IDENTIFICATION AND INTROGRESSION OF NOVEL GENES FOR STEM RUST UG99 RESISTANCE FROM RELATIVE SPECIES OF WHEAT

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Wheat stem rust, caused by *Puccinia graminis* Pers.: Pers f. sp. *tritici* Eriks. & E. Henn. (*Pgt*), is a destructive disease that can cause severe yield losses in wheat. A new *Pgt* race Ug99 (TTKSK), which was first identified in Uganda in 1998, has overcome many important stem rust resistance (*Sr*) genes. There is an ongoing world-wide need to identify new and effective resources of resistance. The objectives of this study were to transfer the Ug99-effective *Sr* genes from wheat-grass species *Thinopyrum junceum* to hexaploid wheat through chromosome engineering and to identify and map new *Sr* genes from tetraploid wheat *Triticum turgidum* ssp. *carthlicum.* A wheat 'Chinese Spring' (CS) –*Th. junceum* disomic addition line, HD3505, was identified to be resistant to *Pgt* races in the Ug99 race group. We transferred the *Sr* gene from HD3505 into CS through chromosome engineering. I identified three BC_2F_1 plants with reduced *Th. junceum* chromatin (BG2133, BG5136, and BG2161) carrying the stem rust resistance. This new gene is located on a wheat group-4 chromosome based on the molecular data. To identify and map the new *Sr* genes in tetraploid wheat, a population of 190 recombinant inbred lines was developed from a cross between *T. turgidum* ssp. *carthlicum* (PI 387696) and susceptible durum wheat line Rusty. This population was screened with TTKSK, TRTTF, and TMLKC and genotyped using the wheat 90K iSelect array. A major QTL was identified and mapped to the genomic region harboring the *Sr13* locus on 6AL. Molecular markers for *Sr13*, including *BE403950, CK207347* and *KASPSr13*, indicated that resistance in PI 387696 was due to the *Sr13* gene. But evaluation of genetic stocks carrying *Sr13* with specific races at different temperature conditions indicated that resistance in PI 387696 is due to new allelic form of *Sr13* or due to other novel *Sr* gene close to *Sr13* locus. The marker validation showed that two newly-developed STARP markers *Xrwgsnp6* and *Xrwgsnp7* can be used for marker-assisted selection of *Sr13* in

wheat breeding programs. The novel genes or alleles identified in this research provide resistance against TTKSK and other emerging *Pgt* races and they can be used in wheat improvement.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. GENERAL INTRODUCTION

Stem rust, caused by *Puccinia graminis* Pers.: Pers. f. sp. *tritici* Eriks. & E. Henn (*Pgt*), is historically a devastating disease responsible for large losses of wheat yields. Several wheat stem rust epidemics occurred in many wheat-growing countries in the 20th century. In the U.S., this disease destroyed more than 20% of the U.S. wheat crops several times between 1919 and 1954 (Roelfs, 1978). Stem rust has been successfully controlled for more than 50 years through theremoval of alternate host barberry (*Berberis vulgaris* L.) and utilization of resistant cultivars (Singh et al., 2006). But in 1999, a highly virulent *Pgt* race, designated Ug99 (TTKSK), was detected in Uganda and caused a major threat to global wheat production. This race possesses broad spectrum virulence to stem rust resistance (*Sr*) genes, including *Sr31* and *Sr38*, used widely by breeding programs worldwide (Pretorious et al., 2000). Furthermore, TTKSK spread rapidly from Africa to other wheat growing regions and evolved rapidly into several new variants such as TTKST and TTTSK, which overcame *Sr24* and *Sr36*, respectively (Jin et al., 2008a; 2008b).

There are several methods that have been used to control stem rust such as utilization of host resistance genes, application of chemicals, and eradication of barberry. But host resistance is most effective, economic, and environmentally friendly approach to control stem rust in wheat (Ellis et al., 2014). The development of resistance cultivars by using the *Sr* genes is now necessary in many wheat breeding programs. To date, 73 numerically designated resistance genes and alleles have been identified. Out of these *Sr* genes, 39 are effective or partially effective against TTKSK and its variants, such as *Sr2*, *Sr13*, *Sr22*, *Sr33*, *Sr35*, *Sr45*, and *Sr46* (Singh et al., 2015). Because new virulent races are constantly emerging to overcome *Sr* genes

that were deployed in the cultivars, it is necessary to identify new *Sr* genes from the untapped germplasm in wheat and its related species.

In the wheat gene pool, tetraploid wheat species (*Triticum turgidum* ssp. *carthlicum*, *dicoccum*, *dicoccoides*, *durum*), and numerous species in the genera *Thionpyrum* (*Th. ponticum, Th. intermedium*), are promising sources of new genes for germplasm improvement of hexaploid common wheat (*T. aestivum* L.) and durum wheat (*T. turgidum* ssp. *durum*) (Mujeeb-Kazi et al., 2013). To date, many *Sr* genes from these species have been transferred into common wheat such as, *Sr13* (Knott, 1962), *Sr14* (Knott, 1962), *Sr25* (McIntosh et al., 1976), *Sr26* (McIntosh et al., 1976), *Sr32* (McIntosh et al., 1995), *Sr43* (Niu et al., 2014), *Sr53* (Liu et al., 2011a), and *Sr51* (Liu et al., 2011a). Gene transfer from the primary gene pool is a straightforward process with direct hybridization, selection, and homologous recombination or by synthetic wheat production. However, transfers of genes from wild relatives into durum and common wheat involve more complex work in chromosome engineering, which includes a series of steps such as intergeneric hybridization, generation of amphiploids, backcrossing, selection, and induction and identification of homoeologous recombination (Gill and Raupp, 1987; Qi et al., 2007). Therefore, current efforts of wheat breeding programs are to utilize these species to acquire novel stem rust resistance.

The objectives of this study were to: 1) introgress novel stem rust resistance gene from *Th. junceum* into wheat, 2) identify and map stem rust resistance gene(s) in tetraploid Persian wheat (*T. turgidum* ssp. *carthlicum*).

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CHAPTER 2. LITERATURE REVIEW

Wheat and its genetic improvement

History and cultivation

Wheat domestication occurred about 10,000 years ago during the Neolithic revolution, which was the transition from hunter-gatherer society to a settled agricultural society (Zeder, 2008).The most important traits in the domestication of wheat included larger seeds, loss of seed dormancy, the free-threshing character, enhanced grain quality, and others (Faris, 2014). As a major cereal crop in human diet, wheat continues to evolve along with society due to advancement of civilization.

Wheat is primarily a self-pollinated species and it belongs to the genus *Triticum* L. of the Triticeae tribe in the Poaceae or Gramineae family. Based on the classification by Van Slageren (1994), the *Triticum* genus includes six wheat species which are classified into three sections, including *Monococcon dumort, Dicoccoides flaksb*, and *Triticum*. The three sections contain 17 subspecies with A, B, D, and G genomes such as diploid species *T. monococcum* L. (A^mA^m) and *T. urartu* Tumanian ex Gandilyan (AA), tetraploid species *T. turgidum* L. (AABB) and *T. timopheevii* (Zhuk.) Zhuk. (AAGG), hexaploid species *T. aestivum* L. (AABBDD) and *T. zhukovskyi* Menabde & Ericz. (AAAAGG). Wheat species that are grown today are primarily of hexaploid common or bread wheat (*T. aestivum* L.ssp. *aestivum*, 2n = 6x = 42, AABBDD) and tetraploid durum wheat (*T. turgidum* L. ssp. durum, 2n = 4x = 42, AABB), which comprises 96% and 4% of wheat production acreage, respectively (Gill et al., 2004).

Tetraploid durum wheat is an allotetraploid with A and B genomes containing 14 pairs of chromosomes, whereas hexaploid bread wheat is an allohexaploid species with genomes A, B, and D, contains 21 pairs of chromosomes. These chromosomes pairs are placed into seven

homoeologous groups (Kimber and Sears, 1987). Both tetraploid and hexaploid wheat originated from one and two interspecific hybridization events between wild ancestors followed by spontaneous chromosome doubling, respectively (Faris et al., 2002). The first event was the spontaneous hybridization between the wild diploid wheat *T. urartu* (2n = 2x = 14, AA), the donor of A genome, and goatgrass species *Aegilops speltoides* Tausch (2n = 2x = 14, SS), a putative donor of the B genome, which led to the formation of wild emmer wheat *T. turgidum* ssp. *dicoccoides* (Körn.) Thell (2n = 4x = 28, AABB). Hybridization of cultivated emmer wheat (*T. turgidum* ssp. *dicoccum,* AABB) with the goatgrass *Aegilops tauchii* (Coss.) Schmal. (2n = 2x = 14, DD) the donor of the D genome, formed bread wheat (AABBDD) (Feldman et al., 2012). These two rounds of hybridization in the evolution process contribute to a large and complex size of common wheat genome. It has a 17 Gb DNA composed of approximately 80% repeats (Brenchley et al., 2012).

Wheat is a significant food for human nutrition and provides food for 35% of the world's population and is the third highest cereal produced worldwide behind rice and maize. In 2016, global wheat production was 749 million tonnes with an average yield of 3.3 tonnes per hectare, with the widest cultivated areas (220.4 million hectares, 2014) (http://faostat.fao.org/). The world population will be around 9 billion in 2050; therefore, the global agricultural production will be increased to meet the food demand of the growing population (Mckenzie and Williams, 2015). For example, wheat production will increase 60% by 2050 to meet the rising demands (Ray et al., 2013). To reach that goal, world wheat output could be increased by either improving the yield per acre or increasing the planting acreage. Based on wheat breeding programs and genetic improvement methods, the world wheat yield has been increased from 25k hectogram per hectare (Hg/Ha) in 1990 to 33k Hg/Ha in 2014 while harvesting areas had decreased from 230 million

hectares in 1990 to 220 million hectares in 2014 (http://faostat.fao.org/). Therefore, improving crop yields to meet these rising demands, rather than clearing more land for agriculture has been a preferred solution to meet that production goal.

World wheat production is presently facing many challenges, such as gradual decrease of wheat genetic variability, emergence of novel pathogens and pests, and abiotic stresses. In recent decades, the dangers of a narrow genetic base of the wheat crops due to extensive utilization of elite cultivars in the past century have become a great global concern (Warburton et al., 2006). Biotic factors such as diseases and pests are also known to reduce grain yield potential and quality. Around 200 diseases and pests have been documented and nearly 50 considered important because they have potential to damage food crops (Weiss, 1987). Overall, it is estimated that approximately 18% of the world wheat grain yield is lost each year due to diseases and pests (Oerke, 2006). Environmental stresses also affect wheat yield, such as drought, cold, minerals, salinity, and water logging (Collins et al., 2008). In the last six decades, a tremendous improvement in wheat production has been achieved through intensive development and utilization of elite wheat cultivars with resistance to various biotic and abiotic stresses. For future wheat improvement, it is essential to broaden the genetic diversity of the wheat germplasm resources, which can provide the resistance against diverse abiotic and biotic stresses (Mujeeb-Kazi et al., 2013).

Wheat gene pools for germplasm improvement

The species in Triticeae tribe are favorable source for wheat research due to their great potential for wheat improvement by utilization of the genetic diversity of wild relatives. The tribe Triticeae consists of about 360 economically important grass species classified under 20–30 genera, such as *Aegilops*, *Agropyron*, *Amblyopyrum*, *Dasypyrum*, *Elymus*, *Eremium*, *Hordeum*,

Hordelymus, *Leymus*, *Psathyrostachys*, *Secale*, *Stenostachys*, *Thinopyrum*, *Triticum*, etc. (Bernhardt, 2015; Barkworth et al., 2009). A majority of the Triticeae species (except for *Triticum* species and *Ae. tauschii*) carry genomes that are homoeologous to wheat genomes A, B, and D and have variable crossability with wheat (Cai et al., 2005). Based on their variable crossability, cytogenetical and evolutionary relationships, homologous and homoeologous chromosome pairings, cultivated wheat and its relatives can be divided into three major gene pools: primary, secondary, and tertiary (Jiang et al., 1994; Chaudhary et al., 2014).

Primary gene pool for wheat improvement

The primary gene pool includes the hexaploid bread wheat landraces, cultivars, and breeding lines, wild and cultivated tetraploid wheat (*T. turgidum*), and *Ae. tauschii* Coss. Gene transfer from the primary gene pool is an easy process using hybridization, backcrossing, selection, and homologous recombination by direct crossing of these species with hexaploid wheat or by making synthetic wheat (Qi et al., 2007; Gill and Raupp 1987). This primary gene pool has been extensively used for wheat improvement both regionally and globally. In 1935, a semi-dwarf wheat cultivar 'Norin 10' was produced in Japan. Dr. Norman Ernest Borlaug and his colleagues at the International Maize and Wheat Improvement Center (CIMMYT) used 'Norin 10' to develop new cultivars which triggered the first Green Revolution in the 1960s (Reitz and Salman, 1968). Besides that, some important genes for biotic and abiotic stresses have also been transferred into common wheat from the primary gene pool, such as stem rust resistance genes *Sr2*, *Sr13*, and *Sr14* from *T. turgidum* ssp. *dicoccum*, *Sr21*, *Sr22*, and *Sr35* from *T. monococcum*; powdery mildew resistance genes *Pm16* and *Pm50* from *T. turgidum* ssp. *dicoccoides;* Hessian fly resistance genes *H26* and *H32* from *Ae. tauschii* (Cox et al., 1994; Sardesai et al., 2005; George Fedak., 2015) and leaf rust resistance genes *Lr14a*, *Lr23*, and *Lr61*

from *T. turgidum* ssp. *durum* (Dyck and Samborski, 1968; McIntosh and Dyck, 1975; Herrera-Foessel et al., 2008), *Lr53* and *Lr64* from *T. turgidum* ssp. *dicoccoides* (Marais et al., 2005; JA Kolmer et al., 2010) and *Lr63* from *T. monococcum* (Kolmer et al., 2010).

Besides the direct interspecific and intergeneric hybridization and backcrossing, amphiploization is another good way for gene introgression from the primary gene pool related species to common wheat (Cox, 1997). Synthetic hexaploid wheat (SHW), which are created from the hybrids between tetraploid wheat (*T. turgidum*) and wild ancestor *Ae. tauschii* (McFadden and Sears, 1946), proved to be the preferred source of new genes for the improvement of bread wheat. In the 1980s, L.R. Joppa developed a number of SHW from the durum wheat cv. 'Langdon'and different *Ae. tauschii* accessions (Friesen et al., 2008; Xu et al., 2010). From 1988 to 2010 at CIMMYT, around 1,300 SHW were developed by using about 50 durum genotypes and 900 *Ae. tauschii* accessions (Ogbonnaya et al., 2013). Many SHW lines have been found to be resistant to the major wheat diseases and pests (Xu et al. 2004; Friesen et al., 2008; Yu et al., 2012) and numerous novel or unique genes for disease and pest resistance in the SHW lines were identified from *Ae. tauschii*, such as *Sr33, Sr45, Sr46, Gb3, Gb7, Cre3, Stb5, Yr28, Rkn, Dn3,* and *H26* for wheat production improvement (Ogbonnaya et al., 2013; Yu et al., 2015).

Secondary and tertiary gene pool for wheat improvement

The secondary gene pool consists of the *Triticum* and *Aegilops* species that share at least one of A, B, or D genomes of hexaploid wheat. The *Triticeae* tribe also contains hundreds of species which carry genomes other than A, B, and D and these species constitute the tertiary gene pool such as the species in genera *Agropyron*, *Amblyopyrum*, *Dasypyrum*, *Eremium*, *Hordeum*, *Hordelymus*, *Secale*, *Psathyrostachys*, *Stenostachys*, *Thinopyrum*, etc. Gene transfer

from alien species in the secondary and tertiary gene pools into cultivated wheat is a complex and difficult process. Chromosome engineering is the best strategy for alien gene introgression in wheat which involves the production of amphiploids and chromosome addition, substitution, and translocation lines (Qi et al., 2007; Mujeeb-Kazi et al., 2013).

Chromosome pairing in wheat is controlled by the *Ph1* (pairing homoeologous) gene on chromosome arm 5BL. It can be manipulated to induce homoeologous recombination between chromosomes in order to achieve gene transfer that normally do not pair (Qi et al., 2007). However, wheat lines possessing gene the mutant *ph1b* showed homoeologous recombination between wheat chromosomes of different genomes (Sears, 1977). Many translocation lines have been developed by using the *ph1b* mutant, including lines carrying the stem rust resistance genes such as *Sr32* (Mago et al., 2013), *Sr39* (Niu et al., 2011), *Sr43* (Niu et al., 2014), *Sr47* (Klinworth et al., 2012), *Sr51* (Liu et al., 2011a), and *Sr53* (Liu et al., 2011b). In addition to the *ph1b* mutant, the *Ph1* gene inhibitor (Ph^I) has been transferred from *Ae. speltoides* to hexaploid wheat 'Chinese Spring' (Chen et al., 1994) to promote the homoeologous recombination between wheat and alien species (Chen et al.,1994). Meanwhile, the Ph^I lines have been successfully used for the integration of alien genes into wheat chromosomes for important traits, such as rust resistance from diverse *Aegilops* species (Aghaee-Sarbarzeh et al., 2002; Chhuneja et al., 2008), or salt tolerance from the species *Th. junceum* (Wang et al., 2003).

In durum wheat, *Ph1*-deficient aneuploids like the durum 5D(5B) disomic substitution (DS) line have been used for alien gene introgression in durum wheat because Ph^I and *ph1b* mutant are not available. Dr. L. R. Joppa used the durum Langdon 5D(5B) DS line to produce a Durum-*Ae. speltoides* 2B/2S translocation line (DAS15) in which the stem rust-resistant gene *Sr47* is present on a large 2S chromosome segment (Faris et al., 2008). Klindworth et al. (2012)

further used the Rusty durum 5D(5B) DS line to create new homoeologous recombinants with very short alien segments carrying *Sr47* from the original translocation DAS15.

Robertsonian translocations have been utilized in a number of resistance breeding studies. Robertsonian translocations are formed by centric misdivision followed by the breakage-fusion mechanism of broken arms (Robertson, 1916). A number of wheat-rye 1RS.1BL Robertsonian translocation lines have been developed and they have contributed to improvement of wheat for disease and insect resistance, such as 1RS.1BL translocation lines carrying the resistance genes *Lr26* for leaf rust, *Yr9* for yellow rust, *Sr31* for stem rust, *Gb2* and *Gb6* for leaf aphids, and *Pm8* for powdery mildew (Mettin, 1973; Zeller, 1973; Bedo and Lang, 2015). A new stem rust *Sr59* gene, from rye was also introgressed into wheat as a 2DS·2RL Robertsonian translocation (Rahmatov et al., 2016). However, the above described mechanism produced random and infrequent homoeologous recombination. For effective utilization of this mechanism, Friebe et al. (2005) made a cross between monosomics of wheat group-1 (1A, 1B, and 1D) chromosomes and disomic chromosomes addition line 1Ht DA derived from wheat-*Elymus trachycaulus* crossing. They found that at anaphase I/telophase I, the 1Ht and 1A univalent underwent misdivision in 6–7% of the pollen mother cells in the hybrids. The frequency of Robertsonian translocations was observed 1–4% in progenies developed from plants monosomic of wheat group-1 (1A, 1B, and 1D) chromosomes and 1Ht chromosome of *E. trachycaulus.* Many wheat-alien species Robertsonian translocation lines have been developed by using monosomics as a tool. These lines carry the beneficial *Sr* genes, such as *Sr44* from *Th. intermedium* (Liu et al., 2013), *Sr51* from *Ae. searsii* (Liu et al., 2011a), and *Sr52* from *Dasypyrum villosum* (Qi et al., 2011).

In addition to the techniques described above, several other approaches, such as ionizing radiations technique used by E.R. Sears to transfer a leaf rust resistance gene from *Ae. umbellulata* (Sears, 1956), somatic cell fusion approach which developed fertile hybrid of wheat × *Agropyron elongatum* (Xia et al., 2003), and gametocidal genes (*Gc*) which induce chromosome breakage, such as *Gc1a* and *Gc1b* identified from *Ae. speltoides* by Tsujimoto and Tsunewaki (1984, 1988). These approaches are not frequently used for alien gene introgression because the translocations induced by these approaches mostly involve two non-homoeologous chromosomes. Therefore, these type changes are not agronomically acceptable (Sharma and Knott, 1966; Sears, 1972).

Numerous wheat lines have been produced by alien introgression and many lines carrying the alien genes for biotic and abiotic stress resistance have been extensively utilized in various breeding programs worldwide. For example, stem rust resistance genes *Sr32*, *Sr39*, and *Sr47* introgressed from the *Ae*. *speltoides* into the common wheat genome (Niu et al., 2011; Klindworth et al., 2012; Mago et al., 2013). Molecular markers linked to these genes were widely utilized in marker- assisted selection in wheat breeding. In addition to it, two more *Sr* genes, *Sr51* from *Ae. searsii* and *Sr53* from *Ae. geniculata* were also introgressed into the wheat genome (Liu et al., 2011a;Liu et al., 2011b).Therefore, alien gene introgression is a good source of agronomically important genes also substantially increased the genetic diversity in wheat.

Techniques used to detect the chromosomes rearrangements

The development of translocation lines with alien chromosome and their characterization largely benefits from the capacity to detect alien chromatin involved. Chromosomal banding techniques such as C-banding were the first technique used for alien chromosome identification and characterization of translocations in wheat (Gill and Kimber, 1974). For example, wheat-rye

translocations were effectively characterized by using this technique (Lukaszewski and Gustafson, 1983). But chromosomal banding is a tedious, laborious, and complex technique. These drawbacks have limited precise and high-throughput identification of alien chromosomes.

The introduction of recent microscopy-based molecular techniques like fluorescence *in situ* hybridization (FISH) and genomic *in situ* hybridization (GISH) accelerated the characterization, improvement, and development of alien introgression lines. The potential utilization of FISH technique depends upon the availability of suitable probes. For example, the probes pAs1and pSc119.2 has been extensively used for identification of D- and B- genome chromosomes, respectively (Rayburn and Gill, 1985; Nagaki et al., 1995; Bedbrook et al., 1980). While, in GISH, genomic DNA from alien species have been commonly used as a probe to determine the size and physical location of the alien chromatin in the wheat chromosomes (Niu et al., 2011, 2014; Klindworth et al., 2012) and the genomic structure of allopolyploid Triticeae (Schwarzacher et al., 1989). Therefore, both these techniques have been widely used together for chromosomal characterization of the wheat-alien translocation lines at the mitotic metaphase stage (Zhang et al., 2001; Danilova et al., 2014).

Cytogenetic techniques are laborious, low-resolution, and time consuming in nature. These drawbacks limit their suitability for large scale selection of wheat-alien introgressions. Therefore, high-resolution and high-throughput techniques are required to enhance the identification and characterization of smaller alien introgressions and chromosome breakpoints. Molecular markers are a method of choice due to their cost-effective and high-throughput procedures. First isozyme, morphological, and seed storage protein markers were used for identification and characterization of wheat-alien introgression lines (Vladova and Petkolicheva, 1996; Guadagnuolo et al. 2001). But, these markers were not useful to reveal chromosomal

rearrangements because they were limited in numbers. DNA based molecular markers, such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), and single nucleotide polymorphism (SNP) markers were used in a number of studies to identify wheat-alien introgression lines. For example, the *Sr22* gene was flanked by SSR markers *Xcfa2123* and *Xcfa2019*. These two markers were used to identify the recombinants between wheat and *T. boeoticum* chromosome in order to find the individuals with reduced *T. boeoticum* chromatin segments with the *Sr22* gene (Khan et al., 2005; Olson et al., 2010). For the *Sr39* gene, a single SSR marker *Xgwm319* was used for screening the segregation population for selection of individuals with reduced alien chromatin (Niu et al., 2011). In addition to it, Tiwari et al. (2014) developed two genome specific SNP markers to identify the introgression segment of *Ae. geniculate* to wheat chromosome carrying leaf rust resistance gene *Lr57* and stripe rust resistance gene *Yr40*. Therefore, molecular markers are now attractive tools to support wheat–alien introgression breeding.

