screening procedures were followed protocols from Liu et al. (2013b).

¶ Note for unique bands present in one line among the pools of lines screened.

Supplementary Table S3. Molecular markers linked to various genes screened on hard winter wheat lines in the Southern Regional Performance Nursery (SRPN) from 2008 to 2012 in the U.S. Great Plains.

Traits	Genes	Chrom-osomes	Markers[†]	Target bands[‡]	2008 SRPN (50)	2009 SRPN(46)	2010 SRPN(48)	2011 SRPN (38)	2012 SRPN (44)	Total unique lines[§] (174=37+46+32+28+31)
Height	*Rht-B1b*	4BS	Rht1BF-MR1	T255	43	42	43	36	37	156 (90)
	Rht-D1b	4DS	Rht2,DF-MR2	T270	2	2	0	0	2	6 (3)
	Rht8c	2DS	Xgwm261	T212	2	0	4	3	1	8 (5)
Photoperiod	*Ppd-D1a*	2DS	PPD-D1,R1,R2	T304	-	14	13	13	13	44 (32)
Rye translocation	*1AL.1RS*	1AL.1RS	Xscm9, Xtsm120	T242, T375	9	7	7	3	5	20 (11)
	1BL.1RS	1BL.1RS	Xscm9, Xtsm120	T225, T361	6	3	7	2	3	17 (10)
Hessian fly	*H9*	1AS	Xsopo05	909	6	7	-	-	0	10
	H9	1AS	Xcfa2153	T198	0	0	-		0	0
	H13	6DS	Xgdm36	T186	0	0	-	-	0	0
	H13	6DS	Xcfd132	T166	1	0	-	-	0	1
Leaf rust or Complex	*Lr19*	7EL:7DL	Lr19-130	130	-	2	2	2	0	6
	Lr21	1DS	Lr21-214	214	1	2	0	0	1	4
	Lr34/Yr18	7DS	Xswm10	T206	12	8	-	-	0	18
	Lr34/Yr18	7DS	csLV34	T171	14	6	10	-	0	26
	Lr34/Yr18	7DS	Lr34JagTM	TaqMan SNP	-	-	3	1	4	6
	Lr34/Yr18	7DS	Lr34TM	TaqMan SNP	-	8	10	9	5	26
	Lr34/Yr18	7DS	Lr34TM & Lr34JagTM & Xcssfr6	TaqMan SNP	-	-	7	2	1	8
	Lr37/Sr38 /Yr17	2NS:2AS	Xventriup-Ln2	T275	24	23	22	12	18	80
	Lr39/Lr41	2DS	Xgdm35	T183	0	0	-	-	24	17

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	L39/Lr41	2DS	Xbarc124	T260	2	1	-	-	0	3
	Lr50	3BL	Xgwm382	T156	0	0	-	-	0	0
Stem rust or complex	*Sr2*	3BS	Xstm559	T100	-	12	6	-	0	15
	Sr2	3BS	X3B028F08	No T260	-	30	19	-	0	40
	Lr24/Sr24	3Ag:3DL	Sr24#12	T512	8	5	-	6	16	29
	Lr24/Sr24	3Ag:3DL	Sr24#50	T213	9	5	11	-	0	18
WSMV	*Wsm1*	4Ai#2S	XBG263898	T357	-	2	0	1	0	3
Gluten strength	*Glu-A1b*	1AL	HMWAx	T1319	41	33			0	63
	A1b	1AL	UMN19	T360	-	28	28	25	33	90 (66)
	Glu-B1a	1BL	BxMAR	T529	-	43	48	37	30	122
	B1al	1BL	BxMAR	T568	-	1	1	0	0	2
	B1e	1BL	BxMAR	T691	-	1	1	1	1	3
	B1i	1BL	HMWBx	T669	12	8	-	3	6	14
	Glu-D1d	1DL	HMWDx	Dx5=T478	42	39	-	-	0	69
	D1d	1DL	UMN25/UMN26	T298/T410	-	34	32	25	34	103 (75)
	D1a	1DL	UMN25/UMN26	T315/T428	-	6	12	13	11	28 (20)
Polyphenol oxidase	*PPO-D1a*	2DL	PPO16	713	-	28	26	32	27	103 (75)
	PPO-D1b	2DL	PPO29	T502	-	38	41	-	38	94
	PPO-A1a	2AL	PPO18	T889/T694	-	3	1	4	4	9 (7)
Grain texture	*Pina-D1b*	5DS	pTa43	No 349	3	10	-	2	0	14 (10)
	Pinb-D1b	5DS	pTa19B2	T240	41	31	-	31	0	85 (60)
Waxy type	*Waxy-A1*	7AS	AFC-AR2	A1a/b= T402/T383; B1a/b= 423/null	0	4	6	5	1	14 (8)
	Waxy-B1	4AL	BDFL-BRD	T243	7	7	5	10	9	37 (21)