Wheat stem rust

History

Wheat stem rust, caused by fungus *Puccinia graminis* Pers. f. sp. tritici Eriks. & E. Henn. (*Pgt*), is one of most feared disease in wheat worldwide. This disease was a destructive problem from Aristotle time (384-322 B.C.) (Schumann and Leonard, 2000). The ancient Romans and Greeks were also plagued by stem rust. Romans made sacrifices to the god of rust, which they called Robigo, because they were not aware about the pathogen at that time (Roelfs et al., 1992). Until the 1700s, the parasitic nature of stem rust was not known, but European farmers identified the link between barberry (*Berberis* vulgaris) and stem rust epidemics in wheat. In 1767, two

Italian scientists Felice Fontana and Giovanni Targioni Tozzetti first provided the information about the stem rust fungus in wheat, which was named *P.graminis* by Persoon in 1797 (Schumann and Leonard., 2000). The evidence that *P.graminis* is heteroecious and requires two hosts, the cereal host and the alternate host barberry, to complete its life cycle (Schumann and Leonard, 2000).

Economic importance of stem rust

Several major epidemics of wheat stem rust pathogens have been reported in the 20th century. These epidemics caused significant yield losses in most of major wheat-growing regions, including eastern and central Europe (with 5% to 20% yield losses) in 1932, Mexico (30%) in 1947-1948, Scandinavia (9% to 33%) in 1951, and Chile (40%) in 1951(Zadoks, 1963; Leonard and Szabo, 2005; Hodson, 2011). It was documented that the severe epidemics of stem rust pathogens resulted in yield losses of around two million tonnes in central India in 1946-1947 (Joshi et al., 1986). In the U.S., many epidemics occurred from 1920 to 1960 with losses from 1.3 to 3.7 million tonnes. In 1935, more than 50% of the wheat yield was lost in North Dakota and Minnesota due to stem rust disease (Roelfs et al., 1992; Hodson, 2011; Leonard, 2001).

The serious damages caused by the stem rust in the 20th century prompted the wheat community to control this disease. Since the 1950's, this disease has come under control by the eradication of alternative host and widespread development and utilization of the stem rust resistant wheat cultivars. However, after about 50 years of successful control on stem rust, a new form of stem rust race called Ug99 originated in Uganda which is a major threat to global wheat production (Pretorius et al., 2000; Singh et al., 2011).One recent severe epidemic occurred in Ethiopia (2013-2014) on variety 'Digalu' which led to serious yield loss (Olivera et al., 2015).

Classification

In 1797, the stem rust pathogen was designated as *Puccinia graminis* Pers. by Christiaan H. Persoon (Schafer et al., 1984). Stem rust fungus *Puccinia graminis* belongs to phylum Basidiomycota, class Urediniomycetes, order Uredinales, and family Pucciniaceae, which contains 17 genera and approximately 4,121 species *P. graminis* has a very broad range of host and is able to infect around 365 species such as wheat, oat, barley and rye (Leonard and Szabo, 2005).Therefore, the pathogen was sub-classified into six formae speciales (f. sp.) based on the host plant species: *P. graminis* f. sp. *tritici* (wheat), *avenae* (oat), *secalis* (rye), *hordeum* (barley), *poae* (bluegrass), and *agrostidis* (bentgrass).

Nomenclature

The wheat stem rust pathogen *P. graminis* f. sp. *tritici* includes different races or pathotypes. Originally, based on the international nomenclature system, *Pgt* races designated based on 12 differential lines, which were divided into three differential sets with four differential lines in each set (Roelfs and Martens, 1988). The nomenclature system modified for designation of new identified races. In the current system, 20 differential lines are divided into five differential sets with four differentials in each set (Jin et al., 2008a). A letter code is given to a certain pattern of infection types (IT) to the four differentials in each set. The letter code illustrates different levels of virulence to the differentials within each set. For example, a race with a higher letter code T can infect more differentials than a low letter code B in the same differential set (Roelfs and Martens, 1988). Therefore, combination of five letter codes represented each race like Ug99 designated as TTKSK, in which first letter T represented a high IT to the first differential set (Jin et al., 2008a) (Table 2.1).

Table 2.1. An international nomenclature system designating *P. graminis* f. sp. *tritici* (*Pgt*) races[a]

	Differential subset	Infection type produced on host lines with *Sr* gene				Ug99[b]
	1	*Sr5*	*Sr21*	*Sr9e*	*Sr7b*	T
	2	*Sr11*	*Sr6*	*Sr8a*	*Sr9g*	T
Pgt code	3	*Sr36*	*Sr9b*	*Sr30*	*Sr17+13*	K
	4	*Sr9a*	*Sr9d*	*Sr10*	*SrTmp*	S
	5	*Sr24*	*Sr31*	*Sr38*	*SrMcn*	K
B		L[c]	L	L	L	
C		L	L	L	H[c]	
D		L	L	H	L	
F		L	L	H	H	
G		L	H	L	L	
H		L	H	L	H	
J		L	H	H	L	
K		L	H	H	H	
L		H	L	L	L	
M		H	L	L	H	
N		H	L	H	L	
P		H	L	H	H	
Q		H	H	L	L	
R		H	H	L	H	
S		H	H	H	L	
T		H	H	H	H	

[a] Roelf and Martens (1998) and Jin et al. (2008b)
[b] An example of *Pgt* code for Ug99
[c] L and H indicate low and high infection type, respectively

Life cycle

P. graminis is an obligate biotrophic fungus, which acquires living host for nutrients and reproduction. It is also a heteroecious and requires two alternate hosts to complete its life cycle (Schumann and Leonard, 2000). The complete life cycle of *P. graminis* has five spore stages: urediniospores, teliospores, basidiospores, pycniospores, and aeciospores (Leonard and Szabo,

2005). The life cycle of *P. graminis* begins with teliospores produced at the end of the wheat growing season in temperate climates. The teliospores have a darker color, thicker cell wall, and are binucleate. As these spores mature, karyogamy occurs and the two nuclei join in each cell. Soon after the karyogamy, meiosis takes place and is not completed until the spring because spores undergo dormancy in winter season. In the spring season, teliospores break dormancy and complete the meiosis. After the meiosis, formation of hypha shape structure called basidium which consists of four haploid nuclei takes place. At this part of the life cycle, the fungus finishes with mitosis which formed the basidiospores with two haploid nuclei. The basidiospores are infecting the upper surface leaves of the barberry through a haploid monokaryotic mycelium. After the colonization of mycelium in the host tissue, production of a flask shape structure called pycnium occurred. Within the pycnium, small and thin-walled pycniospores are formed and disseminate by insects along with rain (Roelf, 1985; Leonard and Szabo, 2005).

Pycniospores have a single haploid nucleus and they act as male gametes, while flexuous hyphae extend from the top of the pycnia as female gametes. After the fusion of pycniospores and flexuous hyphae, a dikaryotic cup-shaped aecium is formed beneath the pycnium. The aecia produce single-celled, dikaryotic aeciospores which are able to infect grass hosts. After aeciospores infect a grass host, uredinium form single-celled dikaryotic urediniospores. These spores infect the grass host mainly on the stems and leaf sheaths under favorable conditions such as moderate temperature, sufficient amount of water on the stem and leaf. Urediniospores germinate by formation of a germ tube which invades the leaf through a stoma. The tip of the germ tube forms an appressorium structure from which branches begin to give the intercellular mycelium and haustoria. The haustoria absorb the food from the host cell and form the hyphae structure that releases the new urediniospores after breaking the host cell. Urediniospores stage is

the repeating stage of stem rust pathogen and is responsible for dissemination of this disease. Late in the season, uredinia mature and begin to produce the teliospores, which initiate the next life cycle (Roelf, 1985; Roelf et al., 1992; Leonard and Szabo, 2005).

Symptoms and sign

In grass hosts like wheat, infection usually occurred on stems and leaf sheaths. After a few days of infection, the initial symptom appears mostly as small chlorotic spots on the infected plant. Infection severity of stem rust is directly related to the level of resistance in the plant. At around 8 to 10 days after infection, pustules called urediospores are developed on susceptible plants. These pustules are red, linear or diamond shaped, and around 10mm long. Another diagnostic symptom is the formation of black color teliospores at the end of the growing season (Leonard and Szabo, 2005). Infection symptoms and signs also appear on the alternative host barberry. In the spring, pycniospores appear on the upper leaf surface. 5 to 10 days after infection, cup-shaped aecium, which contains powdery and orange-yellow color aeciospores, formed on the lower leaf surface (Schumann and Leonard, 2000).

Genetics of the pathogen

Wheat stem rust pathogen, *P. graminis* f. sp. *tritici*, consists of 18 chromosomes with genome 88.6 Mb (Boehm et al., 1992; duplessis et al., 2011). In early studies, Johnson and Newton (1940) and Johnson (1954) found that virulence/avirulence in the wheat stem rust fungus follow the Mendelian laws of inheritance and interaction between host resistance and pathogen avirulence which fits into the gene-for-gene interaction model proposed by Flor (1971). Loegering and Powers (1962) studied the inheritance of pathogenicity on a number of varieties by crossing races 111 and 36. They found the virulence in variety Marquis is controlled by two recessive genes.

Zambino et al. (2000) crossed the two strains of *P. graminis* f. sp. *tritici* and performed the analysis for avirulence segregation on 10 wheat differential lines which contains known stem rust resistance genes *Sr6*, *Sr8a*, *Sr9a*, *Sr10*, *Sr21*, *Sr28*, *Sr30*, and *SrU*, respectively. From this study, they found that segregation of avirulence to virulence fit to 3:1 in eight differentials lines, indicating that avirulence was a dominant phenotype and controlled by a single gene. While avirulence to virulence segregated in the ratio of 15:1 on one differential line, indicating that there are two dominant avirulence genes with epistatic interaction. In another differential line, avirulence to virulence segregated with a ratio of 3:13, which suggested that there are also two genes segregating: one dominant for avirulence and other dominant for avirulence inhibition. Zambino et al. (2000) suggested a nomenclature system for avirulence genes by using the four-prefix letter which indicates the avirulence on a specific host such as *AvrT* (*Triticum*), *AvrS* (*Secalis*), *AvrH* (*Hordeum*), and *AvrA* (*Avena*) and suffix represented the compatible stem rust resistant gene. They analyzed the segregation for 970 RAPD and AFLP markers in their cross population and constructed seven genetic linkage groups with 52 DNA markers. They identified and mapped eight avirulence genes, *Avr*T6, *Avr*T8a, *Avr*T9a, *Avr*T10, *Avr*T21, *Avr*T28, *Avr*T30, and *Avr*TU.

Detection, evolution and movement of Ug99

In 1998, a new *Pgt* race was found in Uganda and it was initially named as Ug99 (Pretorius et al., 2000). This race showed virulence to the large number of cultivars containing *Sr31* gene and caused the epidemics in Kenya in 2004. Based on the North American stem rust nomenclature system (Roelfs and Martens1988), this race was designated as TTKS (Pretorius et al., 2000; Wanyera et al., 2006) and re-designated into TTKSK after the wheat lines monogenic for *Sr24*, *Sr31*, *Sr38*, and *SrMcN* were added as the fifth set of differentials (Jin et al., 2008). The

race TTKSK is a serious threat for wheat production worldwide because it has virulence to most of the wheat cultivars that are being used in production worldwide. Jin and Singh (2006) reported that among 450 U.S. wheat cultivars and breeding lines tested against TTKSK, only 48% of hard red winter wheat, 16% of hard red spring wheat, and 27% of soft winter wheat showed resistance. Moreover, among 174 U.S. spring wheat varieties and breeding lines screened with TTKSK in 2013, only 4% showed the seedling resistance (Singh et al., 2015).

The race TTKSK has the capability to rapidly evolve into new virulence. The evolution of new virulence is occurring by the mutation, recombination, and migration. The race TTKSK and its variants have moved across the African continent, the Middle East, and South Asia through wind (Singh et al, 2006). Presently**,** TTKSK and its 12 variants, commonly known as Ug99 race group, have been detected in 13 countries, namely Uganda, Kenya, Ethiopia, Sudan, Tanzania, Eritrea, Rwanda, South Africa, Zimbabwe, Mozambique, Yemen, Iran, and Egypt (Patpour et al., 2016) and showed broad virulence to deployed *Sr* genes (Table 2.2).These variants are closely related but slightly different in their avirulence and virulence profiles.

Types of host resistances

Host resistance to stem rust is classified into two primary classes: (i) seedling resistance, which is also known as race-specific resistance involved in pathogen recognition and hypersensitive response, and (ii) adult plant resistance (APR), which is a non-race specific resistance and not associated with a hypersensitive response. It is usually considered more durable than the seedling resistance.

Table 2.2. The races belonging to Ug99 race group identified in 2014 in various countries and their avirulence and virulence profiles (Singh et al., 2015)

Race	Resistance genes and their virulence (+) and avirulence (-)	Confirmed countries (year detected)
TTKSK	*Sr31*(+), *Sr21*(+), *Sr24*(-), *Sr36*(-), *Sr9h*(-)	Uganda (1998), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009), Eritrea (2012), Rwanda (2014), Egypt (2014)
TTKSF	*Sr31*(-), *Sr21*(+), *Sr24*(-), *Sr36*(-), *Sr9h*(-)	South Africa (2000), Zimbabwe (2009), Uganda (2012)
TTKST	*Sr31*(+), *Sr21*(+), *Sr24*(+), *Sr36*(-), *Sr9h*(-)	Kenya (2006), Tanzania (2009), Eritrea (2010), Uganda (2012)
TTTSK	*Sr31*(+), *Sr21*(+), *Sr24*(-), *Sr36*(+), *Sr9h*(-)	Kenya (2007), Tanzania (2009), Ethiopia (2010), Uganda (2012), Rwanda (2014)
TTKSP	*Sr31*(-), *Sr21*(+), *Sr24*(+), *Sr36*(-), *Sr9h*(-)	South Africa (2007)
PTKSK	*Sr31*(+), *Sr21*(-), *Sr24*(-), *Sr36*(-), *Sr9h*(-)	Kenya (2009), Ethiopia (2007), Yemen (2009)
PTKST	*Sr31*(-), *Sr21*(+), *Sr24*(-), *Sr36*(+), *Sr9h*(+)	Ethiopia (2007), Kenya (2008), South Africa (2009), Eritrea (2010), Mozambique (2010), Zimbabwe (2010)
TTKSF+	*Sr31*(-), *Sr21*(+), *Sr24*(-), *Sr36*(-), *Sr9h*(+)	South Africa (2010), Zimbabwe (2010)
TTKTT	*Sr31*(+), *Sr24*(+), *SrTmp*(+)	Kenya (2014)
TTKTK	*Sr31*(+), *SrTmp*(+)	Kenya (2014), Egypt (2014), Eritrea (2014), Rwanda (2014), Uganda (2014)
TTHSK	*Sr31*(+), *Sr30*(-)	Kenya (2014)
PTKTK	*Sr31*(+), *Sr21*(-), *SrTmp*(+)	Kenya (2014)
TTHST	*Sr31*(+), *Sr24*(+), *Sr30*(-)	Kenya (2013)

Seedling resistance

Seedling resistance is also called vertical resistance, governed by one gene that provides the resistance against the pathogen at the seedling stage. The seedling resistance can provide effective resistance during the entire stages of plant growth. The mechanism of seedling resistance usually follows gene-for-gene interaction, namely, a resistance gene in the host is matched to an avirulence gene in the pathogen (Flor, 1971). Therefore, recognition of pathogen molecules by the host is presently described as effector-triggered immunity (Jones and Dangle, 2006). For example, *Sr22*, *Sr33*, *Sr35*, *Sr37*, *Sr39*, *Sr43*, and *Sr47* are stem rust seedling resistance genes (Singh et al., 2015). Since seedling resistance is race-specific, it can be overcome by the pathogen with new virulence from sexual recombination and mutation. But defeated race specific genes can still be used in crop improvement with the combination of other resistance genes (Ayliffe et al., 2008).

Adult plant resistance

Adult plant resistance (APR) is also called horizontal resistance and it's generally conferred by multiple genes. APR is expressed in the plant at the adult stage. Generally, this type of resistance doesn't display gene-for-gene interaction. Therefore, host defense generated by APR cannot be easily defeated by the pathogen, making this resistance more durable as compared to seedling resistance. For example, *Sr12* and *Sr57* have been found to act as APR (Rouse et al., 2014). In pyramiding, APR genes can interact with each in epistatic or pleiotropic ways to enhance the resistance and durability (Ayliffe et al., 2008; Rouse et al., 2014; Brown, 2015). The best example of durable APR is *Sr2*/*Yr30*/*Lr27*, *Sr55*/*Yr46*/*Lr67*, *Sr57*/*Yr18*/*Lr34*, and *Sr58*/*Yr29*/*Lr46* (Singh et al., 2005; Herrera-Foessel et al., 2010; Yang et al., 2013; Lan et

al., 2014). However, both seedling and APR genes should be utilized in improvement of wheat cultivars in breeding programs.

Effective resistance genes against Ug99

The most important feature in wheat disease-resistant breeding is to deploy resistance genes into commercial cultivars. Currently, it's a worldwide effort to find the resistance genes against Ug99 race group from wheat gene pools, under the coordination of the Borlaug Global Rust Initiation (BGRI) (Yu et al., 2015). To date, 39 stem rust resistance (*Sr*) genes (Table 2.3) have been identified to have resistance against Ug99 race group. Among these Ug99-effective *Sr* genes, *Sr2*, *Sr13*, and *Sr14* originated from the domesticated emmer wheat (*T. turgidum* ssp. *dicoccum*). *Sr2* was transferred from Yaroslav emmer to cultivar Marquis and located on the short arm of chromosome 3B (McFadden, 1930; Johnson, 1984). This gene showed the APR type resistance and has been widely used in wheat breeding programs, such as 60% CIMMYT breeding germplasm and lines carry *Sr2* (Singh et al.,2011a; Singh et al., 2014). APR of *Sr2* increased by pyramiding *Sr2* with other resistance genes is referred to as 'the *Sr2* complex'. Some wheat cultivars, such as Kiritati, Kingbird, Parula, and Pavon 76 shows APR to Ug99 race lineages due to 'the *Sr2*-complex' (Singh et al., 2011a). While, *Sr13* and *Sr14* originated from Khapli emmer and located on long arm of chromosome 6A and chromosome 1B, respectively (Knott, 1962; McIntosh, 1972). *Sr13* is present in many modern durum cultivars (Simons et al., 2011; Klindworth et al., 2007). Race TRTTF shows virulence to *Sr13* gene and *Sr14* gene is also not effective against Ug99 (Singh et al., 2011a; Jin et al., 2007). Therefore, it is mandatory for deployment of new Ug99 resistance gene into durum wheat. Two *Sr* genes, *Sr22* and *Sr35*, which are derived from *T. monococcum* chromosomes 7AL and 3AL, respectively, are both highly effective against Ug99 race group (Singh et al., 2011).

Table 2.3. Chromosome location and original source of *Sr* genes

Sr gene	Chr location	Original source	References
Sr2	3BS	*T. turgidum* ssp. *dicoccum*	Knott (1968)
Sr13	6AL	*T. turgidum* ssp. *dicoccum*	Knott (1962)
Sr14	1BL	*T. turgidum* ssp. *dicoccum*	Knott (1962)
Sr15	7AL	*T. aestivum* ssp. *aestivum*	Watson and Luig (1966)
Sr22	7AL	*T. monococcum* ssp. *monococcum*	The (1973)
Sr24	3DL	*Th. ponticum*	McIntosh et al. (1976)
Sr25	7DL	*Th. ponticum*	McIntosh et al. (1976)
Sr26	6AL	*Th. ponticum*	McIntosh et al. (1976)
Sr27	3AS	*S. cereale*	Marais and Marais (1994)
Sr28	2BL	*T. aestivum* ssp. *aestivum*	Rouse et al. (2012)
Sr29	6DL	*T. aestivum* ssp. *aestivum*	Dyck and Kerber (1977)
Sr32	2A, 2B, 2D	*Ae. speltoides*	McIntosh et al. (1995)
Sr33	1DS	*Ae. tauschii*	Jones et al. (1991)
Sr35	3AL	*T. monococcum* ssp. *monococcum*	Saintenac et al. (2013)
Sr36	2BS	*T. timopheevii* ssp. *timopheevii*	McIntosh et al. (1995)
Sr37	4BL	*T. timopheevii* ssp. *timopheevii*	McIntosh et al. (1995)
Sr39	2BS	*Ae. speltoides*	Niu et al. (2011)
Sr40	2BS	*T. timopheevii* ssp. *armeniacum*	Dyck (1992)
Sr42/SrCad	6DS	*T. aestivum* ssp. *aestivum*	Hiebert et al. (2011)
Sr43	7DS	*Th. ponticum*	Niu et al. (2014)
Sr44	7DS	*Th. intermedium*	Friebe et al. (1996); Liu et al. (2013)
Sr45	1DS	*Ae. tauschii*	Marais et al. (1998)
Sr46	2DS	*Ae. tauschii*	Yu et al. (2015)
Sr47	2BL	*Ae. speltoides*	Klindworth et al. (2012)
Sr48	2AL	*T. aestivum* ssp. *aestivum*	Bansal et al. (2009)
Sr50	1DS	*S. cereale*	Anugrahwati et al. (2008)
Sr51	3A, 3B, 3DS	*Ae. searsii*	Liu et al. (2011a)
Sr52	6AS	*D. villosum*	Qi et al. (2011)
Sr53	5DL	*Ae. geniculata*	Liu et al. (2011b)
Sr55/*Yr46*/*Lr67*/*Pm46*	4DL	*T. aestivum* ssp. *aestivum*	Herrera-Foessel et al. (2014)
Sr56	5BL	*T. aestivum* ssp. *aestivum*	Bansal et al. (2008)
Sr57/*Yr18*/*Lr34*/*Pm38*	7DS	*T. aestivum* ssp. *aestivum*	Singh et al. (2013a)
Sr58/*Yr29*/*Lr46*/*Pm39*	1BL	*T. aestivum* ssp. *aestivum*	Singh et al. (2013b)
Sr59	2DS	*Secale cereale* L.	Rahmatov et al. (2016)
SrTmp/SrSha7	6DS	*T. aestivum* ssp. *aestivum*	Singh et al. (2015)
SrTA10171	7DS	*Ae. tauschii*	Olson et al. (2013)
SrTA10187	6DS	*Ae. tauschii*	Olson et al. (2013)
SrND234	4AL	*T. aestivum* ssp. *aestivum*	Basnet et al. (2015)
SrHuw234	2BL	*T. aestivum* ssp. *aestivum*	Singh et al. (2011)
Sr1RS^{Amigo}	1AS	*S. cereale*	Olsen et al. (2010)

Common wheat germplasm is also a good source for Ug99-effective *Sr* genes, including race specific and non-race specific, such as *Sr15*, *Sr28, Sr29, Sr42, Sr48, Sr55, Sr56, Sr57, Sr58, SrTmp, SrHuW234, SrND643,* and *SrYaye.* These genes are used in combinations with other Ug99 resistance genes (Singh et al., 2015). *Sr15* originated from cultivars Norka and Thew and it is located on the chromosome arm 7AL. *Sr15* gene is linked with *Lr20* and *Pm1* genes and later it was confirmed that *Sr15* and *Lr20* are the same genes (Watson and Luig, 1966; McIntosh, 1977). *Sr28* was identified in common wheat cultivar Kota and it is located on the long arm of chromosome 2B. Resistance effectiveness of this gene can be increased by pyramiding it with other Ug99 resistance genes (Rouse et al., 2012). *Sr29* originated from wheat cultivar Etoile de Choisy and it is located on chromosome arm 6DL. This gene has been used for stem rust resistance in European wheat (Dyck and Kerber, 1977). *Sr42* is derived from 'Norin 10' and it is located on chromosome arm 6DS (Hiebert et al., 2011; Ghazvini et al; 2012).

In addition to the formally designated race-specific *Sr* genes, several other race-specific genes that are effective against Ug99 races were identified in some common wheat cultivars. Because their relationships with the known genes have not been ambiguously determined, they have only been temporarily designated, such as *SrCad*, *SrND643, SrHuw234*, and *SrYaye*. *SrCad* was identified in several Canadian wheat cultivars and it was mapped to the same location as *Sr42*. It has been suggested that *SrCad* could be the same gene or the allelic form of *Sr42* (Hiebert et al., 2011; Gao et al., 2015). *SrTmp* is present in many Asian, North American and African cultivars. However, race TRTTF is virulent on *SrTmp* (Jin et al., 2008; Singh et al., 2011a). Three other temporarily designated genes *SrND643*, *SrHuw234*, and *SrYaye* were identified or derived from hard red spring wheat line ND643 (Basnet et al., 2015), 'HUW234' (Singh et al., 2011), and Chinese wheat line 'Shanghai#7', respectively. They are mapped to

chromosome arms 4AL, 2BL, and 2BS, respectively (Basnet et al., 2015; Lopez-Vera et al., 2014). Further studies are needed to confirm their effectiveness in stem rust resistance wheat breeding.

Several rust-resistant genes in wheat, including *Lr34*, *Lr46*, and *Lr67*, have been identified to have partial resistance to all races of leaf rust (*Puccinia triticina*; *Pt*), stripe rust (*Puccinia striiformis* f. sp. *tritici*; *Pst*), stem rust and powdery mildew (*Blumeria graminis* f. sp. *tritici*; *Bgt*) at adult plants (Moore et al., 2016). The three APR genes *Lr34*, *Lr46*, and *Lr67* were designated as *Sr57*, *Sr58*, and *Sr55*, respectively, for their stem rust resistance and they are located on chromosome arms 7DS, 1BL, and 4DL, respectively. These pleiotropic genes can provide durable rust resistance in wheat (Herrera-Foessel et al., 2014; Singh et al., 2015). However, these genes are characterized by a slow rusting and a susceptible infection type (Moore et al., 2015). They need to be pyramided with other race-specific and APR genes (Bansal et al., 2014).

In the secondary gene pool of wheat, *T. timopheevii* is a good source of genes for stem rust resistance. So far, three Ug99-effective *Sr* genes, *Sr36*, *Sr37*, and *Sr40* were transferred from the *T. timopheevii* chromosomes 2G and 4G, into common wheat using the chromosome translocation approach. *Sr36* is present in many U.S. wheat cultivars (Olson et al., 2010). Although it is resistant to race TTKSK but it was defeated by race TTTSK (Jin and Singh, 2006). While *Sr37* shows variable expression pattern of resistance during deployment to the other wheat varieties. Therefore, it has not been used in wheat cultivars deployment (McIntosh and Gyarfas, 1971, McIntosh et al., 1995). *Sr40* associated with some undesirable traits. So, it was not suitable for wheat breeding programs (Singh et al., 2015).

Among the wild relatives in the tertiary gene pool, several species in genera *Aegilops*, *Thinoprium*, *Secale*, and *Hanaldia* have been used as the sources of genes for stem rust resistance (Table 2.3). Four of the Ug99-effective *Sr* genes, *Sr24*, *Sr25*, *Sr26*, and *Sr43*, were originated from *Th. ponticum*. The genes *Sr24* and *Sr26* were broadly utilized in wheat breeding and deployed in several wheat cultivars in the U.S. (*Sr24*) and Australia (*Sr26*) (Olson et al., 2010; Dundas et al., 2007). The *Sr26* gene shows resistance to Ug99 race groups while *Sr24* is susceptible to race TTKST (Jin et al., 2008). *Sr25* gene also linked with the leaf rust resistance gene *Lr19* on the long arm of 7D. Initially, utilization of *Sr25/Lr19* in wheat breeding was limited because *Sr25/Lr19* was associated with an undesirable gene for yellow pigment (Friebe et al., 1994). Knott (1980) developed two mutant lines for *Sr25/Lr19* with smaller yellow pigment. Out of these two lines, only one mutant line has been utilized in CIMMYT wheat breeding programs (Liu et al., 2010). Like *Sr25*, the *Sr43* gene was also associated with an undesirable gene for yellow pigment (Knott et al., 1977). Niu et al. (2014) used chromosome engineering to develop two wheat lines with a shorter alien chromosome segment carrying *Sr43,* but the association between the *Sr43* and yellow pigment gene has not broken. The *Sr44* gene, which confers the resistance to the Ug99 race group, was originated from *Th. intermedium* (Friebe et al., 1992; Friebe et al., 1996). Recently, Liu et al (2013) incorporated this gene into wheat chromosome 7DS by Robertsonian translocation.

Several *Aegilops* species have been used as the source of *Sr* genes which were transferred into wheat through chromosome engineering. Three of the Ug99-effective *Sr* genes, *Sr32*, *Sr39*, and *Sr47* are derived from chromosome 2S of *Ae. speltoides. Sr32* was introgressed into hexaploid wheat from *Ae. speltoides*. Several translocation lines with reduced *Ae. speltoides* chromatin containing *Sr32* present on chromosome 2DS have been developed (Mago et al.,

2013). *Sr39* also originated from *Ae. speltoides* present on chromosome 2BS. Multiple genetic stocks with reduced *Ae. speltoides* chromatin containing *Sr39* on chromosome 2BS have been developed and these stocks are currently being used worldwide in various breeding programs (Mago et al., 2009; Niu et al., 2011). *Sr47* was initially introduced into wheat through the translocation involving wheat chromosome 2B and *Ae. speltoides* 2S (Faris et al., 2008). Klindworth et al. (2012) recently developed several new recombinants with reduced alien chromatin containing *Sr47* on chromosome 2BL with associated DNA markers. In addition to the genes from *Ae. speltoides*, two other genes *Sr51* and *Sr53* were transferred from the *Ae. Searsii* and *Ae. geniculata*, respectively (Liu et al., 2011a, b). Moreover, two novel *Sr* resistance genes, *Sr-1644-1Sh* and *Sr-1644-5Sh* were also identified in *Ae. sharonensis* that are effective against stem rust disease (Yu et al., 2017).

Common rye (*Secale cereale*) is a valuable source of genes for resistance to stem rust. So far, five *Sr* genes, *Sr27*, *Sr31*, *Sr50*, *Sr59*, and $Sr1RS^{Amigo}$ have been transferred from rye into wheat (Mago et al., 2015; Rahmatov et al., 2016). These genes provide the resistance to the Ug99 race group except for *Sr31*, which is susceptible to race TTKSK (Marais and Marais, 1994; Mago et al., 2002). In addition, *Dasypyrum villosum* is also a good source of genes for resistance to stem rust. Qi et al., (2011) evaluated 95 accessions of *D. villosum* for stem rust reaction to find the novel source of resistance to Ug99. After evaluation, they found that all the accessions showed resistance reaction towards stem rust. So far, only one *Sr* gene, *Sr52*, has been introduced from *D. villosum* into wheat through a 6AL.6VS Robertsonian translocation line, but this gene is temperature sensitive (Qi et al., 2011).

Gene cloning of stem rust resistance genes

Several *Sr* genes for seedling resistance have been isolated from common wheat and its related species. The genes *Sr33* and *Sr35* were isolated from *Ae. tauschii* and *T. monococcum* genomes, respectively, through map-based cloning (Periyannan et al., 2013; Saintenac et al., 2013). The gene *Sr50* was cloned from common rye using physical mapping cloning. During this study, it was identified that *Sr50* gene and *Mla* gene from barley are homologous and encoded a coiled-coil, nucleotide-binding, leucine-rich repeat (CC-NB-LRR) protein (Mago et al., 2015). In recent studies, *Sr22* and *Sr45* were cloned by using a new technique called MutRenSeq, which is based on a three-step method for rapidly cloning of resistance genes (Steuernagel et al., 2016). So far, five dominant S*r* genes for seedling resistance were cloned in wheat that encodes a coiled-coil, nucleotide-binding, leucine-rich repeat (CC-NB-LRR) protein (Periyannan et al., 2013; Saintenac et al., 2013). The results from these studies provided crucial information for better understanding of the functionality of these genes in wheat and for new knowledge of the mechanism of resistance.

In addition to cloning the race-specific genes described, two APR genes *Sr56* (i.e. *Lr67*) and *Sr57* (i.e. *Lr34*) were also cloned. The *Lr67* gene is a pleiotropic gene that provided the partial resistance against three rust diseases (stem, leaf, and strip) and to powdery mildew in wheat. Recent cloning of this gene explained that this gene was encoded a hexose transporter protein. This protein was differing in susceptible wheat by two amino acids (Moore et al., 2015). Similarly, the *Lr34* gene also acts like a pleiotropic gene that encoded an ATP-binding cassette (ABC) transporter protein (Krattinger et al., 2009). Therefore, increasing number of cloned wheat stem rust resistance genes now makes pyramiding of multiple resistance genes together on a small chromosomal region in wheat which enhance the durability of resistance.

Molecular markers in breeding

A molecular marker is a DNA fragment that can be genetically recognized to be associated with a certain location within the genome (Jonah et al., 2011). Since the late 1980s, various DNA marker technologies have been developed and several marker systems have been widely used in investigating genetic diversity, dissecting complex traits, generating linkage maps, and tagging genes of interest across almost all biological organisms (Gupta et al., 1999). Based on the marker technologies, DNA markers are classified into three categories: low-throughput hybridization-based markers, such as restriction fragment length polymorphisms (RFLPs), medium-throughput PCR-based markers, such as randomly amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs) and simple sequence repeats (SSRs), and high-throughput sequence-based markers, such as single nucleotide polymorphism (SNP) powerful tools in genetic studies and improvement in plant species.

Botstein et al (1980) first used RFLPs for linkage mapping in humans. RFLPs were considered to be the first-generation DNA markers for plant genome mapping. These are co-dominant, locus specific, highly reproducible, and southern blotting based markers. But RFLPs are expensive, laborious, and time consuming. RAPDs were first used for wheat genetic linkage mapping by Devos and Gale (1992). RAPDs are dominant markers and they do not require hybridization and blotting steps like RFLPs. But, their reproducibility level is very low and they cannot be used to identify allelic differences in heterozygotes. AFLP combined restriction digestion with PCR amplification. AFLP markers are dominant in nature, highly reproducible, and do not need prior sequence information.

The SSRs are mostly based on differences in number of di-, tri- or tetra- nucleotide repeats at a specific locus (Powells et al., 1996). The SSR markers are highly polymorphic,

reproducible, locus specific, co-dominant in nature, and require small amounts of DNA (Röder et al., 1998). Therefore, SSR markers have been extensively used in various genetic studies, genome mapping, gene and QTL mapping and cloning, and marker-assistant selection in various crop species (Gupta and Varshney, 2000). In wheat, SSR markers are now available for a majority of the genes and QTLs, such as *Xgwm533* for *Sr2*, *Xbarc152*, and *Xcfd15* for *Sr33*, *Xgpw4382* for *QGpc.2B-yume* (QTL for wheat grain protein content) (Spielmeyer et al., 2003; Sambasivam et al., 2008; Terasawa et al., 2016). These markers are valuable genetic resources in wheat breeding. However, SSR markers still have some limitations such as high cost in time and labor.

During recent years, SNP markers have gained great consideration in molecular genetics and plant breeding because of their abundance in genomes of every organism. SNPs are biallelic in nature and no gel based assays are generally required for it. High-throughput DNA chip-based technologies including wheat 9K iSelect array based on the Illumina Infinium I(Cavanagh et al. 2013) and 90K iSelect array based on Infinium I and Infinium II assay technology (Wang et al., 2014). The 90K iSelect array was developed with 81,587 functional SNPs in which 46,977 SNPs were genetically located on a consensus map (Wang et al., 2014). Presently, wheat 9K and 90K iSelect arrays have been abundantly used in mapping wheat genes and genome through linkage and association analysis. For example, using 9K SNP chip, the *Sr56* gene was mapped on chromosome 5BL and novel QTL was identified for resistance to leaf spot disease in wheat (Bansal et al., 2014; Gurung et al., 2014). Similarly, Babiker et al. (2017) used the 90K SNP chip for molecular mapping of stem rust TTKSK resistance locus linked to the *Sr28* gene on chromosome 2BL, and Gao et al. (2016) used the 90K chip for leaf rust resistance association study in wheat.

The SNP markers identified from chip-based technology are not suitable for direct use for single assay. Therefore, PCR-based SNP marker techniques are required for genotyping individual SNPs in marker-assisted selection in wheat breeding. Currently, different kinds of PCR based SNPs genotyping approaches are used, such as allele-specific PCR, Mini-sequencing, AS-probe hybridization, and restriction site cleavage (Syvänen et al., 1990; Pastinen et al., 1997; Livak et al., 1995; Livak., 1999; Semagn et al., 2014; Konieczny et al., 1993; Neff et al., 1998). Among these techniques, only the allele-specific Kompetitive Allele Specific PCR (KASP) assay, which is a homogenous fluorescence-based genotyping technology, has been widely used because it is more cost-effective, flexible, and robust than other methods in QTL analysis and marker-assisted selection (Semagn et al., 2014). A number of the KASP markers have been developed for Ug99-effective genes, such as KASP_IWB1208 for *Sr28* (Babiker et al., 2016), KASP_2RL_c25837C1, KASP_2RL_c21825C1, and KASP_2RL_c20194C2 for *Sr59* (Rahmatov et al., 2016).

Recently, Long et al. (2017) developed a novel SNP genotyping method known as Semi-Thermal Asymmetric Reverse PCR (STARP). The STARP assay included two universal priming element adjacent primers (PEA-primers) and two asymmetrically modified allele specific primers (AMAS-primers) and one common reverse primer for genotyping. This method has high platform compatibility, low time and labour cost and more flexible throughputs. By using this method, Klindworth et al. (2017) developed five STARP markers for the *Sr47* gene (Table 2.4). Therefore, markers have accelerated the plant breeding programs. Once gene flanking or gene diagnostic markers were identified, breeders used these markers for Marker assisted selection (MAS) program and for pyramiding.

Table 2.4. A list of molecular markers, chromosome location, and type linked to stem rust genes

Sr gene	Chromosome location	Marker name	Marker type[a]	References
Sr2	3BS	*Xgwm533*	SSR	Spielmeyer et al. (2003)
Sr13	6AL	*Xbarc104b, XCD926040, XCK207347, XBE403950*	SSR, EST	Simons et al. (2011)
Sr22	7AL	*Xwmc633, Xcfa2123, Xcfa2019*	SSR	Olson et al. (2010b), Khan et al. (2005)
Sr24	3DL	*Xbarc71, XSr24#12,XSr24#50*	SSR, AFLP	Mago et al. (2005)
Sr25	7DL	*XBF145935, XGb*	EST	Ayala et al. (2007); Liu et al. (2010); Yu et al. (2010)
Sr26	6AL	*XSr26#43, XBE518379*	EST	Mago et al. (2005); Liu et al. (2010)
Sr28	2BL	*XwPt-7004-PCR, Xwmc332,KASP_IWB1208*	DArT, SSR, KASP	Rouse et al. (2012); Babiker et al. (2016)
Sr32	2A, 2B, 2D	*csSr32#1, csSr32#2*	AFLP	Mago et al. (2013)
Sr33	1DS	*Xbarc152, Xcfd15, XBE405778, XBE499711*	SSR, EST	Sambasivam et al. (2008); Periyannan et al (2013)
Sr35	3AL	*Xcfa2170, XAK335187*	SSR, Indel	Jin et al. (2007); Zhang et al. (2010); Saintenac et al. (2013)
Sr36	2BS	*Xgwm319, Xwmc477, Xstm773-2*	SSR	Tsilo et al. (2008)
Sr39	2BS	*XSr39#22r, Xrwgs27*	EST	Mago et al. (2009); Niu et al. (2011)
Sr40	2BS	*XSr39#22r*	SSR	Bernardo et al. (2013)
Sr42/SrCad	6DS	*XFSDRSA*, *Xbarc183*	SCAR, SSR	Hiebert et al. (2011); Ghazvini et al. (2012)
Sr43	7DS	*Xrwgs30, Xcfa2040*	EST, SSR	Niu et al. (2014)
Sr44	7DS	*Xbe404728, Xbe473884*	EST	Liu et al. (2013)
Sr45	1DS	*Xcssu45*	AFLP	Periyannan et al. (2014)
Sr46	2DS	*Xgwm210, Xwmc111*	SSR	Yu et al. (2015)
Sr47	2BL	*Xgwm501, Xrwgs33, Xrwgsnp1, Xrwgsnp2, Xrwgsnp3, Xrwgsnp4, Xrwgsnp5*	SSR, STARP	Faris et al. (2008); Klindworth et al. (2012); Klindworth et al. (2017)
Sr48	2AL	*Xstm673acag*	SSR	Bansal et al. (2009)
Sr52	6AS	*XBE497099, XWMS570*	STS, SSR	Qi et al. (2011)
Sr53	5DL	*XBE500291/MboI, XBE443021/MboI, XBE442600/MseI*	STS	Liu et al. (2011b)
Sr54		*Xcfd283,* Xwmc167	SSR	Ghazvini et al. (2013)
Sr55/Yr46/Lr67/ Pm46	4DL	*Xcfd71, Xcfd23*	SSR	Herrera-Foessel et al. (2014)
Sr56	5BL	Xsun209, X sun320	SSR, EST	Bansal et al. (2014)
Sr59	2DS	*KASP_2RL_c25837C1, KASP_2RL_c21825C1, KASP_2RL_c20194C2*	KASP	Rahmatov et al. (2016)
SrTmp/SrSha7	6DS	*Xgpw518, Xkwm864, Xkwm929*	SSR, SNP	Hiebert et al. (2016)
SrTA10171	7DS	*Xgdm88, Xwmc827, Xcfd30*		Olson et al. (2013)
SrTA10187	6DS	*X6DS0027, X6DS0039, X6DS0050*	KASP, STS	Olson et al. (2013); Wiersma et al. (2016)
SrND234	4AL	*Xgwm350, Xwmc219, Xwmc776*	SSR	Basnet et al. (2015)

[a] EST: expressed sequence tagged; STS: Sequence tagged sequence; DArT: Diversity Array Technology; Indel: Insertion deletion; SCAR:Sequence-characterized amplified regions AFLPs: Amplified Fragment Length Polymorphisms; KASP: Kompetitive Allele Specific PCR; STARP: Semi-thermal Asymmetrical Reverse PCR

Usage of Ug99 resistance genes in wheat breeding

The most effective measure to control the stem rust epidemics caused by Ug99 race group is to utilize the resistance cultivars which contain the Ug99-effective *Sr* genes. The major breeding programs that target the Ug99 race group are now utilizing the resistance genes in their wheat breeding for development of resistance cultivars. From 2009 to 2010, CIMMYT, in collaboration with other local breeding programs in Africa, released 14 resistant varieties such as Koshan 09, Muqawim 09, Baghlan 09 and Chonte #1 in Afghanistan, Frankolin#1 in Bangladesh, Misr 1, Misr 2 in Egypt, Danda and Kakaba in Ethiopia, Super152, Super172, Baz and Ufan in India, Robin and Eagle in Kenya, Frankolin#1, Picaflor#1, and Danphe#1 in Nepal, and NR356 in Pakistan (Singh et al., 2011). All these varieties mostly carried the *Sr2* gene alone or its combinations with the other resistance genes. In 2007, the wheat breeders in Iran evaluated their promising germplasm in Kenya and then released 11 bread wheat varieties which showed resistance to stem rust. These varieties are being used as the parents for generating the new Ug99 resistant cultivars (Najafian et al., 2013). In the U.S., two spring wheat varieties, 'Tom' and'Linkert', having APR to the Ug99 race group, were recently released by the University of Minnesota (USA), (Anderson et al. 2012; Singh et al., 2015). These early breeding endeavors have provided initial protection of wheat crops from Ug99 threat in the target region.

It is well recognized that pyramiding several *Sr* genes together is the most effective way for achieving durable resistance. Recently, a number of resistant cultivars with different combinations of race specific-resistance and APR genes were released in Ethiopia, Kenya and other countries. For example, Njau et al. (2013) developed a population of recombinant inbred lines (RILs) from a cross between cultivar 'Avocet S' containing race specific gene *Sr26* and cultivar 'Pavon 76' containing APR *Sr2* gene, and found transgressive segregates with a higher

level of resistance expression as compared to the parents. As an effort in searching for novel Ug99-effective genes is continued, more Ug99-effective genes and their diagnostic or closely-linked markers will become available. Therefore, it is expected that the Ug99 threat can be eventually eliminated through a global effort in extensive development and widespread utilization of wheat cultivars carrying various combinations of Ug99-resistance genes.

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CHAPTER 3. INTROGRESSION OF A NOVEL STEM RUST RESISTANCE GENE FROM *THINOPYRUM JUNCEUM* INTO WHEAT

Abstract

Stem rust (*Puccinia graminis* Pers.: Pers. f. sp. *tritici*) (*Pgt*) is one of the most destructive diseases of wheat. Virulent races in the Ug99 (TTKSK) lineage are threatening wheat production globally. The best strategy for protection of the wheat crop is to explore the wild wheat relatives for identification of novel effective genes against *Pgt* races. A wheat 'Chinese Spring' (CS) – *Thinopyrum junceum* disomic addition line, HD3505 (2n = 44), was identified to be resistant to *Pgt* races in the Ug99 race group and several North American *Pgt* races. In this study, we transferred the resistance gene from the *Th. junceum* chromosome 4E derived from HD3505 into CS through chromosome engineering. In this research, HD3505 was crossed to CS monosomic for chromosome 4D and a Robertsonian translocation line with the short arm of the wheat chromosome and the long arm of the *Th. junceum* chromosome were developed. To further reduce the *Th. junceum* chromatin carrying the stem rust resistance gene, a BC_2F_1 population of 1,209 plants was developed by backcrossing the Robertsonian translocation plant to CS *ph1b*. Three BC_2F_1 plants with reduced *Th. junceum* chromatin (BG2133, BG5136, and BG2161) carrying the stem rust resistance were identified. After molecular analysis, only 4 SSRs markers *Xcfd31*, *Xgwm608*, *Xgwm133*, and *Xwmc182* belonging to group 4, produced polymorphic bands between CS, HD3505 and newly-developed translocation lines, suggesting that this novel stem rust resistance gene was located on a wheat group-4 chromosome. The genomic *in situ* hybridization analysis revealed that the *Th. junceum* chromosome segments carrying the resistance gene in the three translocation lines are located in the distal region of the long arm with the sizes of aproximately 35% of the translocated chromosomes. Therefore, approximately

65% of *Th. junceum* chromatin surrounding the stem rust resistance gene was eliminated. This novel gene is temperature insensitive and effective against at least six *Pgt* races at lower (18°C) and high (25°C) temperature conditions. These newly developed wheat lines are new resources of resistance to Ug99 and other *Pgt* races, and may be useful in wheat improvement.

Introduction

Wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is a major staple food crop for the world's population and the best source of calories and proteins for human diet. As the global population steadily grows, to meet food demands, we need to increase the wheat production (FAO, 2015). Wheat crop production is affected by various abiotic and biotic factors. Stem rust, caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. (*Pgt*), is one of the serious diseases for world wheat production (Singh et al., 2011). This disease is historically the most devastating disease of wheat. In the 20th century, many serious stem rust epidemics occurred in Europe, Asia, Australia, and the United States (U.S.) that caused severe wheat yield losses (Roelfs, 1977; Watson, 1981; Leonard and Szabo, 2005). In the U.S., from 1920 to 1960, several severe epidemics occurred and they caused up to 50% wheat yield losses (Leonard and Szabo 2005). Since the 1960s, stem rust had been effectively controlled by utilizing stem rust resistance genes (*Sr*) and removing the alternative *Pgt* host, barberry (*Berberis vulgaris* L.) (Singh et al., 2011).

A new *Pgt* race that is virulent to *Sr31*, a widely deployed gene from rye (*Secale cereal*e L.) that provided effective resistance to stem rust for three decades, was identified in Uganda in 1999 (Pretorius et al., 2000). This race was initially named Ug99, and later designated as TTKSK according to the North American Stem Rust Nomenclature System (Pretorius et al., 2000; Jin et al., 2007). TTKSK has the capability to quickly spread and evolve into new

virulence (Jin et al., 200a; Jin et al., 2009). Since 1999, 12 other *Pgt* races (TTKSF, TTKST, TTTSK, TTKSP, PTKSK, PTKST, TTKSF+, TTKTT, TTKTK, TTHSK, PTKTK and TTHST) belonging to the Ug99 lineage have been identified in East Africa (Fetch et al., 2016). TTKSK and the other *Pgt* races in the Ug99 lineage, commonly known as the Ug99 race group, are currently a significant threat to wheat crops in East Africa and potentially in other wheat-growing regions because they have broad virulence to many *Sr* genes that are widely deployed in wheat cultivars worldwide. More than 90% of wheat cultivars have susceptible reactions to the Ug99 race group (Singh et al., 2011). Besides the Ug99 race group, another *Pgt* race, TKTTF, originated in Ethiopia in 2012 and showed virulence against several major genes such as *Sr9a, Sr9b, Sr9d, Sr9e, Sr36, Sr38, SrTmp*, and *SrMcN* that were present in many wheat cultivars and including genes effective against the Ug99 race group (http://rusttracker.cimmyt.org/?page_id=6811) (Singh et al., 2015). For example, in 2013-2014, two varieties 'Digalu', and 'Robin', which carry *SrTmp,* were defeated by TKTTF causing significant yield losses in Ethiopia and Kenya, respectively (Olivera et al., 2015; Singh et al., 2015).