	Waxy-D1	7DS	BDFL-DRSL	T314	0	0	-	2	0	1 (1)
Xgwm261.165	-	2DS	Xgwm261	T183	-	23	21	17	21	65
Xgwm261.174	-	2DS	Xgwm261	T192	-	1	4	0	5	7
Xgwm261.210	-	2DS	Xgwm261	T228	-	4	14	12	13	33
Aluminum tolerance	*ALT QTL*	4D	Xwmc331	T149	11	14	14	7	5	43
	ALT QTL	4DL	ALMT1-SSR3A	T220-250	7	10	-	-	0	14
Fusarium head blight	*Fhb1*	3BS	UMN10	T258	-	1	1	0	0	2
	Fhb1	3BS	Xgwm533	T159	1	4	-	-	0	5
Pre-harvest sprouting	*PHS-3AS*	3AS	Xbarc12	T218	8	5	2	4	0	18 (10)
	PHS-3AS	3AS	Xbarc321	T187	9	8	-	-	0	15 (9)
	PHS-4AL	4A	Xbarc0170	T202 or T214	-	2	21	0	3	20
Vernalization	*Vrn-A1*	5AL	Xcdo708	T129 (winter)	-	39	34	30	25	128 (74%)
	Vrn-A1	5AL	Vrn-A1-SNP	SNP	-	9	7	-	0	16
	Vrn-D3	7D	Vrn-D3-F6R8	T422 (early)	-	26	30	16	24	96 (55%)
Soil borne mosaic virus	*Sbm1*	5D	Xgwm0469		-	-	18	10	0	22
Gluten strength	*Glu-B3c*	1BS	Glu-B3c	T486	-	19	0	0	0	19
	Glu-B3e	1BS	Glu-B3e	669	-	46	-	-	0	46

† The markers data were summarized from the Southern Regional Performance Nursery (SRPN) for the hard winter wheat screened at the USDA-ARS Central Small Grain Genotyping Laboratory and Hard Winter Wheat Genetics Research Unit, Manhattan, KS (http://www.ars.usda.gov/Research/docs.htm?docid=11932, accessed on August 10, 2013).

‡ Base pair size may change based on the platform for screening. Most of them are based on ABI M13 tailed forward primers (with "T" in the front of band size).

Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

[§] Percentage inside of the parentheses has been adjusted based on the number of unique lines screened that year.

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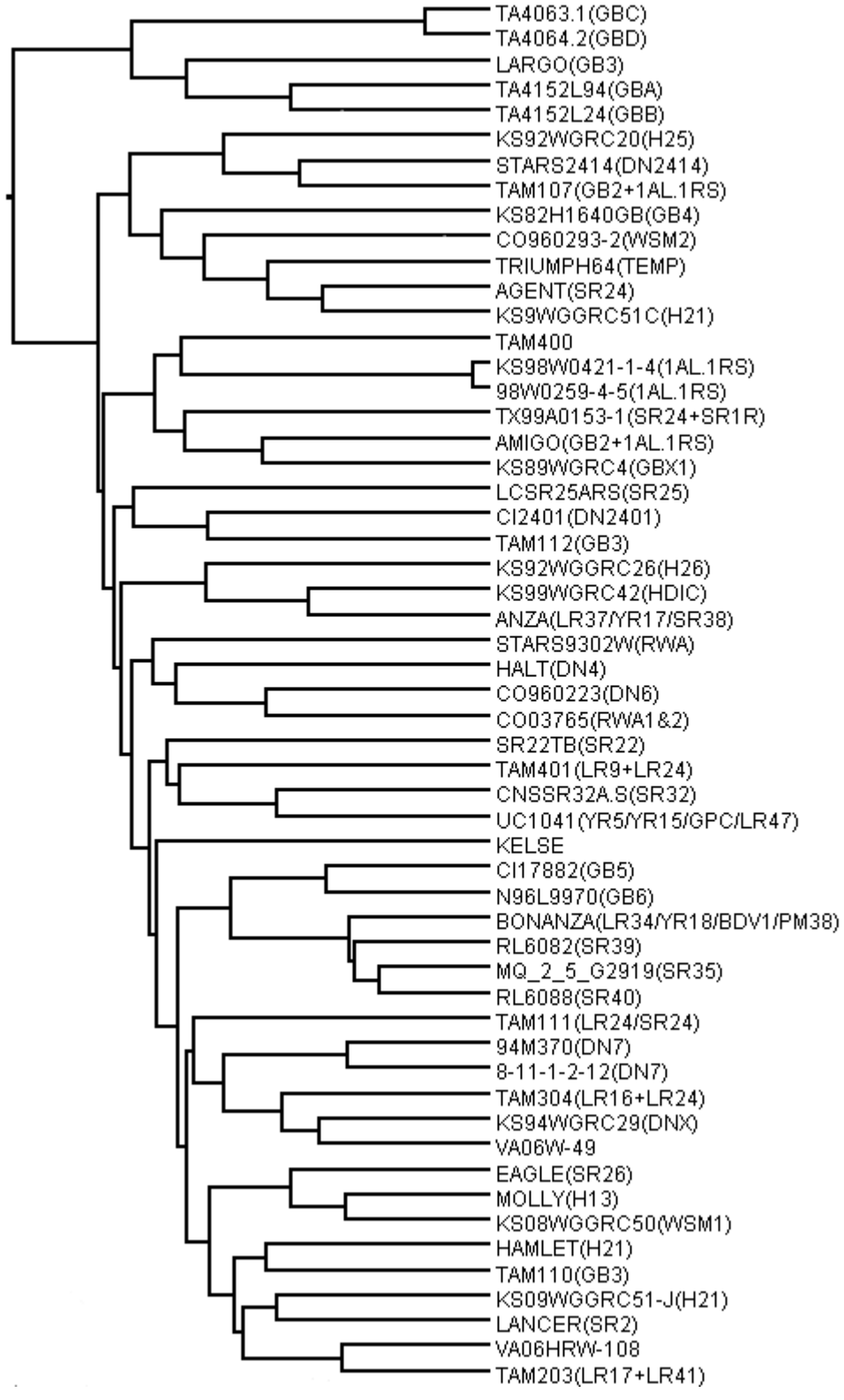
Supplementary Fig. S1



Crop Science Accepted paper, posted 02/21/2014. doi:10.2135/cropsci2013.08.0564

Supplementary Fig. S2