Host resistance is the most preferred way to control stem rust. To date, 73 *Sr* genes/alleles have been identified and about 35 are effective against the Ug99 race lineages (Singh et al., 2015). Nevertheless, due to rapid mutation in *Pgt* races, most *Sr* genes become ineffective within short periods of time (Singh et al., 2015). Therefore, it is necessary to identify and characterize novel sources of Ug99 resistance from various germplasm of wheat gene pools (Mujeeb-Kazi et al., 2013). The secondary and tertiary gene pools of wheat are good sources of new genes for cultivated wheat. Many important *Sr* genes, such as *Sr27*, *Sr31*, *Sr50*, $Sr1RS^{Amigo}$, and *Sr59* derived from rye (Marais and Marais, 1994; Mago et al., 2005; Anugrahwati et al.,

2008), *Sr24*, *Sr25*, *Sr26*, and *Sr43* from tall wheatgrass (*Thinopyrum ponticum* (Podp.) Barkworth & D.R. Dewey) (McIntosh et al., 1976; Niu et al., 2014), *Sr32*, *Sr39*, and *Sr47* from goatgrass (*Aegilops speltoides* Tausch) (McIntosh et al., 1995; Niu et al., 2011; Klindworth et al., 2012), *Sr36* from *Th. timopheevii* (Zhuk.) Zhuk. (McIntosh et al., 1995), *Sr44* from *Th. intermedium* (Host) Barkworth and D.R. Dewey (Liu et al., 2013), *Sr51* from *Ae. searsii* Feldman & Kislev ex Hammer (Liu et al.,2011a), *Sr52* from *Dasypyrum villosum* (L.) Candargy (Qi et al., 2011), and *Sr53* from *Ae. geniculate* Roth (Liu et al., 2011b). Most of these genes have not been deployed into wheat cultivars due to association with linkage drag (Singh et al., 2015).

Chromosome engineering is a useful technique for transferring desirable genes from wild relatives into common wheat by homoeologous recombinations between wheat chromosomes and their homoeologues from wild relatives (Qi et al., 2007). In wheat, regular pairing between homologous chromosomes is strictly controlled by the *Ph1* (pairing homoeologous) locus on chromosome 5B (Qi et al., 2007). Meiotic pairing and recombination between homoeologues in wheat and its wild relative species can be induced by using the *ph1b* mutant or *Ph1* deletion stocks (Klindworth et al., 2012). For example, the new wheat-alien chromosome translocation lines with smaller alien chromatin carrying *Sr39*, *Sr43*, and *Sr47* were recently developed by using using *ph1b* mutant or *Ph1* deletion stock (Niu et al., 2011; Niu et al; 2014; Klindworth et al., 2012).

In the tertiary gene pool of wheat, genus *Thinopyrum* is a valuable source of beneficial traits for wheat improvement (Dewey, 1984). Around 20 perennial grass species belong to this genus and display a wide range of ploidy levels that consist of the J, E, and St genomes. Two diploid species, *Th. elongatum* (Host) D.R. Dewey (2n = 2x = 14, EE or J^eJ^e) and *Th. bessarabicum* (Savul. and Rayss) A. Löve (2n = 2x = 14, JJ or E^bE^b), have E (or J^e) and J (E^b),

genomes, respectively (Wang, 2010; Wang et al., 2010). The polyploid species *Th. intermedium* (Host) Barkworth & D.R. Dewey (2n = 6x = 42, $EEE^{st}E^{st}StSt$) and *Th. ponticum* (Popd.) Barkworth& D.R. Dewey (2n = 10x = 70, $EEEEEEE^{st}E^{st}E^{st}E^{st}$ or EEEEEEStStStSt) have E and St genomes (Dewey, 1984; Wang, 2010). Although *Thinopyrum* species are an excellent source of stem rust resistance (Zhang et al., 2014), only two species *Th. intermedium* (*Sr44*) and *Th. ponticum* (*Sr24*, *Sr25*, *Sr26*, and *Sr43*) have been used as sources of *Sr* genes (Liu et al., 2013; McIntosh et al., 1976; Niu et al., 2014). To further broaden the *Sr* gene pool for confining the Ug99 threat, it is necessary to identify and transfer new *Sr* genes from other *Thinopyrum* species.

In a previous study, a wheat 'Chinese Spring' (CS) –*Th. junceum* (L.) A. Love (2n = 6x = 42, JJJJEE or $E^bE^bE^bE^bE^eE^e$) disomic addition line, HD3505 (2n = 44), was identified to be resistant to TTKSK and several North American *Pgt* races (Xu et al., 2009). The *Th. junceum* chromosome in HD3505 was determined to be homoeologous to the group 4 chromosomes of wheat (McArthur et al., 2012). The objective of this study was to transfer the *Sr* gene from the *Th. junceum* chromosome in HD3505 into a homoeologous chromosome in wheat through chromosome engineering and develop molecular markers for the *Sr* gene for marker assisted selection.

Material and methods

Plant materials

The wheat CS-*Th. junceum* disomic addition line HD3505 (2n = 44), originally developed by Charpentier (1992), and CS were utilized as donor and recipient parents, respectively, for crossing and population development. Chromosome translocations between wheat chromosome 4D and the *Th. junceum* group-4 chromosome in HD3505 were induced using the CS monosomic for chromosome 4D (CSM4D) and CS *ph1b* mutant. CS N4A-T4B

(nullisomic for 4A and tetrasomic for 4B), CS N4B-T4D (nullisomic for 4B and tetrasomic for 4D), and CS N4D-T4B (nullisomic for 4D and tetrasomic for 4B) were used as controls for molecular marker analysis. *Th. junceum* accession D3668 was used as source of the DNA probe in fluorescent genomic *in situ* hybridization (GISH).

Chromosome manipulation

In this study, we first used the monosomic method to induce a Robertsonian translocation between wheat chromosome 4D and the *Th. junceum* group-4 chromosome in HD3505 as decribed by Friebe et al. (2005). The *Th. junceum* chromatin carrying the *Sr* gene was further reduced through homoeologous recombination induced by the *ph1b* mutant (Figure 3.1). Specifically, HD3505 was first crossed to CS M4D. The meiotic pairing of the F_1 plants was examined using chromosome preparation methods as described by Xu and Joppa (1995). The F_2 progeny derived from the F_1 plants with meiotic pairing configuration 20″ + 2′ were tested for reaction to *Pgt* race TMLKC. The resistant F_2 plants with 42 chromosomes were analyzed for the presence of an induced Robertsonian translocation chromosome using GISH. The resistant F_2 plants that carried a Robertsonian translocation chromosome were immediately backcrossed to CS *ph1b*. The BC_1F_1 plants were tested for reaction to *Pgt* race TMLKC and the resistant plants were analyzed with the molecular markers *Xpsr128*, *Xpsr574*, and *Xawjl3* to select plants homozygous for *ph1b* (Roberts et al., 1999; Niu et al., 2011). The resistant BC_1F_1 plants that were homozygous for *ph1b* were backcrossed to CS as shown in Figure 3.1. The BC_2F_1 plants were used for the selection of new translocations lines carrying the stem rust resistance gene on shortened *Th. junceum* chromatin. The selection of new translocations was performed based on the stem rust evaluation, GISH, and the molecular marker analysis.

Stem rust inoculation and evaluation procedure

The *Pgt* race TMLKC was used for screening of the parents, F_2, BC_1F_1, and BC_2F_1 populations at USDA-ARS Northern Crops Science Laboratory, Fargo, ND. For this test, two seeds per line were grown in super-cell cones (Stuewe and Sons, Inc., Corvallis,OR, U.S.A) filled with soil mix Sunshine SB100 (Sun Gro Horticulture Distribution Inc., Bellevue, WA, U.S.A.) and fertilized with Osmocote Plus 15-19-12 fertilizer (Scotts Sierra Horticultural Product Company, Marysville, OH, U.S.A.). The seedlings were grown in a greenhouse at 20 to 23°C with a 16/8 hr (day/night) photoperiod. The inoculum was prepared by suspending the uredospores in paraffinic oil. Seedlings that were approximately 6-8 days old were inoculated following the procedure of Williams et al. (1992). The plants remained in the mist chamber under subdued light for 24 h after inoculation. Inoculated seedlings were then transferred to a greenhouse maintained at 20 to 23°C. Seedlings were scored for infection types (IT) 13 or 14 days after inoculation by evaluating the infected primary leaf of each plant. Each leaf was evaluated using the scale of Stakman et al. (1962) where 0 = immune, ; = necrotic fleck, 1 = small necrotic pustules, 2 = small to medium sized chlorotic pustules with green island, 3 = medium sized chlorotic pustules, and 4 = large pustules without chlorosis. The plants with an IT score of 2 or lower were considered resistant while plants with scores of 3 or greater were considered susceptible. The selected translocation lines with shortened *Th. junceum* chromosome segment were also tested with TMLKC and nine additional races, TTKSK, TRTTF, TTTTF, QTHJC, QFCSC, RTQQC, MCCFC, MCMJC, TPMKC, and TPPKC at different temperatures (18° and 23°C) in the controlled conditions in growth chambers.

Molecular marker analysis

For F_2, BC_1F_1 and BC_2F_1 genotyping, 220 SSR markers (Somers et al., 2004; Sourdille et al., 2004, Xue et al., 2008), 101 *Th. bessarabicum* chromosome 4J-specific EST-STS markers (Pu et al., 2015), and 14 E-genome specific EST-SSR markers (Wang et al., 2010) were used. For chromosome 4J-specific EST-STS markers, 45 and 56 were previously assigned to short arm (4JS) and long arm (4JL), respectively (Pu et al., 2015).

For marker analysis, genomic DNA was extracted following the protocol described by Pallotta et al. (2003) with some modifications. The young leaf tissues were collected in a Qiagen 96-well plate with one 3-mm tungsten carbide bead in each well along with leaf tissue. After leaf tissues were collected, 400 µl of preheated extraction buffer (0.1M tris-HCl, pH 7.5, 0.05 EDTA pH8.0, 1.25% SDS) was added to each well and the plate was shaken thoroughly using a Retsch MM300 Shaker at a frequency 30/sec for 90 seconds. The plate was flipped and shaken for another 90 seconds.The plate was incubated at 65°C for 40 min and then put into a refrigerator for about 15 min. After cooling, 250 µl of cold (4°C) 6M ammonium acetate was added to each well, the plate was strongly shaken to mix the ammonium acetate, and the plate was returned to the refrigerator for 15 min. The plate was centrifuged for 15 min at 4,000 rpm and then put into a refrigerator for 20 min at 4°C. After centrifugation, 350 µl of supernatant was collected from each well into a new Qiagen 96-well plate, which contained 300 µl of iso-propanol in each well. After the solutions were thoroughly mixed, the DNA was allowed to precipitate for 5 min. The plate was centrifuged again for 20 min at 4,000 rpm under 4°C to pellet the DNA. After the supernatant was discarded, the DNA pellet was washed in 500 µl of 70% ethanol. The plate was centrifuged for 20 min at 4,000 rpm under 4°C. After the supernatant was discarded, the DNA

pellets were dried overnight and then dissolved in 300 ml TE buffer (10 mm Tris, pH 8.0, 1mm EDTA).

The polymerase chain reactions (PCR) for the wheat group-4 SSR,4E- specific and 4J-specific EST-STS markers were performed using the procedures described by Röder et al (1998), Wang et al. (2010), and Pu et al. (2015), respectively. The amplified product was electrophoresed on 6% non-denatured poly-acrylamide gel in 0.5× TBE for 90-120 min (varies according to marker size) using constant 40-60W per gel. Gels were stained with Gel-Red and scanned using the Typhoon 9410 variable mode imager (GE Healthcare, Inc. Waukesha, WI).

Florescent genomic *in situ* hybridization

Florescent genomic in situ hybridization was performed following the procedure of Cai et al (1998). Roots of 1-2 cm in length were collected and pretreated in ice water for 24 h. After the pretreatment, roots were fixed in a mixture of 3 ethanol: 1 glacial acetic acid for 48 h at room temperature. For preparation of slides, the root tips were stained in 1% acetic carmine for 2-3 min and then squashed in 45% acetic acid under the cover slip. Prepared slides were microscopically examined and slides with good chromosome spreads were frozen at -80°C after removing the cover slips. The total genomic DNA of *Th. junceum* accession D3668 was used as probe DNA and labeled with biotin-16-dUTP via nick translation following the manufacture's protocol (Enzo Life Sciences, Inc. NY, USA). The genomic DNA of CS was used as blocking DNA, which was prepared by shearing total genomic DNA in 0.4 M NaOH in boiling water for 40-50 min. The hybridization of probe DNA to chromosomes and signal detection were performed using the protocol of Cai et al. (1998). The *Th. junceum* segments were detected using fluorescein isothiocyanate-conjugated avidin (FITC-avidin) and wheat segments were counter-stained using 4'-6-Diamidino-2-phenylindole (DAPI). The slides were examined under the Zeiss

Axioplan 2 Imaging Research Microscope and images were captured using an Axiocam CCD camera (Carl Zeiss Light Microscopy, Germany). In the images, the wheat chromatin (painted red) was differentiated from the *Th. junceum* chromatin (painted yellow green).

Results

Development and identification of wheat-*Th. junceum* chromosome translocation lines

To develop a wheat-*Th. junceum* group-4 chromosome Robertsonian translocation line using the monosomic method, HD3505 was crossed to CS M4D and the resultant F_1 plants were examined for meiotic parings. Among F_1 plants examined, two and three plants had meiotic pairing configuration of 20″ + 1′ and 20″ + 2′, respectively. A total of 471 F_2 plants derived from the three F_1 plants (12N3, 12N6, and 12N9) with 20″ + 2′ were evaluated for reaction to *Pgt* race TMLKC. The F_2 plants segregated 155 resistant (ITs1 to 23) and 316 susceptible (ITs 32 to 43) (Table 3.1, Figure 3.2). The observed segregation ratio did not fit a 3:1 ratio ($\chi^2 = 3.992$, $p = 0.0457$), suggesting the presence of segregation distortion (Table 3.1). A total of 24 F_2 plants with ITs ranging from 1 to 2, were cytologically examined for the presence of a Robertsonian translocation chromosome by GISH analysis. An F_2 plant with 2n = 41 chromosomes (12N6-32) was identified to carry a Robertsonian translocation chromosome with the short arm of wheat chromosome and the long arm of the *Th. junceum* chromosome (Figure 3.4).

To further reduce the size of the *Th. junceum* chromatin containing the *Sr* gene, the Robertsonian translocation plant was backcrossed to CS *ph1b* to initiate *ph1b*-induced homoeologous recombination, (Figure 3.1). Among 974 BC_1F_1 plants tested with race TMLKC. 84 and 890 plants were identified as resistant and susceptible, respectively. This segregation did not fit to 1:1 ratio ($\chi^2 = 666.97$, $p < 0.001$), indicating that segregation distortion occurred at this gene locus (Table 3.1). Resistant BC_1F_1 plants were further analyzed with chromosome arm

5BL-specific markers *Xpsr128*, *Xpsr574*, and *Xawjl3* for *ph1b*, and 18 BC_1F_1 plants were recognized as homozygous for *ph1b* by failure to amplify the *Xpsr128* and *Xpsr574* alleles. The 18 resistant BC_1F_1 plants that were homozygous for *ph1b* were backcrossed to CS and 1,209 BC_2F_1 seeds were produced and used in selection of new recombinant lines.

The 1,209 BC_2F_1 plants were tested with race TMLKC, and there were 172 resistant (ITs;1 to 12^-) and 1,028 susceptible (ITs 33^+ to 4) plants. Segregation of resistance in the BC_2F_1 population also significantly deviated from a 1:1 ratio ($\chi^2 = 617.04$, $p < 0.001$) (Table 3.1). Based on GISH analysis, 3 BC_2F_1 plants (BG2133, BG5136, and BG2161) were identified to carry a translocation chromosome with reduced *Th. junceum* chromatin (Figure 3.4). The results from GISH analyses of the translocation chromosomes indicated that the stem rust resistance gene is located in the distal region of a wheat group-4 chromosome. BG2133, BG5136, and BG2161 have only small reductions of *Th. junceum* chromatin in the subtelomeric region of 4AL or 4DL (Figure 3.4). The GISH analysis of their progenies (BC_2F_2 or BC_2F_3) revealed that the *Th. junceum* chromatin in BG2133, BG5136, and BG2161 comprised 35.8%, 36.5%, and 37.4% of the translocation chromosome, respectively (Table 3.5). Therefore, approximately 65% of the *Th. junceum* chromatin segment surrounding the stem rust resistance gene was eliminated.

Characterization of wheat-*Th.junceum* translocation lines with molecular markers

The progenies (F_3, BC_2F_2) of the F_2 plant carrying a Robertsonian translocation chromosome and three BC_2F_1 plants with reduced *Th. junceum* chromatin (BG2133, BG5136, and BG2161) were further characterized with markers. A total 220 SSRs, 101 EST-STS and 14 E-genome specific EST-SSRs markers were used to detect the polymorphism between CS and disomic addition line HD3505. Out of these markers, 45 were polymorphic between CS and disomic addition line HD3505 (Table 3.6). The majority of these polymorphic markers produced

a dominant coupling-phase band belonging to five homeologous groups, including 3 SSRs to group 2, 40 SSRs and EST-STS/SSRs to group 4, 1 SSR to group 5, 2 SSRs to group 6, and 1 SSR to group 7 (Table 3.6). After analysis, only 4 SSRs markers (*Xcfd31*, *Xgwm608*, *Xgwm133*, and *Xwmc182*) belonging to group 4 produced polymorphic bands between CS, HD3505 and newly-developed translocation lines (Figure 3.3). Marker *Xcfd31*was previously located at the distal region of chromosome arm 4AL and the other three markers, *Xgwm608*, *Xgwm133*, and *Xwmc182* were mapped near the centromeric region of chromosome arm 4DL (Somers et al., 2004; Sourdille et al., 2004). The molecular marker data indicated that the resistance gene was located on a wheat group 4 chromosome (i.e. 4A or 4D), but the exact chromosome is still not clear due to lack of co-dominant markers. Because CS M4D was used in the cross, the Robertsonian translocation chromosome most likely consists of chromosome arm 4DS (T4DS·4EL) and the stem rust gene was located on the long arm of the *Th. junceum* group-4 chromosome in HD3505.

Evaluation of the selected translocation lines for stem rust resistance

The CS, HD3505, Robertsonian translocation line (12N6-32) and three new translocation lines (BG2133, BG5136, and BG2161) were evaluated with races TTKSK, TRTTF, and TTTTF and eight North American *Pgt* races (Table 3.3). Virulence and avirulence responses of these *Pgt* races to major *Sr* genes are summarized in Table 3.2. Stem rust testing revealed that *Th. junceum* resistance gene was effective against TTKSK and TTTTK races with ITs ;1 to 12^{-}, but was ineffective against TRTTF with ITs 3^{+} (Table 3.3 and 3.4). For reactions to North American *Pgt* races, this gene conditioned resistance to QFCSC, RTQQC, MCCFC, TCMJC, and TMLKC (ITs: 0; , 1^{-}, 2^{-}, and 21), but was ineffective against races QTHJC, TPMKC, and TPPKC (ITs: 33^{-}, 33^{+}, and 34). Translocation lines BG2133, and BG5136 were in homozygous conditions with

fixed reaction, while lines BG2161 and 12N6-32 were still segregating (Table 3.3 and 3.4). The resistance gene in *Th. junceum* was not temperature sensitive, having similar reaction at different temperature conditions.

Discussion

As stem rust becomes a new threat to world wheat production, many wheat-related grass species and their derivatives have been used as sources of the *Sr* genes effective against Ug99 and other *Pgt* races (Xu et al., 2009; Zheng et al., 2014; Niu et al., 2014). In the tertiary gene pool of wheat, wild Triticeae species are good resources of stem rust resistance genes (Zheng et al., 2014). Many effective *Sr* genes were transferred from alien species into wheat using additions, substitutions, and translocations lines (McArthur et al., 2012). These lines cannot be utilized directly in wheat breeding because alien chromatin contains many undesirable genes (Cai et al., 2005). Chromosome engineering techniques overcome the deleterious effects of alien chromosomes by reducing the size of the alien chromosome segments transferred into the wheat genome (Qi et al., 2007). A large amout of alien chromatin surrounding seveal *Sr* genes such as *Sr26* (Dundas et al., 2007), *Sr32* (Mago et al., 2013), *Sr39* (Niu et al., 2011), and *Sr47* (Faris et al., 2008; Klindworth et al., 2012) were previously eliminated by using chromosome engineering.

In this study, we used a wheat-*Th. junceum* group-4 chromosome disomic addition line HD3505 to introgress a *Sr* gene from *Th. junceum* into wheat. By using the monosomic method (Friebe et al., 2005), we successfully developed a Robertsonian translocation line 12N6-32. To further reduce the alien chromatin in the wheat genome, we used the CS *ph1b* mutant to develop BC_1F_1 and BC_2F_1 populations. In the BC_2F_1 population, three plants, BG2133, BG5136, and BG2161 were detected with reduced alien chromosome segments. These three plants were

selfed to select homozygous progeny. A homozygous line was selected for BG2133 and BG5136, but BG2161 remained in a heterozygous condition. The original disomic addition line, HD3505, was resistant to *Pgt* races TTKSK, TTTSK, QFCSC, RCRS, and TTTTF (ITs, '2^-' to 2^+), but susceptible to TTKST, QTHJC, RKQQC, and TPMKC (ITs '3^-' to '4') (Xu et al., 2009). In this study, the two homozygous translocation lines BG2133 and BG5136 had similar reactions to the *Pgt* races tested in this study as their donor parent HD3505, with resistance reaction to TTKSK, TTTTF, QFCSC, RTQQC, MCCFC, TCMJC, and TMLKC (ITs 0; to 21) and susceptible reaction to TRTTF, QTHJC, TPMKC, and TPPKC (ITs: 33- to 34). Even when the translocation lines were evaluated under different temperature conditions, their ITs did not change, indicating that the *Sr* gene derived from *Th. junceum* was not temperature sensitive. Being effective at both low (18°C) and high (25°C) temperature conditions increases the utility of this gene.

Segregation distortion is a deviation of segregation ratios from the expected Mendelian ratio (Xu, 2008). Segregation distortion is a common genetic phenomenon associated with alien chromosomes that are transferred into wheat background (Niu et al., 2011). We observed segregation distortion in BC_1F_1 and BC_2F_1 populations in this study. Segregation distortion may be a common characteristic in *Thinopyrum* chromosomes in wheat backgrounds. The *Lr19* gene derived from *Th. ponticum* chromosome $7e1_1$ exhibited normal Mendelian segregation in Thatcher and CS backgrounds, but showed significant segregation distortion when transferred into other wheat backgrounds (Sharma and Knott, 1966; McIntosh et al., 1976; McIntosh et al., 1995). Similarly, Niu et al. (2014) also observed segregation distortion of the *Th. ponticum* chromosome $7e1_2$ carrying *Sr43* in CS background. In another study, Kong et al (2009) found deviation from normal Mendelian ratios when the *Th. intermedium* chromosome 7E

segment carrying the *Bdv3* gene for resistance barley dwarf virus was transferred to wheat. This indicated there may have been a stronger effect of gametocidal (*Gc*) and segregation distortion (*sd*) genes on gamete formation that caused segregation distortion of *Thinopyrum* chromosomes in wheat backgrounds.

To make this new *Sr* gene usable in wheat breeding programs, there is a need to develop gene linked molecular markers, which help to stack multiple *Sr* genes in one variety. During this study, we found four molecular markers that co-segregated with the *Sr* gene in our developed lines. Of these four markers, three markers located close to the chromosome 4DL centromeric region and one marker located at the distal region of chromosome 4AL. The chromosomal location of this new *Sr* gene was still undetermined. We produced the Robertsonian translocation line using CS M4D as a parent. Therefore, most likely the Robertsonian translocation chromosome consists of chromosome arm 4DS (T4DS·4EL). But we have not identified any co-dominant markers and a chance of involvement of chromosomes 4A or 4B is also possible. Therefore, based on the present data, we can only assume that the *Sr* gene is translocated to a wheat group-4 chromosome.

We determined the size, location, and breakpoint of the alien chromosome segment introgressed into the wheat genome using GISH analysis. Approximately 65% of *Th. junceum* chromatin of the chromosome was eliminated in the new wheat translocation lines. The remaining 35% of *Th. junceum* chromatin was located in the distal region on the long arm of a wheat group-4 chromosome, probably 4D. To determine if the new translocations lines can be used in wheat breeding programs, they need to be evaluated for agronomic performance and quality characteristics. If the *Th. junceum* chromatin is still associated with deleterious linkage

drag, the translocation lines developed in this study will be the useful donors for further reducing the size of the alien chromosome segment using *ph1b*-induced homoeologous recombination

This study demonstrates the potential utility of *Thinopyrum* species in wheat improvement. Alien introgression is a useful approach to enhace the utility of *Thinopyrum* species. Through this study, we identified a novel stem rust resistance gene from *Th. junceum* and successfully transferred the gene into the wheat genome using chromosome engineering. This is the first time this species has been utilized for incorporating a stem rust resistance gene into wheat. This novel gene was not temperature sensitive and was effective against many *Pgt* races. Therefore, it should be a useful gene in wheat breeding and provides additional resources for pyramiding *Sr* genes in wheat for effective and durable resistance to stem rust.

Table 3.1. Infection type (IT) of F_2 families derived from a cross between disomic addition line HD3505 and CS M4D with *Pgt* race TMLKC at greenhouse conditions

F_2 family	No. of susceptible plants with IT		No. of resistant plants with IT	
	43	32	23	1-21
12N3	90	16	23	29
12N6	48	4	24	10
12N9	136	22	47	22
Total	274	42	94	61
	S[a] = 316		R[b] = 155	

[a] S: Susceptible
[b] R: Resistant

Table 3.2. Virulence and avirulence responses to major *Sr* genes for the races used in this study (Olivera et al., 2012; Jin et al., 2007)

Race	Isolate	Origin	Avirulence	Virulence
TTKSK	13ETH18-1	Ethiopia	*Sr24 36 Tmp*	*Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN*
TRTTF	06YEM34-1	Yemen	*Sr8a 24 31*	*Sr5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McNTmp*
TTTTF	01MN84A-1-2	USA	*Sr24 31*	*Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McNTmp*
TMLKC	72-41 (sp2)	USA	*Sr6 8a 9a 9b 17 24 30 31 38*	*Sr5 7b 9d 9e 9g 10 11 21 36 McNTmp*
QTHJC	64E-C1	USA	*Sr7b 9a 9e 24 30 31 38 36 Tmp*	*Sr5 6 8a 9b 9d 9g 10 11 17 21 McN*
QFCSC	A48	USA	*Sr6 7b 9b 9e 11 24 30 31 36 38 Tmp*	*Sr5 8a 9a 9d 9g 10 17 21 McN*
RTQQC	72.00	USA	*Sr9e 10 17 24 30 31 38 Tmp*	*Sr5 6 7b 8a 9a 9b 9d 9g 11 21 36 McN*
MCCFC	A-5	USA	*Sr6 8a 9a 9b 9d 9e 11 21 24 31 36 38*	*Sr5 7b 9g 10 17 30 TmpMcN*
TCMJC	A-21	USA	*Sr6 8a 9a 9b 11 24 30 31 38 Tmp*	*Sr5 7b 9d 9e 9g 10 17 21 36 McN*
TPMKC	TNMKsp2	USA	*Sr6 9a 9b 24 30* 31 38	*Sr5 7b 8a 9d 9e 9g 10 11 17 21 36 McNTmp*
TPPKC	81AC-46(2)	USA	Sr6 9a 9b 24 31 38	*Sr5 7b 8a 9d 9e 9g 10 11 17 21 30 36 McNTmp*

Table 3.3. Resistance Infection types (ITs) of wheat-*Th. junceum* translocation lines when tested with different *Pgt* races at different temperature conditions[a].

Line	TTKSK	TTTTF	QFCSC			RTQQC			MCCFC			TCMJC			TMLKC		
	GH	GH	18[b]	25[b]	GH[b]	18	25	GH	18	25	GH	18	25	GH	18	25	GH
CS	3+	3+	33-	43	3+4	33-	43	43	34	43	34	33-	34	3-3	34	43	34
HD3505	;1	12-	1-	0;	0;	23-	2-2	12-	22+	21	1'13	0;1	0, 1-	0;1-	2	11+	1
BG2133	12-	12-	0;-2	1	11+	23-	23	2+3-	23-	23-	2+3	12-	12	2-	23-	22+	22+
BG5136	1;	12-	21	12	0;	2+3	23	2' 2+	23-	23-	2+3-	12	12	1-	23-	22+	2-2
BG2161	3+/12-	2-/3+	21-/34	34	1-	34/2+3-	23/34	34/2+3-	34	23-	34	33-	34/1-	234	32	34/23-	2+/43
12N6-32	3+/;1	2-/3+	34/23	2/34	11+/34	34	23/34	2+/334	34	23-/34	3+4	34/33-	34/12	34	34/23-	22+/34	34/2+3

[a] ITs score 0, ; , 1, 2 are showed resistant reaction, and 3, 4 are showed susceptible reaction. Plants showed combinations of ITs scores, like IT score 32 is primarily 3 score with lesser 2 score. Signs plus (+) and minus (-) indicated small and large size of the pustules (Stakman, 1962).[b]18 and 25 indicated the temperatures 18°C and 25°C, respectively, in growth chambers, and GH indicated greenhouse.

[c] GH, greenhouse

Table 3.4. Susceptible Infection types (ITs) of wheat-*Th. junceum* translocation lines when tested with different *Pgt* races[a] at different temperature conditions.

Line	TRTTF	QTHJC			TPMKC			TPPKC		
	GH	18[b]	25[b]	GH[c]	18	25	GH	18	25	GH
CS	3+	33+	43	43	34	43	3+4	34	43	3+4
HD3505	3+	33-	34	3+4	32	34	34	32	34	3
BG2133	3+	33-	34	34	33+	34	34	32	34	34
BG5136	3+	33-	34	34	34	34	34	32	34	34
BG2161	3+	33-	34	34	34	34	34	34	34	34
12N6-32	3+	33+	34	3+4	34	34	3+4	34	34	34

[a]ITs score 0, ; , 1, 2 are showed resistant reaction, and 3, 4 are showed susceptible reaction. Plants showed combinations of ITs scores, like IT score 32 is primarily 3 score with lesser 2 score. Signs plus (+) and minus (-) indicated small and large size of the pustules (Stakman, 1962).
[b] 18 and 25 indicated the temperature 18°C and 25°C, respectively.
[c] GH, greenhouse.

Table 3.5. Measurement and size calculation of *Th. junceum* 4E chromosome segments carrying stem rust resistance gene in BG2133, BG5136, and BG2161

Line	Cell No. examined	Average length (μm) of 4E segments	Average lengh (μm) of whole chromosome	Average 4E%[a]
BG2133	5	4.94	13.81	35.8
BG5136	8	4.51	12.41	36.5
BG2161	6	5.94	15.90	37.4

[a] Percentage of *Th. junceum* 4E chromosome segment carrying resistance gene in the translocation chromosome.

Table 3.6. A list of molecular markers polymorphic between HD3505 and Chinese Spring

Marker	Chromosome location	References
Xwmc602	2A/2B	Somers et al. (2004)
Xgwm304	2A/5A	Sourdille et al. (2004)
Xwmc335	5B	Somers et al.(2004), Sourdille et al. (2004)
Xcfd31	4A	Sourdille et al. (2004)
Xbarc78	4A	Somers et al.(2004), Sourdille et al. (2004)
Xbarc52	4A	Somers et al.(2004), Sourdille et al. (2004)
Xgwm160	4A	Somers et al.(2004), Röder et al. (1998)
Xwmc219	4A	Somers et al.(2004)
Xwmc497	4A/7A	Somers et al.(2004)
Xmag3273	4A	Xue et al. (2008)
Xwmc776	4A	Xue et al. (2008)
Xhbg403	4D	Torada et al. (2006)
Xhbe341	4D	Torada et al. (2006)
Xhbe217	4A	Torada et al. (2006)
Xhbe484	4A	Torada et al. (2006)
Xhbg452	4A	Torada et al. (2006)
Xgwm608	4D	Somers et al.(2004), Sourdille et al. (2004)
Xgwm133	4D	Somers et al.(2004), Sourdille et al. (2004)
Xwmc182	4D	Somers et al.(2004), Sourdille et al. (2004)
Xbarc98	4D/2B	Somers et al.(2004), Sourdille et al. (2004)
Xbarc178	6B	Somers et al.(2004), Sourdille et al. (2004)
Xgwm88	6B	Somers et al.(2004), Sourdille et al. (2004)
4EST236	4JS	Pu et al. (2015)
4EST262	4JS	Pu et al. (2015)
4EST79	4JS	Pu et al. (2015)
4EST300	4JS	Pu et al. (2015)
4EST335	4JS	Pu et al. (2015)
4EST397	4JS	Pu et al. (2015)
4EST394	4JS	Pu et al. (2015)
4EST401	4JS	Pu et al. (2015)
4EST403	4JS	Pu et al. (2015)
4EST408	4JS	Pu et al. (2015)
4EST426	4JS	Pu et al. (2015)
4EST429	4JS	Pu et al. (2015)
4EST475	4JS	Pu et al. (2015)
4EST561	4JS	Pu et al. (2015)
4EST573	4JS	Pu et al. (2015)
4EST627	4JS	Pu et al. (2015)
4EST643	4JS	Pu et al. (2015)

Table 3.6. A list of molecular markers polymorphic between HD3505 and Chinese Spring (continued)

Marker	Chromosome location	References
4EST655	4JS	Pu et al. (2015)
Xmag1682	4JS	Pu et al. (2015)
Xlfz564	4JS	Pu et al. (2015)
Ltc1481-116	4E	Wang et al. (2010)
Ltc1506-94	4E	Wang et al. (2010)
Ltc1141-91-93	4E	Wang et al. (2010)

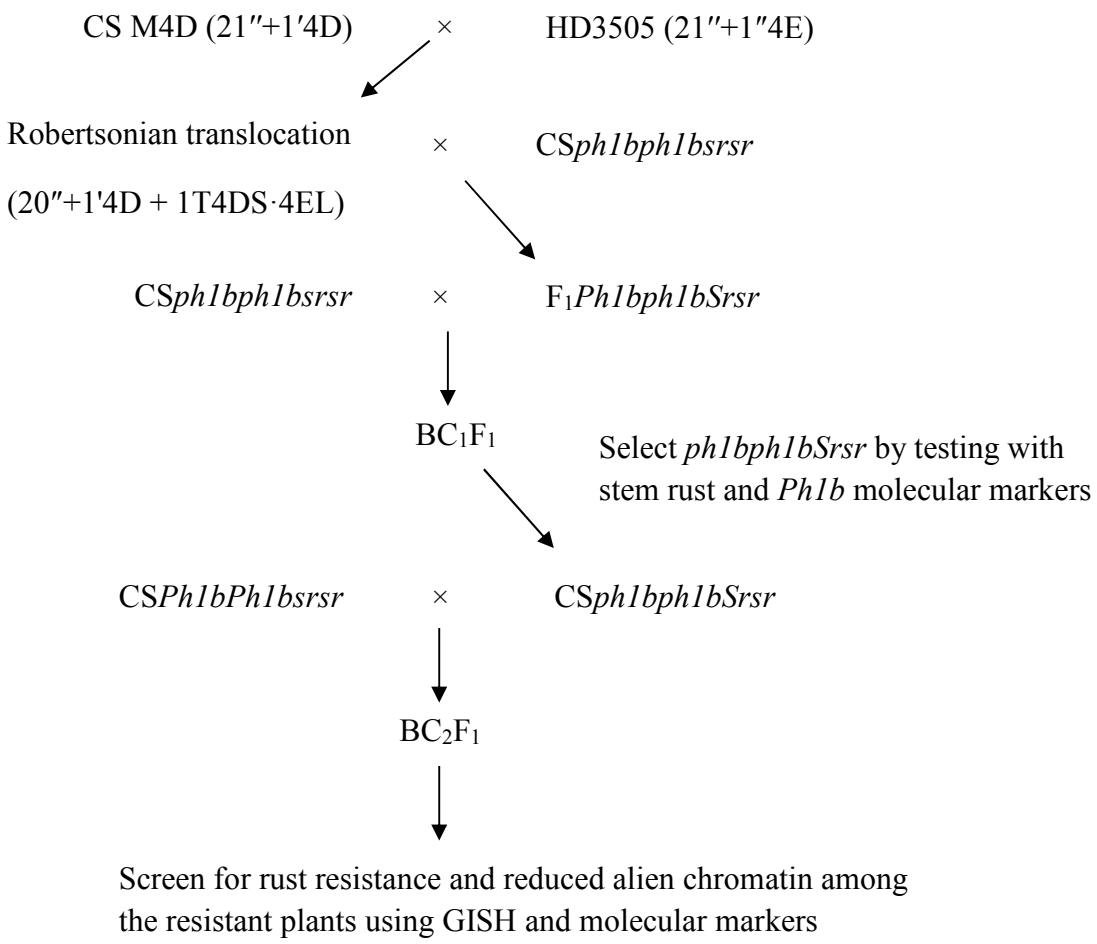
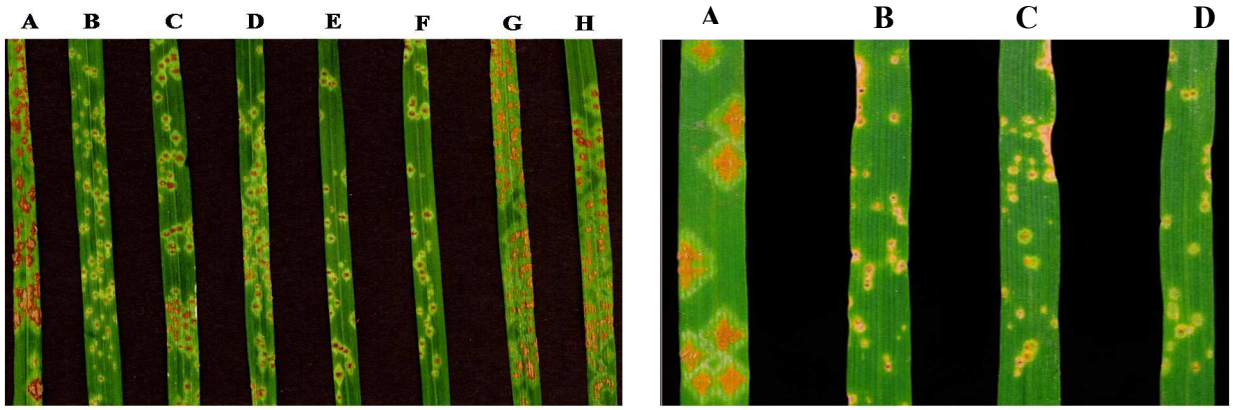


Figure 3.1. The procedure used to transfer a stem rust resistance gene from wheat-*Th. junceum* chromosome disomic addition line HD3505.



(a) TMLKC (b) TTKSK

Figure 3.2. (a) Reactions to *Pgt* race TMLKC of A) CS, B) HD3505, C) 12N6-32, D) BG2161, E) BG2133, F) BG5136, G&H) BC_2F_1 susceptible plants and race (b) Reactions to *Pgt* race TTKSK of A) CS, B) HD3505, C) BG5136, D) BG2133

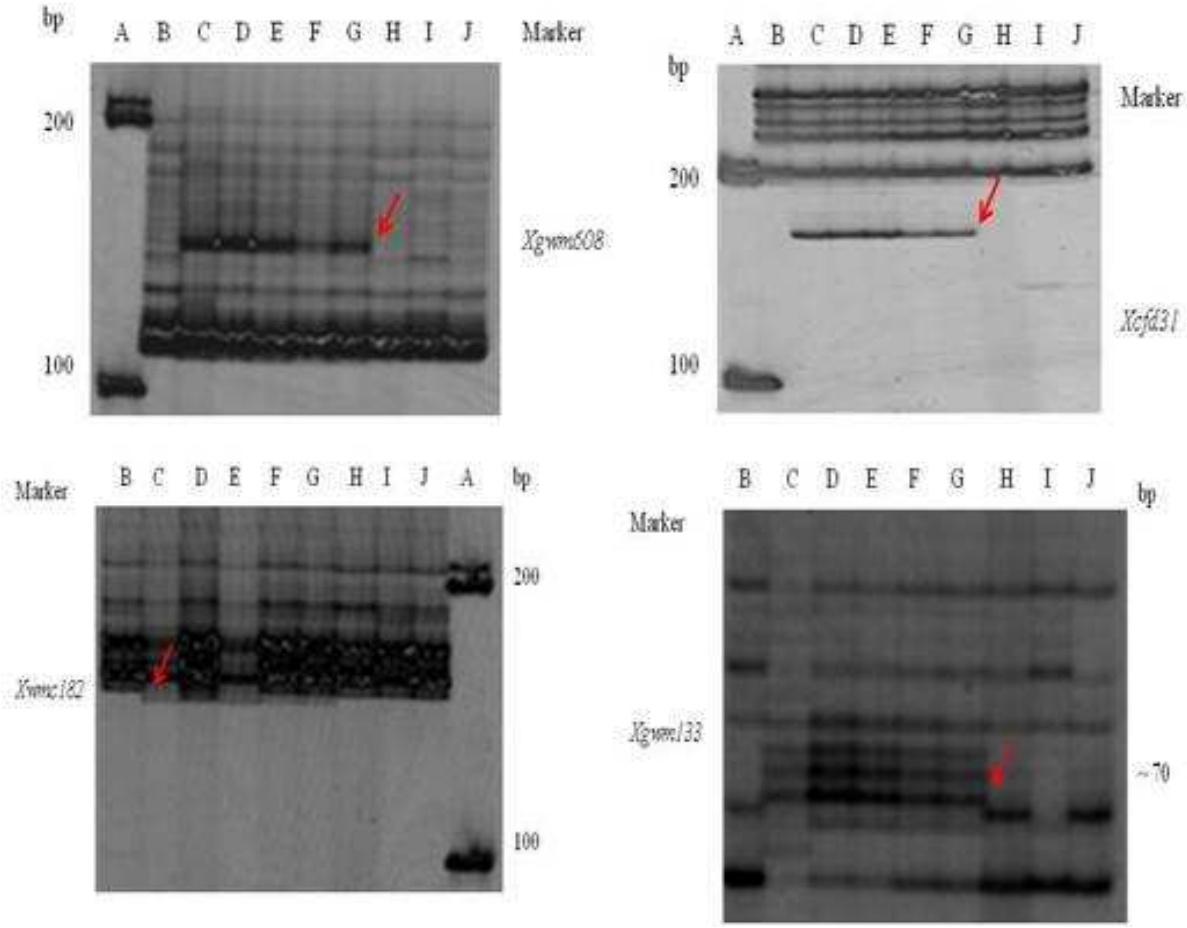


Figure 3.3. Gel images of the PCR products of four dominant markers (*Xgwm608, Xcfd31*, *Xwmc182*, and *Xgwm133*) run on 6% non-denaturing polyacrylamide gel. Gel sequence A) Ladder (100bp), B) CS, C) HD3505, D) BG2133, E) BG5136, F) BG2161, G) BG866, H) N4AT4B, I) N4BT4D, J) N4DT4B. Red arrow indicated the target band in the gel.

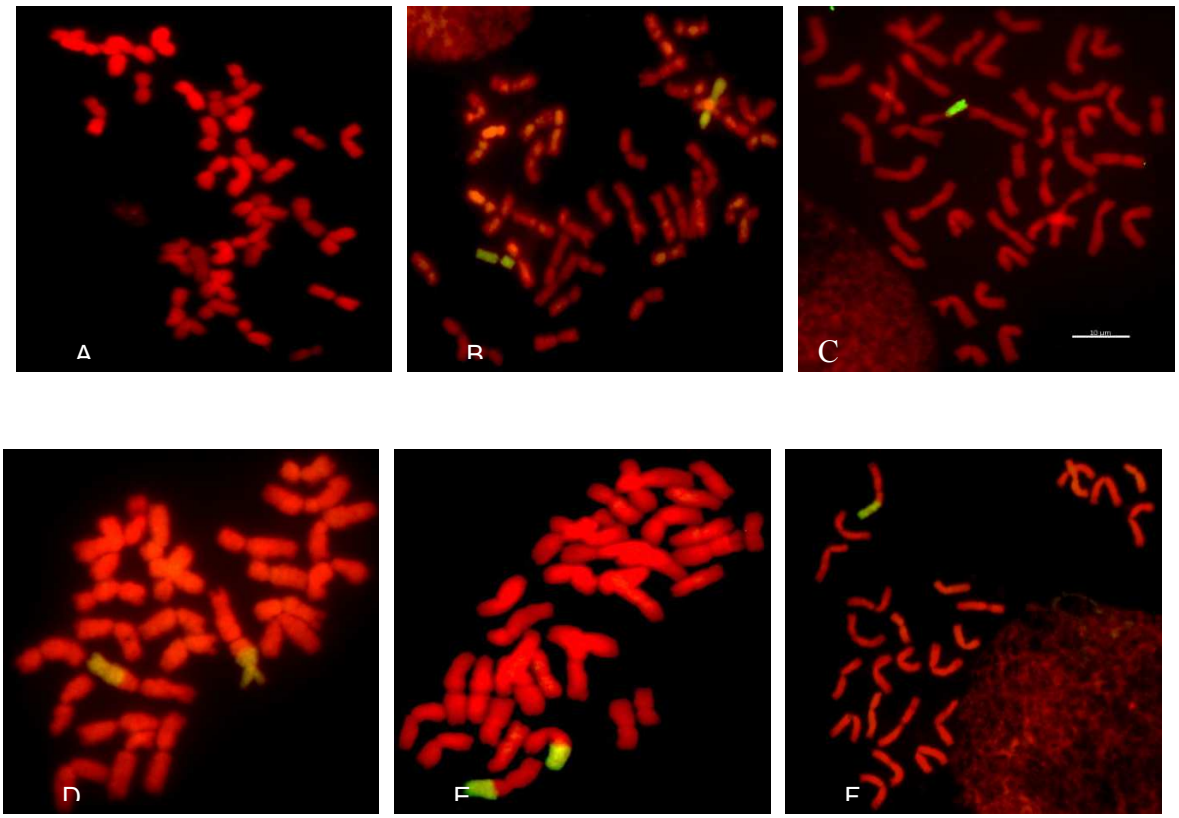


Figure 3.4. Images from GISH analysis of wheat-*Th. junceum* translocation lines carrying stem rust resistance gene. Green fluorescence is alien chromatin from *Th. junceum* labeled with FITC-avidin and red fluorescence from wheat chromatin labeled with PI. A) CS, B) HD3505, C) 12N6-32 (Robertsonian translocation line), D) BG5136 (homozygous), E) BG2133 (homozygous), F) BG2161 (heterozygous)

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CHAPTER 4. IDENTIFICATION AND MAPPING OF STEM RUST RESISTANCE GENES FROM TETRAPLOID PERSIAN WHEAT (*T. TURGIDUM* SUBSP. *CARTHLICUM*)

Abstract

Puccinia graminis Pers.: Pers f. sp. *tritici* Eriks. & E. Henn., (*Pgt*) is the causal agent of wheat stem rust and can cause significant yield losses. A new *Pgt* race, Ug99 (TTKSK) and its variants have defeated several important genes which are widely deployed in wheat cultivars. To confine this threat, researchers have been devoted to identifying effective Ug99 resistance genes. Here, we report the identification and mapping of a resistance gene from an accession (PI 387696) of *Triticum turgidum* ssp. *carthlicum* that conditions resistance against TTKSK. To find the mode of inheritance of resistance, 190 recombinant inbred lines (RILs) were developed by crossing PI 387696 to susceptible line Rusty. The parents and 190 RILs were evaluated for seedling resistance to three *Pgt* races TTKSK, TRTTF, and TMLKC and genotyped using the wheat 90K iSelect array. Genetic and mapping analysis indicated that one dominant gene in PI 387696 conferred the resistance to the three *Pgt* races and the resistance locus was mapped to the genomic region harboring the *Sr13* locus on chromosome arm 6AL. Molecular markers diagnostic for *Sr13*, including *BE403950, CK207347*and *KASPSr13*, indicated that resistance in PI 387696 was due to the *Sr13* gene. But evaluation of genetic stocks Kl-B, ST464-C1, Langdon, and Medea Ap9d with specific races at different temperature conditions indicated that resistance in PI 387696 was due to a new allelic form of *Sr13* or due to other novel *Sr* gene close to *Sr13* locus. The marker validation showed that two closely linked Semi-thermal Asymmetric Reverse PCR **(**STARP) markers *Xrwgsnp6* and *Xrwgsnp7* can be used for marker assisted selection in

wheat breeding programs. This new *Sr13* allele can be useful in enhancing the durability of resistance against stem rust in wheat by its pyramiding with other important *Sr* genes.

Introduction

Stem rust, caused by the pathogen *Puccinia graminis* Pers. f. sp. *tritici* Eriks and E. Henn (*Pgt*), is historically the most damaging disease to wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD). During the 1920s and 1960s, serious epidemics occurred in many wheat-growing countries and caused significant yield losses (Leonard and Szabo, 2005). In the past several decades, wheat crops around the world have been protected from stem rust through effective utilization of stem rust resistance (*Sr*) genes, and eradicating the alternate host (*Berberis vulgaris* L.) (Singh et al., 2006). However, in 1999, a new *Pgt* race, which broke down the resistance conferred by *Sr31*, was detected in Uganda (Pretorious et al., 2000). This new *Pgt* race was initially named Ug99 (Pretorious et al., 2000) and was designated as TTKSK according to the North American Stem Rust Nomenclature System (Jin et al., 2008b). TTKSK is virulent on many *Sr* genes (Pretorious et al., 2000; Singh et al., 2015), and has the ability to mutate rapidly into new virulent variants. Variants of TTKSK detected in Kenya were also found with virulence to resistance genes *Sr24* and *Sr36* (Jin et al., 2008a; 2009). To date, 13 *Pgt* races, TTKSK, TTKSF, TTKST, TTTSK, TTKSP, PTKSK, PTKST, TTKSF+, TTKTT, TTKTK, TTHSK, PTKTK, and TTHST have been confirmed under the Ug99 lineages (Fetch et al., 2016). These races are now commonly referred to as the Ug99 race group.

There are additional *Pgt* races unrelated to the Ug99 race group that have broad virulence against *Sr* genes. A new *Pgt* race, TRTTF, was detected in Yemen in 2006 (Singh et al., 2011). TRTTF is the first known race with virulence to $Sr1RS^{Amigo}$, which is an Ug99 effective gene in US winter wheat cultivars (Olivera et al., 2012; Singh et al., 2015). Another *Pgt* race, TTTTF,

was first detected in the United states in 2003 (Jin et al., 2005). The TTTTF race showed virulence against the combination of *Sr9e* and *Sr13* genes, which are present in many durum wheat cultivars (http://rusttracker.cimmyt.org/?page_id=7). Recently, TTTTF caused a serious stem rust epidemic in Sicily (Europe) and damaged both durum and common wheat crops (Bhattacharya, 2017). In addition, race TKTTF was first detected in Turkey in 2005. Like the Ug99 race group, this race rapidly distributed into eleven other wheat growing countries (http://rusttracker.cimmyt.org/?page_id=6811). Many *Sr* genes that are successfully utilized in resistant wheat cultivars are ineffective against TKTTF, such as *Sr9e*, *Sr36*, *SrTmp*, and *SrMcN*. The TKTTF race recently caused severe epidemics in Ethiopia in 2013 on cultivar Digalu that carried the *SrTmp* gene (Olivera et al., 2015). A second race also coding as TKTTF has been detected in Germany (Olivera et al., 2017), and when tested on wheat lines carrying *Sr7a*, *Sr33*, *Sr45*, and *SrTt-3*, this race differs from TKTTF of Ethiopian origin.

Due to the emergence of Ug99 and other races with broad virulence to *Sr* genes, worldwide efforts were made to identify effective resistance to the Ug99 race lineage and other emerging *Pgt* races, in both cultivated and wild relatives of wheat. Host resistance is an economic and environmentally friendly strategy for controlling stem rust disease (Ellis et al., 2014). Stem rust has been effectively controlled for over 50 years through utilization of resistance genes in wheat cultivars (Singh et al., 2011). To date, 73 *Sr* genes and alleles have been identified from wheat and its relatives (Singh et al., 2015). Out of these genes, the Ug99 race group has been found to be virulent on 34 *Sr* genes. The other 39 *Sr* genes, such as *Sr13, Sr25, Sr26, Sr33, Sr35, Sr39, Sr45, Sr46*, and *Sr47* showed moderate or high resistance to the Ug99 race group (Singh et al., 2015). Some of the Ug99-effecteve *Sr* genes are associated with undesirable traits or do not have consistent resistance under different environmental conditions

(Singh et al., 2011). Therefore, there is a continuous need to search for novel *Sr* genes which are effective against the Ug99 race group and other newly emerging races of stem rust disease.

The best strategy for identification of new *Sr* genes is combining phenotypic data of stem rust inoculation with genotypic data of molecular markers. Recently, wheat 9K and 90K single nucleotide polymorphism (SNP) iSelect assays (Illumina Inc., San Diego, CA. U.S.A) have revolutionized wheat mapping (Cavanagh et al, 2013; Wang et al, 2014) by speeding up the mapping of *Sr* genes to specific chromosomes. For example, Bansal et al (2014) used the 9K SNP iSelect array to map *Sr56* in the winter wheat cultivar Arina and identified molecular markers linked with the resistance locus. Similarly, Babiker et al (2015) used the 90K SNP array for mapping the resistance locus in spring wheat landrace PI 374670 to chromosome 7A and identified the flanking SNP markers. Identification of molecular markers that are tightly linked to the new *Sr* genes is essential for transferring the genes into wheat cultivars and for pyramiding several resistance genes (Todorovska et al., 2009). These markers are also useful in minimizing linkage drag. Therefore, many *Sr* genes with closely-linked or diagnostic markers have been identified, such as *Sr2* (Spielmeyer et al., 2003; Mago et al., 2011; Bernardo et al., 2013), *Sr13 (*Simons et al., 2011), *Sr43* (Niu et al., 2014)*, Sr45* (Periyannan et al., 2014), *Sr47* (Klindworth *et al.* 2017), *SrND463* (Basnet et al., 2015), *SrTA10171* (Olson et al., 2013), and *SrTA10187* (Wiersma et al., 2016). Some of these markers have been broadly utilized in wheat breeding programs for stem rust resistance breeding (Bernardo et al., 2013; Yu et al., 2010; Olson et al., 2010a).

Tetraploid wheat is a good source of stem rust resistance. Many *Sr* genes, such as *Sr2* (Knott, 1968), *Sr12* (Knott, 1984), *Sr13*, and *Sr14* (Knott, 1962; Simons et al., 2011) originated from tetraploid wheat. *Triticum turgidum* ssp. *carthlicum* (Neyski) A. Love & D. Love (2n = 4x

= 28, AABB) is a cultivated tetraploid wheat, also known as Persian wheat. It is an early-maturing wheat species with a spring habit and is an important source of food consumption for humans (Zhuang et al., 2011). It is cultivated in the Transcaucasia region in countries such as Armenia and Georgia (Zhuang et al., 2011; Takumi and Morimoto, 2015). It possesses many useful agronomic traits including resistance to powdery mildew and stem rust, higher tiller numbers, good fertility, and higher storage protein (gliadin) content (Zhu et al., 2005; Raut et al., 1984; Belay et al., 1994; Zhuang et al., 2007; Jørgensen and Jensen, 1972).

Olivera et al. (2011) evaluated tetraploid wheat accessions for seedling resistance to stem rust, and they found *T. turgidum* ssp. *carthlicum* accession PI 387696 was resistant to Ethiopian races of stem rust pathogen (Olivera et al., 2011; Zhuang et al., 2011). To date, no *Sr* genes have been identified from this species. Therefore, the aim of this study was to study the inheritance of resistance in this line, determine chromosomal location of the resistance genes, and identify closely linked markers.

Materials and methods

Plant Materials

Tetraploid accession PI 387696 of *T. turgidum* ssp. *carthlicum* was obtained from the USDA-ARS National Small Grain Collection in Aberdeen, Idaho (https://npgsweb.ars-grin.gov/gringlobal/accessiondetail.aspx?id=1291239). A population 190 recombinant inbred lines (RILs) was developed by firstly crossing PI 387696 to Rusty (PI 639869), a genetic stock of durum wheat (*T. turgidum* L. ssp. *durum*) that is near-universally susceptible to stem rust (Klindworth et al., 2006), followed by single-seed descent through the F_7 generation.

Additional genetic stocks used in this study included Kl-B, ST464-C1, Langdon (CItr13165), and Medea Ap9d. Kl-B and ST464-C1 are both durum wheat lines which are

monogenic for stem rust resistance. Kl-B was derived from Khapli emmer (Williams and Miller, 1982), the original source of *Sr13*, and because it conditions infection type (IT) '2', it is postulated to carry *Sr13*. The gene in ST464-C1 was located to chromosome 6A, and based on ITs on eight stem rust races, was postulated to be *Sr13* (Klindworth et al., 2007). Durum wheat 'Langdon' and Medea Ap9d carry multiple stem rust resistance genes (Knott, 2000). Langdon derives stem rust resistance from Khapli (Heerman and Stoa, 1956) and is therefore postulated to carry *Sr13*. Medea Ap9d carries *Srdp-2* (Roelfs and McVey, 1979), and McIntosh et al. (1995) indicated *Srdp-2* is allelic to *Sr13*.

Evaluation of stem rust

Rusty, PI 387696, and their F_2 and RIL (F_7) populations (Rusty/PI 387696) were evaluated for reactions to *Pgt* races: TMLKC (North American isolate), TTKSK (Ug99 isolate) and TRTTF (Yemen isolate). The F_1 hybrid (Rusty/PI 387696) was also evaluated with these three *Pgt* races. Virulence and avirulence responses of these three races to major *Sr* genes are summarized in Table 4.1. Stem rust evaluation with races TTKSK and TRTTF were conducted in USDA-ARS Cereal Disease Laboratory, St. Paul, MN using the protocol reported by Rouse et al. (2011). Testing of race TMLKC was conducted at USDA-ARS Northern Crops Science Laboratory, Fargo, ND. For TMLKC testing, two to four seeds per line were grown in super-cell cones (Stuewe and Sons, Inc., Corvallis, OR, U.S.A) containing soil mix Sunshine SB100 (Sun Gro Horticulture Distribution Inc., Bellevue, WA, U.S.A) and fertilized with OsmocotePlus 15-19-12 fertilizer (Scotts Sierra Horticultural Product Company, Marysville, OH, U.S.A) into two replicates. The seedling plants were grown in a greenhouse at 20 to 23°C with a 16/8 h (day/night) photoperiod. The urediospores of TMLKC were suspended in paraffinic oil, and eight-day-old seedlings were inoculated following the procedure described by Williams et al.

(1992). After inoculation, the plants were kept for 24 h in the mist chamber under subdued light and then transferred to a greenhouse maintained at 20 to 23°C. Seedlings were scored for ITs at 13 or 14 days after inoculation by evaluating the infected primary leaf of each plant. Each leaf was evaluated using the scale reported by Stakman et al. (1962) where 0 = immune, ; = necrotic fleck, 1 = small necrotic pustules, 2 = small to medium sized chlorotic pustules with green island, 3 = medium sized chlorotic pustules and 4 = large pustules without chlorosis, and signs "-" and "+" to demonstrate smaller and larger pustules, respectively, for each IT (Roelfs and Martens, 1988; Klindworth et al., 2012). The plants with IT 2 or lower were considered resistant while the plants with IT 3 or greater were considered susceptible. For linkage analysis, the original seedling IT scores were converted to a 0–9 linear single-value disease scale using the method described by Zhang et al. (2014). In this method, Stakman's ITs 0, ; (fleck); 1^-, 1, 1^+, 2^-, 2, 2^+, 3^-, 3, 3^+, and 4 were converted to 0, 0, 1, 2, 3, 4, 5, 6, 7, 8, and 9 respectively, with double minus ($^=$) and double plus ($^{++}$) being converted to single minus ($^-$) and single plus ($^+$), respectively. For the lines with combination of ITs, the middle score(s) and the letters C and N were ignored, and the predominant IT was weighted double than the last score. For example, to covert Stakman's IT score ;21^{++}, the IT was first collapsed to ;1^+, and then converted to linear single value 1. These linearized 0 to 9 scale values for the RIL population and parents were further utilized for the QTL analysis.

Genotyping of PI 387696

Total genomic DNA was extracted from the Rusty × PI 387696 RIL population (F_7) using the protocol described by Niu et al. (2011). The RIL population and parents were genotyped using the wheat 90K SNP iSelect assay. The SNP genotyping assay was carried out on the Beadstation and iScan instruments following the manufacturer's protocols (Illumina Inc.,

San Diego, CA. U.S.A). The SNP markers were designated with “IWA”, and “IWB” followed by their index number as suggested in Wang et al. (2014). SNP genotype calling was performed with Genome Studio polyploidy clustering v2011.1 software (Illumina Inc., San Diego, CA. U.S.A) and accuracy of SNP clustering was visually inspected. Incorrect clustering was manually organized for accuracy of SNP genotype calling.

Several SSR markers with known chromosome locations were selected from each chromosome to confirm genetic linkage groups of particular chromosomes. These SSR markers included *Xwmc* (Somers et al., 2004), *Xcfa* and *Xcfd* (Sourdille et al., 2004), *Xbarc* (Song et al., 2005), *Xgdm* (Pestsova et al., 2000), and *Xgwm* (Röder et al., 1998). The selected SSR set was checked for polymorphism between Rusty and PI 387696 using the polymerase chain reaction (PCR) conditions described by Röder et al. (1998) with some modifications. A volume of 15 µl reaction mixture consisted of 3 µl of 5× green GoTaq buffer with 7.5 mM $MgCl_2$ (Promega Corporation, Madison, WI), 0.48 µl of 2.5 mM each dNTP, 1.2 µl of 5,000 nM each forward and reverse primer, 0.2 µl of 5 unit Taq polymerase, 2 µl of template DNA (50 ng/µl), and 8.12 µl of distilled water. The PCR amplification was conducted following one cycle of 94°C for 4 min, 35 cycles of 94°C for 30 sec, 55°C annealing for 45 sec, and 72°C for 45 sec, and one cycle of 72°C for 10 min for final extension. The PCR products were electrophoresed on 6% non-denatured poly-acrylamide gel, which were made using 37.5 ml of distilled water, 5 ml 0.5× TBE (Tris-borate-EDTA) buffer, 7.5 ml acrylamide/bis-acrylamide, 500 µl of 10% ammonium persulfate (APS), and 30 µl tetramethylethylenediamine (TEMED). After loading PCR products in wells, the poly-acrylamide gel was run for 90-120 min (depends on the size of the marker) using a DDH-400-33 sequencer (C.B.S. Scientific Company, Inc., Del Mar, CA, U.S.A) under constant 40-60W per gel. The gel was stained with 1× GelRed (Phenix Research Products, Candler, NC,

U.S.A) for 5-10 min, and then scanned with a Typhoon 9410 imager (GE Healthcare, Inc. Waukesha, WI, U.S.A). Molecular markers that showed the polymorphism between the two parents were used to genotype the 190 RILs and used for linkage map construction.

Stem rust testing of *Sr13* genotypes

Rusty, Kl-B, Langdon, Medea Ap9d, PI 387696, and ST464-C1 were included in a test of eight local *Pgt* races. Races/isolates used in the test were QTHJC/64E-(1), QFCSC/370C, RTQQC/72.00, RHFSC/72.22, TMLKC/72-41, TPMKC/TNMK, THTSC/A12, and TCMJC/A21. Two of these races, THTSC and TCMJC, are notable because in tests conducted with 21 North American stem rust races by J.D. Miller (unpublished, 1995), these were the only two races virulent on Kl-B; and hence virulent on *Sr13*. Based on local records, TCMJC was originally identified as race 15-WL (Gough et al., 1964), and noted for its virulence on *Sr13*.

Linkage map and QTL analysis

A linkage map was constructed using the computer program Mapdisto v1.8.2.1 (Lorieux, 2012). The markers were first organized into groups by using the command 'find groups', with minimum logarithm of odds (LOD) 3.0 and an r_{max} value of 0.3, and the command 'order' was used to determine the initial order of markers in the linkage group. Next, the commands 'check inversions', 'ripple order', and 'drop locus' were used to find the best map. The Kosambi mapping function was used to calculate the map distance in centiMorgans (cM) (Kosambi, 1944). The genotypic and phenotypic data of the RIL population was used in QTL analysis. The critical LOD threshold was calculated using a permutation test with 1000 iterations. For QTL analysis, composite interval mapping (CIM) was carried out using the computer program QGene 4.3 (Joehanes and Nelson, 2008).

Development and validation of semi-thermal asymmetric reverse PCR (STARP) markers

STARP markers were developed by utilizing the source sequences from the wheat 90K SNP iSelect assay for SNP markers IWB34398 and IWB71956 that were linked to the resistance locus and identified based on the seedling resistance analysis of the RILs population. During this study, two STARP markers (*Xrwgsnp6* and *Xrwgsnp7*) were developed by following the protocol of Long et al. (2017) (Table 4.2). Genotyping with the STARP assay was performed using two-universal priming element-adjustable primers (PEA-primers), two asymmetrically modified allele-specific primers (AMAS-primers) and one common reverse primer (Long et al., 2017). The PEA-primer sequences used during this study were similar to those reported in Long et al. (2017) and AMAS-primers and common reverse primer was designated using the sequence of SNP markers IWB34398 and IWB71956. These STARP markers were first evaluated on 6% non-denatured poly-acrylamide gel following the protocol described by Long et al. (2017). The polymorphic STARP markers were then evaluated using the CFX384^{TM}Real-Time System (Bio-Rad Laboratories, Inc., Hercules, CA, USA) by following the PCR reaction mixture conditions and protocol described by Long et al. (2017). The STARP markers were validated using a diverse set of 16 durum and 32 common wheat cultivars or lines originating from different geographic regions.

Results

Seedling reactions of Rusty × PI 387696 hybrid and populations to stem rust pathogen

Stem rust evaluation showed that Rusty and PI 387696 had susceptible and resistant reactions, respectively, to *Pgt* races TTKSK, TRTTF and TMLKC (Figure 4.1). To identify the stem rust resistance gene(s) in PI 387696, the F_1 hybrid and F_2 and RIL (F_7) populations were developed from the cross Rusty × PI 387696. Sixteen F_1 plants were evaluated with *Pgt* race

TMLKC and 4 F_1 plants with races TTKSK, and TRTTF. In addition, 83, 90, and 167 F_2 plants were tested with *Pgt* races TTKSK, TRTTF, and TMLKC, respectively. All F_1 plants had a level of resistance similar to PI 387696, suggesting that the resistance was controlled by a dominant gene(s). In the F_2 populations, the plants tested with TTKSK, TRTTF, and TMLKC segregated for resistant and susceptible phenotypes in ratios of 63:20, 68:22, and 128:39, respectively (Table 4.3). A chi-square goodness-of-fit test showed that the segregation fit the expected 3:1 ratio (TTKSK: $\chi^2 = 0.922$, p = 0.860; TRTTF: $\chi^2 = 0.015$, p = 0.903; TMLKC: $\chi^2 = 0.241$, p = 0.623) for a single dominant gene. Among the 190 RILs tested with TTKSK, TRTTF, and TMLKC, 85 and 98 lines had resistant (ITs ;, 1, ;2, and 22^+) and susceptible (ITs 3^+, 4) reactions, respectively, to all three *Pgt* races; and, seven lines had ambiguous reactions with either heterozygous or intermediate (ITs $2/3^+$, $2^+/3^+$, $3^+/2$, and $22^+/3^+$) reactions. Therefore, we excluded those seven lines for further linkage analysis study. The segregation of 85 resistant versus 98 susceptible fit an expected 1:1 ratio for a single gene ($\chi^2 = 0.922$, p = 0.336) (Table 4.3). Therefore, the stem rust data from evaluation of the F_1 hybrid and F_2 and RIL populations all substantiate that the stem rust resistance against three *Pgt* races in PI 387696 was controlled by a single dominant gene.

Mapping and QTL analysis of resistance to stem rust

A total of 9,996 polymorphic SNP markers between Rusty and PI 387696 were identified by analyzing 190 RILs (Rusty/PI 387696) with the 90K iSelect SNP array. Because many of these polymorphic markers were co-located (Appendix A2), only 1,551 of the polymorphic SNP markers were used for genetic map construction by choosing one marker from each set of co-located markers (Appendix A2). In addition to the SNP markers from the 90K iSelect SNP array, 76 SSR and two EST-STS markers were identified to be polymorphic between the two parents

(Table 4.4 and Figure 4.2). In addition, two STARP markers (*Xrwgsnp6* and *Xrwgsnp7*) were also included in linkage map construction (Table 4.4 and Figure 4.3). Therefore, a total of 1,629 polymorphic markers were finally used to construct the genetic linkage groups and to map the resistance gene in PI 387696.

For genetic linkage analysis, the 1,629 polymorphic markers were assigned to 14 linkage groups representing 14 (A and B genome) tetraploid wheat chromosomes with a total map length of 2,394.26 cM and average marker density 1.47 cM/marker. The A genome consisted of 720 markers with 1,189.50 cM map length and average marker density of 1.65 cM/marker. The B genome consisted of 909 polymorphic markers with 1204.76 cM map length and average marker density of 1.32 cM/marker. Chromosome 3B was the longest linkage group with 248.03 cM and an average marker density of 1.62 cM/marker. Chromosome 4B was the shortest linkage group with 125.20 cM map length and average marker density of 1.37 cM/marker (Table 4.4). Among the 1,629 polymorphic markers, 462 markers exhibited segregation distortion and they were present on all 14 chromosomes. The B genome had a high number of distorted markers (382 markers) as compared to the A genome (80 markers) (Table 4.4; Appendix A1; Figure A1).

QTL analysis

In this study, the critical LOD threshold value ranged from 2.7 to 3.0 ($P = 0.01$) after performing a permutation test at 1000 iterations. Therefore, the critical LOD threshold value of 3.0 was used to identify the significant QTL. A QTL for resistance to three *Pgt* races was mapped to the distal region on the long arm of chromosome 6A using Composite Interval Mapping (CIM) analysis. This QTL, designated as *QSr.rwg-6A* spanned at interval 28.3 cM between the SNP markers IWB6825 and IWB59051. Markers *BE403950* and *IWB5885.1* were the most significant markers underlying the *QSr.rwg-6A* at a distance of 0.3 cM and 2.6 cM from

the resistance locus for races TRTTF and TMLKC and markers *BE403950* and *IWB59051* were significant for race TTKSK at a distance 0.3 cM and 5.2 cM, respectively (Figure 4. 4). The *QSr.rwg-6A* QTL had a LOD value of 13.2, 10.8 and 26.8 with phenotypic variations 86%, 91%, and 96% for TTKSK, TRTTF, and TMLKC, respectively (Table 4.5).

The QTL (*QSr.rwg.6A*) was present in the similar region on chromosome arm 6AL that is associated with *Sr13* (Simons et al., 2011). To verify the *Pgt* resistance gene in PI 387696 is the same or different from *Sr13,* we used the *Sr13* gene specific KASP marker *KASPSr13* (J. Dubcovsky, unpublihsed) for genotyping the RIL population. After QTL analysis, the marker position of *KASPSr13* indicated that the *Sr* gene in PI 387696 maps to the same position as *Sr13* (Figure 4.4b). In addition, the *Sr13* markers *BE403950* and *CK20734* (Simons et al. 2011) also co-segregated with marker *KASPSr13* (Figure 4.4b).

Comparison of the *Sr* gene in *T. turgidum* ssp. *carthlicum* to *Sr13* genotypes

Infections were very heavy in the multi-race test, especially in the low temperature test. Since *Sr13* was originally identified from Khapli, the Kl-B genotype served as the check for the *Sr13* phenotype. As expected, at 25°C, Kl-B expressed resistant IT (23^- or lower) to six races, but had susceptible IT (3^-2^+ or higher) to THTSC and TCMJC. The *Sr13* gene is normally effective at high temperature (25°C) and ineffective at low temperature (18°C), and this was observed for Kl-B (Table 4.6). In contrast to Kl-B, the four other genotypes expressed differential reactions to the races and temperature treatments. At high temperature, ST464-C1 was resistant to all eight races, Medea Ap9d was susceptible to QTHJC, QFCSC, and TCMJC, and PI 387696 were susceptible to QFCSC (Figure 4.5). PI 387696 had a lower IT to race THTSC at high temperature and expressed more necrosis. While Kl-B exhibited the temperature

sensitivity normally associated with *Sr13*, temperature sensitivity was not pronounced in the four other genotypes.

Validation of STARP markers

Two STARP markers *Xrwgsnp6* and *Xrwgsnp7* which are closely linked to the *Pgt* resistance locus (*QSr.rwg.6A*) in PI 387696 were analyzed on a diverse set of 16 durum and 30 common wheat cultivars. Marker *Xrwgsnp6* amplified Rusty allele (A1) in three durum and one common wheat cultivars/lines and the remaining 41cultivars/lines amplified the PI 387696 allele (A2) (Table 4.7, and Figures 4.6 and 4.7). For marker *Xrwgsnp7*, the Rusty allele (A1) was present only in one durum cultivar, 19 cultivars/lines amplified the PI 387696 allele (A2), and 25 cultivars/lines had both Rusty and PI 387696 allele (H) (Table 4.7, and Figures 4.6 and 4.7). Based on this validation data, 98% durum and common wheat cultivars/lines carried the PI 387696 allele (A2).

Discussion

Currently, the Ug99 race group and other emerging races of stem rust pathogen are a serious threat to many wheat growing countries and potentially jeopardize world food security (Singh et al., 2015). The current efforts of wheat breeding programs are to identify and deploy Ug99 resistance *Sr* genes into wheat cultivars (Singh et al., 2011). For example, the *Pgt* resistance gene *SrND643* identified from hard red wheat line ND643 (Basnet et al., 2015) and *Sr56* originated from Swiss winter wheat cultivar Arina (Bansal et al., 2014). As part of this effort, we have focused on the identification and introgression of novel Ug99-effective *Sr* genes from wheat-related species and derivatives. Most research studies have focused on the stem rust resistance in hexaploid common wheat and wheat-alien species of wheat, while in durum wheat, stem rust resistance, mode of inheritance, and genetics is less studied. Molecular markers linked

to *Sr* genes produced for common wheat may not always be useful for durum wheat stem rust resistance studies (Haile et al., 2013). Therefore, efforts are needed to find the novel *Sr* genes or alleles in durum wheat and its related tetraploid subspecies. In this study, we attempted to identify novel effective *Sr* gene from tetraploid *T. turgidum* ssp. *carthlicum* PI 387696 originating from Ethiopia. Genetic analysis of F_2 and RIL populations revealed that a single dominant *Sr* gene present in PI 387696 was effective against TTKSK, TRTTF, and TMLKC. By molecular mapping, a major QTL, *QSr.rwg-6A*, identified from PI 387696 was located on the distal end of the long arm of chromosome 6A.

Simons et al. (2011) showed that stem rust resistance gene *Sr13* was also located on the distal end chromosome arm 6AL within a 1.2-2.8 cM interval based on the mapping population used for analysis. Khapli emmer (CItr 4013) and landrace ST464 (PI 191365) were the main sources of the *Sr13* gene (Knot, 1962; Klindworth et al., 2007). In addition, *Sr13* is also present in many durum cultivars such as Kronos, Kofa, Medora, Sceptre, Langdon, Wells, and Leeds (Simons et al., 2011; Klindworth et al., 2007*)*. In this study, *Sr13* markers *BE403950*, *CK207347*, and *Xgwm427* were polymorphic between Rusty and PI 387696 and mapped 0.3 cM (*BE403950* and *CK207347*) and 6.3 cM (*Xgwm427*) proximal to the resistance locus *QSr.rwg-6A*. Molecular marker *CK207347* was mapped 0.5 cM proximal to the *Sr13* region and *BE403950* was completely linked with this region in the mapping population Mindum × Medora (Simons et al., 2011). Marker *Xgwm427* mapped at 17.6 cM proximal to the *Sr13* gene in UC1113 × Kofa mapping population (Simons et al., 2011). In addition, *Sr13* gene specific KASP marker *KASPSr13* co-segregated with markers *BE403950* and *CK207347* in our study. The molecular data analysis indicated that stem rust resistance in PI 387696 was conditioned by a gene at the *Sr13* locus.

In North American and CIMMYT durum cultivars/lines, *Sr13* is one of the main genes effective against TTKSK. During this study, PI 387696 *s*howed resistant reactions towards TTKSK, TRTTF, and TMLKC with IT scores ';', '1', and ';2', respectively. In addition, we performed the race specificity test on different cultivars that carried *Sr13* or an allele at different temperature range. Results from the multi-race test indicated that Kl-B (*Sr13*) was susceptible to races TCMJC and THTSC. Differential reactions were observed on the other four genotypes in the test, and this suggested that the genes were not the same. The gene *Srdp2* in Medea Ap9d has long been recognized as different from *Sr13*, but allelism to *Sr13* was suggested by McIntosh et al. (1995). The differential reactions of ST464-C1 and PI 387696 to the eight races suggest that they are either alleles of *Sr13* or that these genotypes carry an additional gene(s) that modifies resistance to stem rust. Even though molecular data did not provide any proof for differences between the PI 387696 gene and *Sr13*, based on the race analysis data, we concluded that *T. turgidum* ssp. *carthlicum* PI 387696 carries a novel allele of *Sr13*

In this study, two STARP markers *Xrwgsnp6* and *Xrwgsnp7* were identified using the RIL population and they were mapped at 3.4 cM and 1.5 cM proximal to *QSr.rwg.6A* locus, respectively. These markers were validated in different genetic backgrounds. These markers may be more useful than it would appear from the tests with these cultivars. *Sr13* is present in many durum cultivars. In particular, we know that Alkabo, Grenora, and Langdon have *Sr13* and in this study, they have the same allele as found in PI 387696. So perhaps these markers cannot differentiate between lines having different *Sr13* alleles. However, Divide also has the same alleles as PI 387696, and it does not have *Sr13*. So, the presence of *Sr13* does not fully explain why so few cultivars do not differ from PI 387696. Therefore, additional new STARP markers

are needed which can be effectively utilized for marker-assisted selection of this novel PI 387696 allele.

The original *Sr13* gene in durum wheat was derived from Khapli emmer [*T. turgidum* ssp. *dicoccum* (Schrank ex Schübler) Thell.] and in our study, we found a new *Sr13* allele from *T. turgidum* ssp. *carthlicum.* In addition, different allelic forms of *Sr13* are found in different durum wheat lines such as Medea Ap9d (*Srdp-2*), ST464-C1, and Kl-B (Roelfs and McVey, 1979; Klindworth et al., 2007; McIntosh et al., 1995). This finding may indicate that *Sr13* is a complex locus in which substantial allelic variations might have occurred in durum and other tetraploid wheat subspecies. Genetic diversity is a key factor in breeding for improvement of wheat beneficial traits. Apparently, this new *Sr13* allele identified from *T. turgidum* ssp. *carthlicum* will be useful in developing new durum and bread wheat cultivars with an increased genetic diversity of TTKSK-resistant *Sr* genes.

Table 4.1. Virulence and avirulence responses to major *Sr* genes for the races used in this study (Olivera et al., 2012; Jin et al., 2007)

Race	Isolate	Origin	Avirulence	Virulence
TTKSK	04KEN156/04	Kenya	*Sr24 36 Tmp*	*Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN*
TRTTF	06YEM34-1	Yemen	*Sr8a 24 31*	*Sr5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McNTmp*
TMLKC	72-41 (sp2)	USA	*Sr6 8a 9a 9b 17 24 30 31 38*	*Sr5 7b 9d 9e 9g 10 11 21 36 McNTmp*

Table 4.2. STARP markers developed this study and their details including their SNP sources, primer sequence, and T_m values

Marker	SNP source	Primer name	Primer type[b]	Primer sequence (5'-3')[a]	T_m(°C)
Xrwgsnp6	IWB71956	*Xrwgsnp6F*	F - primer 1	[Tail 2]GGAAAACGACGACGACT	54.45
		Xrwgsnp6F	F - primer 2	[Tail 1]GGAAAACGACGACGCTC	56.07
		Xrwgsnp6R	R - primer 2	TGGAAAATCAGCGCTCGACAG	61.27
Xrwgsnp7	IWB34398	*Xrwgsnp7F*	F - primer 1	[Tail 2]AGCACACTACTACGAGAACAT	56.50
		Xrwgsnp7F	F - primer 2	[Tail 1]AGCACACTACTACGAGACAAG	57.17
		Xrwgsnp7R	R - primer 2	CGACCCATACTCAAGACCATCTG	60.49

[a]Tail 1 sequences: GCAACAGGAACCAGCTATGAC-3′

[a]Tail 2 sequence: GACGCAAGTGAGCAGTATGAC-3′ (Long et al., 2017)

[b]Primers type; F: Forward, R: Reverse

Table 4.3. Segregation of resistance to three races of stem rust pathogen in the F_2 and recombinant inbred line (RIL) poplations derived from the cross Rusty × *T. turgidum* ssp. *carthlicum* PI 387696

Race	F_2 plants				RILs			
	R	S	χ^2 (3:1)	*p* value	R	S	χ^2 (1:1)	*p* value
TTKSK	63	20	0.031	0.860	85	98	0.922	0.336
TRTTF	68	22	0.015	0.903	85	98	0.922	0.336
TMLKC	128	39	0.241	0.623	85	98	0.922	0.336

Table 4.4. Detail of markers mapped in each chromosome/genome in the Rusty × PI 387696 RIL population

Chromosome	SSR[a]	EST[a]	SNP[a]	STARP[a]	Total	Length (cM)[b]	Marker density (cM/marker)	No. of markers with distorted ratios
1A	5	–	93	–	98	126.27	1.3	11
1B	6	_	154	–	160	158.36	1.0	43
2A	7	–	81	–	88	192.08	2.2	13
2B	5	–	141	_	146	152.79	1.1	119
3A	7	–	94	–	101	206.03	2.0	1
3B	10	–	143	–	153	248.03	1.6	89
4A	2	–	89	–	91	148.59	1.6	16
4B	3	–	84	–	87	125.20	1.4	25
5A	3	–	112	–	115	202.21	1.8	22
5B	7	–	130	_	137	187.82	1.4	18
6A	4	2	94	2	102	142.66	1.4	8
6B	6	–	110	–	116	170.38	1.5	77
7A	5	–	120	–	125	171.66	1.4	9
7B	4	–	106	–	110	162.18	1.5	11
A genome	33	2	683	2	720	1,189.50	1.7	80
B genome	41	_	868	_	909	1,204.76	1.3	382
Total	76	2	1551	2	1629	2,394.26	1.5	462

[a] SSR = simple sequence repeat, EST = expressed sequence tagged, STRAP = semi-thermal asymmetric reverse PCR, SNP = single nucleotide polymorphism,
[b] Length in centiMorgans (cM)

Table 4.5. CIM analysis of QTLs associated with resistance to stem rust caused by *Pgt* races TTKSK, TRTTF, and TMLKC

QTL	Chromosome	Marker interval	Marker position	TTKSK			TRTTF			TMLKC		
				LOD	R^2	Add.[a]	LOD	R^2	Add.[a]	LOD	R^2	Add.[a]
QSr.rwg-6A	6AL	IWB6825-IWB59051	103.1cM-131.4cM	13.2	0.86	1.8	10.8	0.91	1.8	26.8	0.96	2.3

[a]Add.: Additive effects of the QTL

Table 4.6. Infection types (ITs) of different cultivars/lines when tested with different *Pgt* races at different temperature conditions (18°C and 25°C) [a]

Line	QTHJC		QFCSC		RTQQC		RHFSC		TMLKC		TPMKC		THTSC		TCMJC	
	18[b]	25	18	25	18	25	18	25	18	25	18	25	18	25	18	25
Rusty	34	43	34	4	33^{-}	4	3^{-}2	34	34	34	34	43	34	34	34	34
Langdon	0;1^{-}	1^{+}2^{-}	0;	2^{-}cn[c]	0;	2^{-}c	1;c	1^{-}n	22^{-}c	12^{-}c	2^{-}cn	2^{-}	;1^{-}	0;	22^{+}	13c
KI-B	34	22^{+}	3^{-}2	2^{+}3^{-}	3^{-}2^{+}	2	3^{-}2	2, 2^{++}	3^{-}2	2^{-}c	23^{-}	2^{-}	3^{-}2	3^{-}2^{+}	3^{-}2	3^{-}2^{+}
ST464-C1	2, 22^{+}	2	2	2^{-}	2	2	22^{+}	2	22^{-}c	2^{-}c	2^{-}c	2^{-}	23^{-}	2^{-}2^{+}	3^{-}2	2
Medea Ap9d	34	32	2	3^{-}2^{+}	2	2^{+}	2	2	2	2	2^{-}	22^{-}	22^{+}	2	23^{-}	32^{+}
PI 387696	0;1^{-}n	2	2	32^{+}	1c	2	2	2^{-}2c	1^{-}n^{+}	2^{-}c	1^{-}c^{+}	2^{-}	22^{-}cn	0;1^{-}c	2	2^{-}c

[a]ITs score 0, ; , 1, 2 are resistant reactions, while 3, 4 are susceptible reactions. Plants having combinations of ITs scores, like IT score 32 is primarily 3 score with less 2 score. Signs plus (+) and minus (-) indicate small and large size of the pustules (Stakman, 1962).

[b] 18 and 25 indicated the temperature 18°C and 25°C, [c] c = chlorosis, n = necrosis.

Table 4.7. Analysis of 48 cultivars or lines with two STARP markers linked to the *Pgt* resistance locus in PI 387696

Cultivar/line	Type	Habit	Origin[a]	*Xrwgsnp6*[b]	*Xrwgsnp7*
Strongfield	Durum	Spring	Canada	A1	A2
Transcend	Durum	Spring	Canada	A1	A2
Cappelli	Durum	Spring	Italy	A1	A1
Svevo	Durum	Spring	Italy	A2	A2
15FAR344-6(255)	Durum	Spring	ND, USA	A2	A2
D09557	Durum	Spring	ND, USA	A2	A2
D09690	Durum	Spring	ND, USA	A2	A2
D101073	Durum	Spring	ND, USA	A2	A2
Alkabo	Durum	Spring	ND, USA	A2	A2
Carpio	Durum	Spring	ND, USA	A2	A2
Divide	Durum	Spring	ND, USA	A2	A2
Grenora	Durum	Spring	ND, USA	A2	A2
Joppa	Durum	Spring	ND, USA	A2	A2
Langdon	Durum	Spring	ND, USA	A2	A2
Lebsock	Durum	Spring	ND, USA	A2	A2
Line E	Common	Spring	Australia	A1	A2
BR34	Common	Spring	Brazil	A2	H
LMPG-6	Common	Spring	Canada	A2	A2
Chinese Spring	Common	Spring	China	A2	H
Jimai 22	Common	Winter	China	A2	H
Jinqiang 5	Common	Spring	China	A2	H
Sumai 3	Common	Spring	China	A2	H
Yangmai 16	Common	Spring	China	A2	H
Zhengmai 9023	Common	Facultative	China	A2	H

Table 4.7. Analysis of 48 cultivars or lines with two STARP markers linked to the *Pgt* resistance locus in PI 387696 (continued)

Cultivar/line	Type	Habit	Origin[a]	*Xrwgsnp6*[b]	*Xrwgsnp7*
Zhoumai 27	Common	Winter	China	A2	H
Alsen	Common	Spring	ND, USA	A2	H
Barlow	Common	Spring	ND, USA	A2	H
Elgin-ND	Common	Spring	ND, USA	A2	H
Faller	Common	Spring	ND, USA	A2	A2
Glenn	Common	Spring	ND, USA	A2	H
Grandin	Common	Spring	ND, USA	A2	A2
ND830	Common	Spring	ND, USA	A2	H
ND833	Common	Spring	ND, USA	A2	H
NDHRS16-12-19	Common	Spring	ND, USA	A2	H
Reeder	Common	Spring	ND, USA	A2	H
Steele-ND	Common	Spring	ND, USA	A2	H
VitPro-ND	Common	Spring	ND, USA	A2	H
IL06-14262	Common	Winter	IL, USA	A2	H
Newton	Common	Winter	KS, USA	A2	H
Ada	Common	Spring	MN, USA	A2	H
Bolles	Common	Spring	MN, USA	A2	H
Linkert	Common	Spring	MN, USA	A2	H
Tom	Common	Spring	MN, USA	A2	A2
Brick	Common	Spring	SD, USA	A2	H
Granger	Common	Spring	SD, USA	A2	H
Rusty	Durum	Spring	ND, USA	A1	A1
T. turgidum ssp. *carthlicum* (PI 387696)	Durum	Spring	ID, USA	A2	A2

[a]Origin:CO, Colorado; KS, Kansas; ND, North Dakota; SD, South Dakota; IL, Illinois MN,Minnesota; ID, Idahob A1 Rusty allele; A2, PI 387696 allele; H, both Rusty and PI 387696 alleles

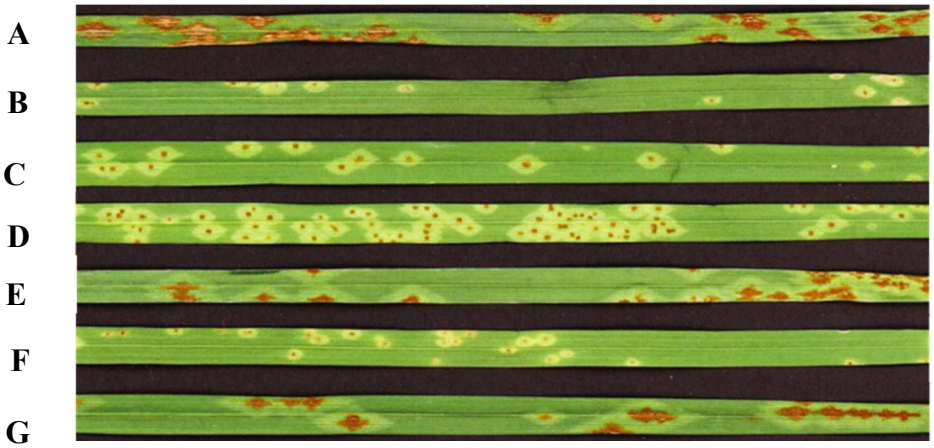

Figure 4.1. Infection types of F_1 and F_2 plants and recombinant inbred lines (RILs) from the cross Rusty × PI 387696 after inoculation with *Pgt* race TMLKC. A) Rusty (IT 34), B) PI 387696 (IT 1) (C) F_1 plant with (IT 1;) (D) F_2 resistant plant (IT 1) (E) F_2 susceptible plant (34) (F) RILs resistant plant (IT 1;) (G) RILs susceptible plant (IT 34).

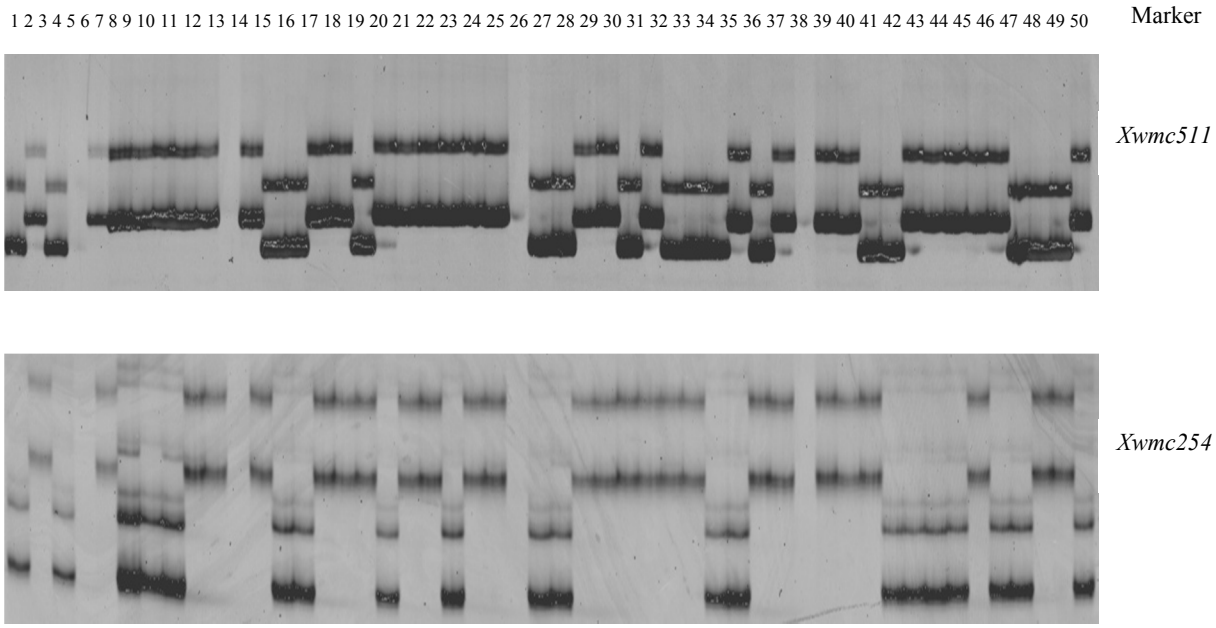

Figure 4.2. Gel images of SSR markers *Xwmc511* and *Xwmc254* which showed polymorphism between Rusty and PI 387696 and used for linkage map construction. Representative wheat lines: 1) Rusty, 2) PI 387696, 3) Rusty, 4-50 RIL population.

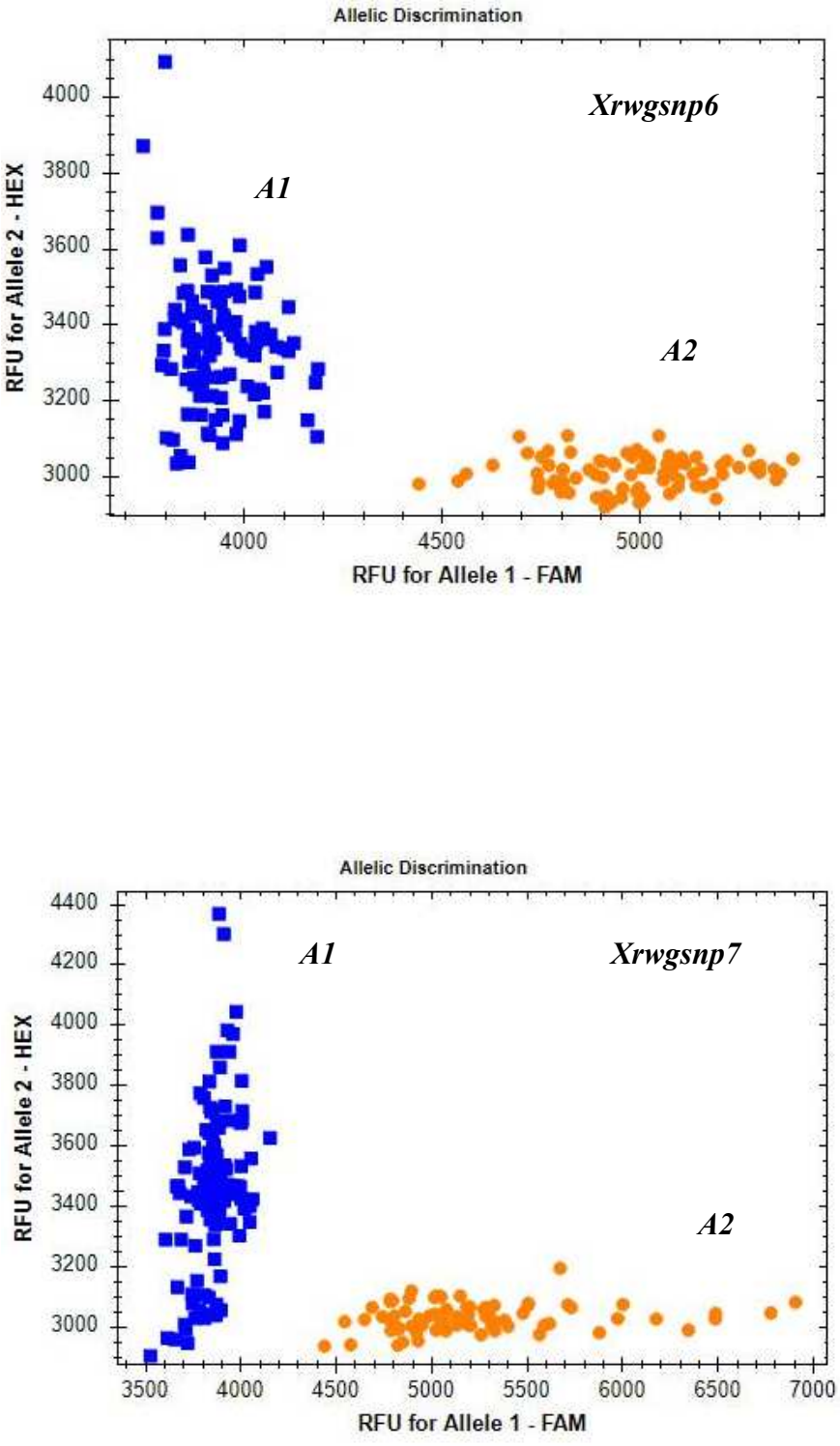

Figure 4.3. Analysis of two STARP markers (*Xrwgsnp6* and *Xrwgsnp7*) on RIL population and parents (Rusty, *T. turgidum* ssp. *carthlicum*) using the CFX384^{TM}Real-Time System. An A1 and A2 cluster represents the homozygous Rusty and *T. turgidum* ssp. *carthlicum* alleles, respectively. RFU represents the relative fluorescence unit.

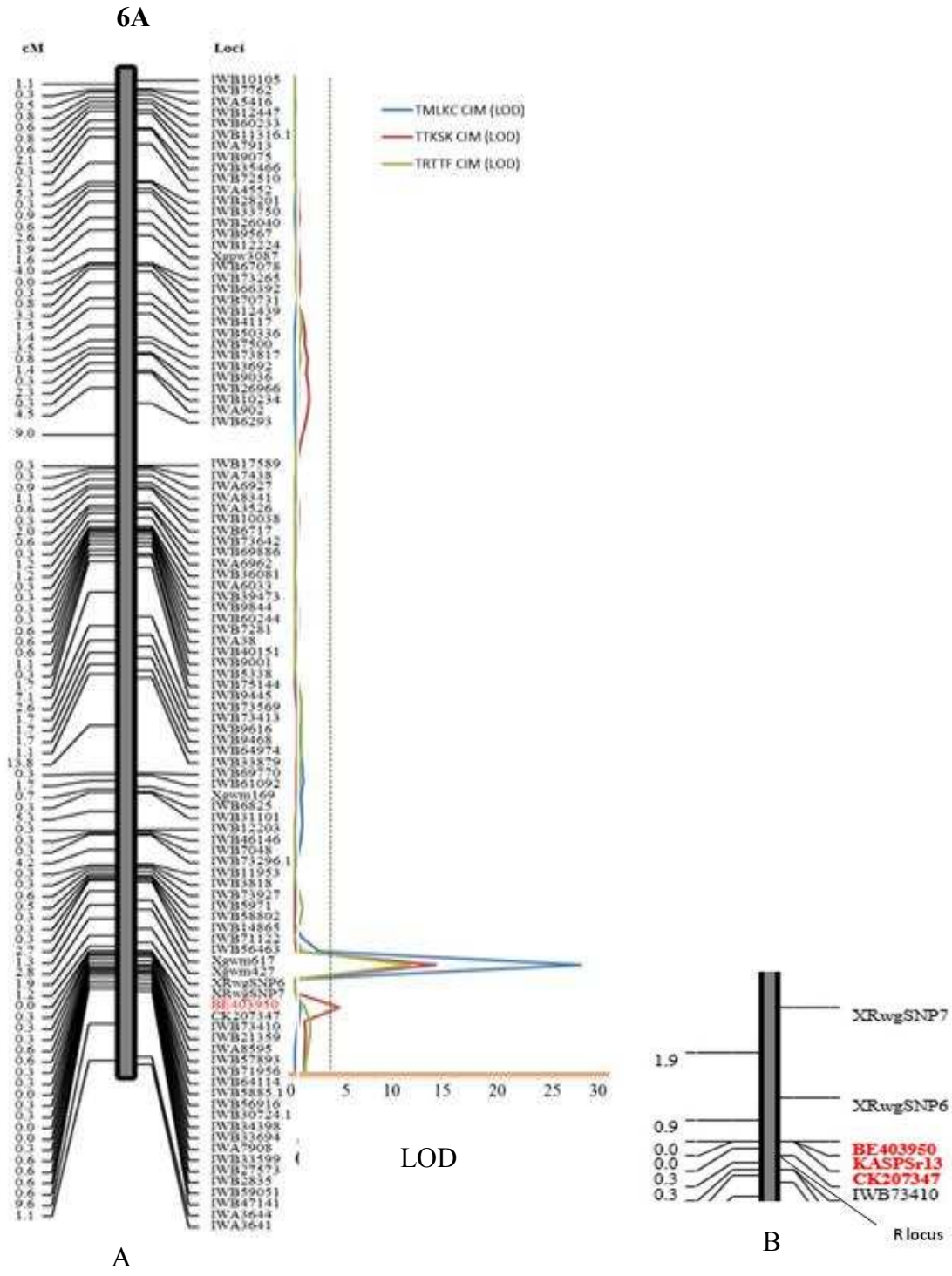

Figure 4.4. (a) Regions of linkage map for chromosome 6A harboring QTL for stem rust resistance to *Pgt* races (TMLKC, TRTTF, and TTKSK) in RILs population. The centiMorgen (cM) distances between the markers loci indicated to the left side of the linkage map and markers loci are present on the right side of the linkage map. The critical LOD threshold is 3.0 indicated by a black dotted line and LOD score scale is represented at the bottom. (b) QTL analysis to verify the resistance gene in PI 387696 is same or different from *Sr13* by using the *Sr13* gene specific KASP marker *KASPSr13*.

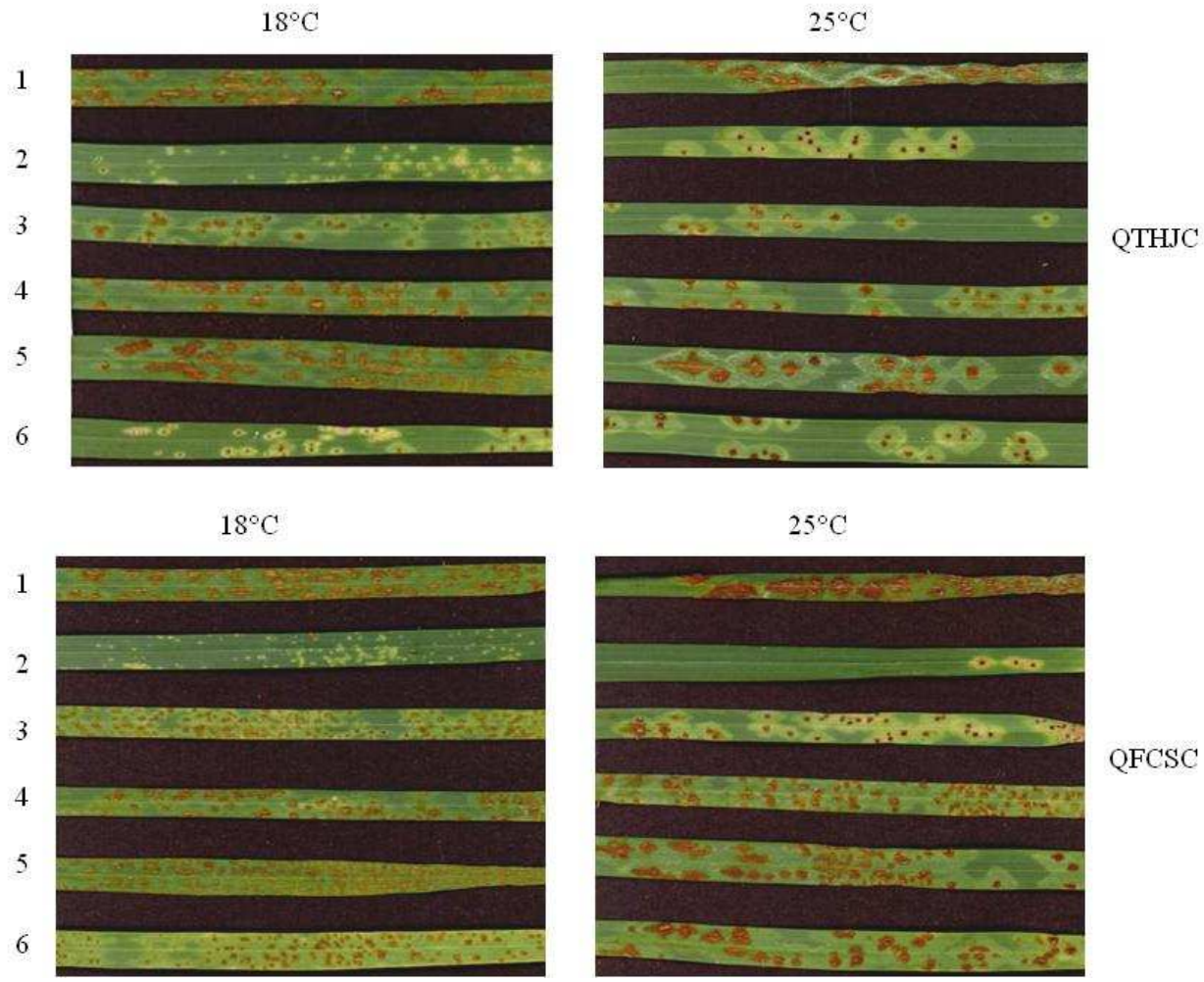

Figure 4.5. Infection types of durum lines and PI 387696 inoculated with *pgt* race QTHJC and QFCSC at 18°C and 25°C: 1) Rusty, 2) Langdon, 3) ST464-C1, 4) K1-B, 5) Medea Ap 9d, 6) PI 387696.

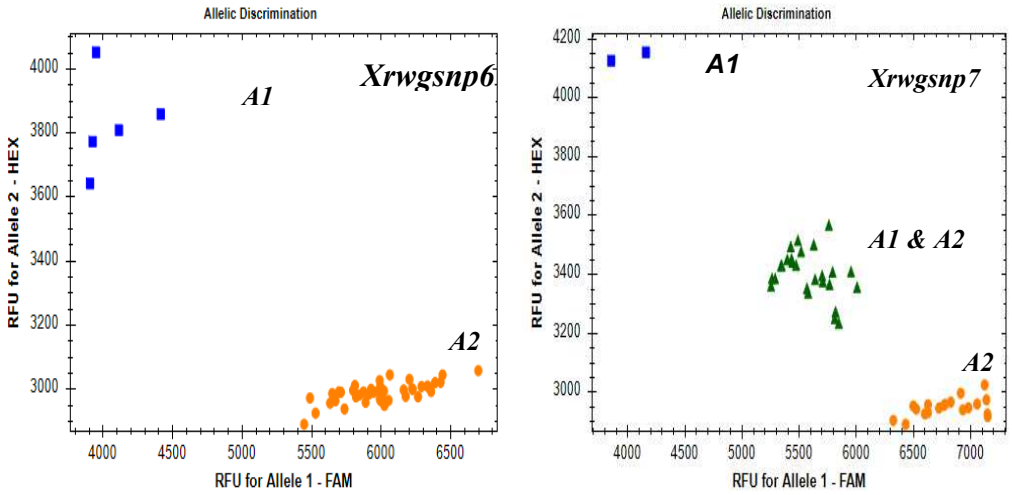

Figure 4.6. Analysis of two STARP markers (*Xrwgsnp6* and *Xrwgsnp7*) on a diverse set of 48 cultivars using the CFX384^{TM}Real-Time System. An A1 and A2 cluster represents the homozygous Rusty and *T. turgidum* ssp.*carthlicum* alleles, respectively

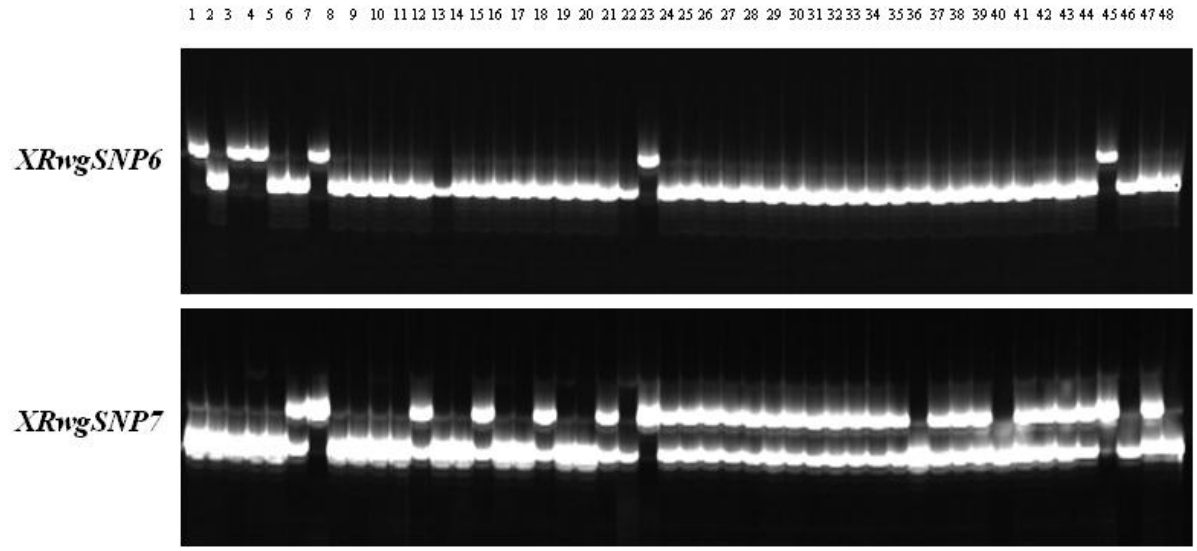

Figure 4.7. Validation of two STARP markers on 48 common and durum wheat cultivars. (1) Strongfield, (2) Alkabo, (3) Line E, (4) Transcend, (5) Carpio, (6) BR34, (7) Cappelli, (8) Divide, (9) LMPG-6, (10) Svevo, (11) Grenora, (12) Chinese Spring, (13) 15FAR344-6(255), (14) Joppa, (15) Jimai 22, (16) D09557, (17) Langdon, (18) Jinqiang 5, (19) D09690, (20) Lebsock, (21) Sumai 3, (22) D101073, (23) Rusty, (24) Yangmai 16, (25) Zhengmai 9023, (26) ND830, (27) Ada, (28) Zhoumai 27, (29) ND833, (30) Bolles, (31) Alsen, (32) NDHRS16-12-19, (33) Linkert, (34) Barlow, (35) Reeder, (36) Tom, (37) Elgin-ND, (38) Steele-ND, (39) Brick, (40) Faller, (41) VitPro-ND, (42) Granger, (43) Glenn, (44) IL06-14262, (45) Rusty, (46) Grandin, (47) Newton, (48) PI 387696

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APPENDIX A. MOLECULAR MARKERS MAPPED IN THE RUSTY × *T. CARTHLICUM* (PI 387696) RILs POPULATION

Marker	Chromosome	Position	Segregation distortion
IWB7436	1A	0	ns
IWB12616	1A	2.035938593	ns
IWB71424.1	1A	2.310658246	ns
IWB57448	1A	3.125923537	ns
IWB6172	1A	3.950148854	ns
IWB7590	1A	4.502640475	ns
IWB71687.1	1A	4.774374166	ns
IWB61182	1A	5.04759268	ns
IWB10922	1A	6.444560025	ns
IWB63610	1A	8.179301174	ns
IWB63712	1A	10.25141917	ns
IWB36053	1A	11.37516798	ns
IWA414	1A	11.37516798	ns
IWB7727	1A	12.22267941	ns
IWB7233	1A	13.0560639	ns
IWB3519	1A	13.0560639	ns
IWB11044	1A	15.98327903	ns
IWB3334.1	1A	18.5568931	ns
IWB31932	1A	23.33310172	ns
IWB31602	1A	23.60483541	ns
IWB47933	1A	25.0096545	ns
IWA7048	1A	25.56521558	ns
IWB72800	1A	25.83694927	ns

Marker	Chromosome	Position	Segregation distortion
IWB7717	1A	26.94820864	ns
IWB49926	1A	27.49766453	ns
IWB47241	1A	30.07127861	ns
IWB52279	1A	33.87966443	ns
IWB35115	1A	35.55621724	ns
IWB21167	1A	35.83554094	ns
IWB57257.1	1A	37.24830056	ns
Xgwm164	1A	40.37725504	ns
Xbarc120	1A	42.53901148	ns
IWA8506.1	1A	43.36779108	ns
IWB6962	1A	43.90255537	ns
IWB71416	1A	44.16992987	ns
IWA3883	1A	44.43730437	ns
IWB8898	1A	44.70467887	ns
IWB13492	1A	44.97063122	ns
IWB15064	1A	45.23517646	ns
IWB71889	1A	45.50691016	ns
IWB8273	1A	46.33113547	ns
IWB61236	1A	46.60140039	ns
IWB66378	1A	46.60140039	ns
IWB64464	1A	48.56864425	ns
IWB20695	1A	49.97346334	ns
IWB35308	1A	52.37828243	ns
IWA8070	1A	54.69199304	ns
IWB58903	1A	54.97288591	ns
IWB11515	1A	55.81092675	ns

Marker	Chromosome	Position	Segregation distortion
IWB5406	1A	56.35441019	ns
IWB25487	1A	57.45345472	ns
IWB35691	1A	57.72371964	ns
IWB31863	1A	57.99545333	ns
IWB34337	1A	59.09449785	ns
IWB11628	1A	59.36330979	ns
IWB43838	1A	59.64108176	ns
IWB65763	1A	60.19664284	ns
IWA7871	1A	61.02542244	ns
IWB46385	1A	61.30165981	ns
IWB75761	1A	61.57192473	ns
Xwmc312	1A	62.39615005	ns
IWB11543	1A	62.9426034	ns
Xcfa2129	1A	63.77138299	ns
IWB60627	1A	64.04311669	ns
IWB58118	1A	65.98848147	ns
IWB27132	1A	66.5319649	ns
IWB44683.1	1A	67.35168572	ns
IWB8167	1A	68.75650481	ns
IWB35531	1A	72.90788294	ns
IWB6517	1A	74.30485029	ns
IWB12579	1A	76.30585181	*
IWB29580	1A	77.14389266	*
IWB4075	1A	77.41861231	*
IWB35025	1A	77.690346	*
IWB11406	1A	78.77744133	ns

Marker	Chromosome	Position	Segregation distortion
IWB7472	1A	80.41732385	ns
IWB64554	1A	87.47577279	*
IWB9746	1A	88.56881006	*
IWB52732	1A	90.56981158	ns
IWB52033	1A	90.85229134	ns
IWB31208.1	1A	93.48621293	ns
IWB66930	1A	95.52215152	ns
IWB31445	1A	96.92697061	ns
IWB3536	1A	102.3045608	ns
IWB3034	1A	112.0275128	**
IWB67875	1A	113.1576122	*
IWB62751	1A	113.9909967	*
IWB13639	1A	114.5315424	*
IWB4244	1A	115.0750258	*
IWB61091	1A	115.9177753	ns
IWB12293	1A	120.1963199	ns
IWA4898	1A	120.7549847	ns
IWB6426	1A	121.0297044	ns
IWB43929	1A	121.5946819	ns
IWB30871	1A	123.9773509	ns
IWB3413	1A	124.2551228	ns
IWB65294	1A	124.5313602	ns
Xbarc17	1A	125.8136392	ns
IWB15041	1B	0	ns
IWB10856	1B	0	ns
IWB65421	1B	1.111259369	ns

Marker	Chromosome	Position	Segregation distortion
IWB44730	1B	1.395344059	ns
IWB43880	1B	1.686035067	ns
IWB44816	1B	2.848995671	ns
IWB52018	1B	3.985517898	ns
IWB11925.1	1B	6.895676942	ns
IWB27496	1B	8.349525197	ns
IWB57219	1B	8.641916073	ns
IWB12208	1B	10.70183216	ns
IWB12603	1B	11.27987305	ns
IWB29507	1B	11.86127472	ns
IWB70626	1B	13.58603883	ns
IWB14010	1B	15.6101969	*
IWB31845	1B	16.15074253	*
IWB65685	1B	16.70019843	*
IWB9714.1	1B	18.40534895	ns
IWB14060	1B	18.96715242	ns
IWB12048	1B	24.29956744	ns
IWB72109	1B	24.57889113	ns
IWB13124.1	1B	32.60867458	*
IWB58765	1B	33.16733941	*
IWB62647.1	1B	33.7167953	*
IWB8310.1	1B	34.54102062	ns
IWB64708	1B	34.82191348	*
IWB72704	1B	35.39995438	ns
IWB9932	1B	35.68084724	ns
IWB9627	1B	36.51423174	ns

Marker	Chromosome	Position	Segregation distortion
IWB29515	1B	36.78895139	ns
IWB8781	1B	37.0796424	ns
IWB72487	1B	37.0796424	ns
IWB16228	1B	37.64144586	ns
IWB69962	1B	37.91768324	ns
IWB68665	1B	38.1954552	ns
IWB10753	1B	38.47634807	ns
IWB63352	1B	38.76043276	ns
IWB60559	1B	42.61406267	ns
IWB67741	1B	43.4568122	ns
IWB67742	1B	44.02824677	ns
IWB10361	1B	49.32729449	ns
IWB15647	1B	49.87675038	ns
IWB14738	1B	50.43541521	ns
IWB66125	1B	50.99408005	ns
IWB39745	1B	51.86118968	ns
IWB9998	1B	52.45291231	ns
IWB63944	1B	53.84987966	ns
IWB7205	1B	55.81712351	ns
IWB35618	1B	56.09336089	ns
IWA6965	1B	56.37268459	ns
IWB73157	1B	58.0974487	ns
IWB34334	1B	58.3767724	ns
IWB67338	1B	58.94820697	ns
IWB40109	1B	59.24059785	ns
IWB69550	1B	64.67569466	ns

Marker	Chromosome	Position	Segregation distortion
IWB65744	1B	64.97330655	ns
IWA5348	1B	65.5581083	ns
IWB40146	1B	65.83588026	ns
Xbarc302	1B	67.53139039	ns
IWB5590	1B	68.90532054	ns
IWB2337	1B	70.28684484	ns
IWB5511	1B	71.38588937	ns
IWB10551	1B	71.65326387	ns
IWB39521	1B	73.05023121	ns
IWB35922	1B	76.27094125	ns
IWB2788	1B	78.85937158	ns
IWB46080	1B	79.6790924	ns
Xwmc694	1B	79.98772639	ns
IWB7183	1B	79.98772639	ns
IWB65754	1B	80.25653833	ns
IWA270	1B	82.51789298	ns
IWB66204	1B	83.06434633	ns
IWB68866	1B	83.33172082	ns
IWA4203	1B	83.59909532	ns
IWB9661	1B	85.56633918	ns
IWB26948	1B	86.6964386	ns
IWB6215	1B	86.6964386	ns
IWA1231	1B	87.51170389	ns
IWA775	1B	87.51170389	ns
IWB13393	1B	87.51170389	ns
IWB14729	1B	87.51170389	ns

Marker	Chromosome	Position	Segregation distortion
IWB31909	1B	87.78642354	ns
IWB8507	1B	88.05964206	ns
IWB39291	1B	89.15267932	ns
IWB73745	1B	89.42005382	ns
IWB57391	1B	89.42005382	ns
IWB73964	1B	90.50714915	ns
IWB28518	1B	91.04478857	ns
IWB57368	1B	91.32411227	ns
IWB71902	1B	91.60659203	ns
IWB8999	1B	91.87685695	ns
IWB73514	1B	92.68771489	ns
IWB58168	1B	92.95797981	ns
IWB72552	1B	93.23269946	ns
IWB8187	1B	93.50443315	ns
IWB71822	1B	94.59152848	ns
IWB64623	1B	95.1291679	ns
IWB8944	1B	95.39797984	ns
IWB70038	1B	95.66252509	ns
IWB61202	1B	95.93133703	ns
IWB7534	1B	95.93133703	ns
IWB60916	1B	96.73783501	ns
IWB67348	1B	97.00378736	ns
IWB7151	1B	97.26833261	ns
IWB8066	1B	97.53287786	ns
IWB35875	1B	98.07636129	ns
IWB59663	1B	98.89608211	ns

Marker	Chromosome	Position	Segregation distortion
IWB3067	1B	99.16345661	ns
Xwmc134	1B	99.78458231	ns
IWB12504	1B	101.042659	ns
IWB69351	1B	101.3114709	ns
IWB63855	1B	101.8491103	ns
IWB72499	1B	103.5071252	ns
IWB59602	1B	104.9040926	ns
IWB60525	1B	105.1788122	ns
IWB9764	1B	105.7282681	ns
IWB9256	1B	106.539126	ns
IWB64093	1B	107.6442442	ns
IWB31201	1B	108.7555036	*
IWB72580	1B	109.8485409	*
IWB72607	1B	112.4369712	**
IWB35890	1B	113.2657508	**
IWB5074	1B	113.530296	**
IWB29141	1B	114.0622158	**
IWB37326	1B	114.326761	**
IWB11512	1B	114.8732144	**
IWB66919	1B	115.7112552	*
IWB12325	1B	115.9844737	**
Xbarc188	1B	122.2062937	ns
IWB66189	1B	124.0087269	**
IWB35108	1B	124.2849643	**
IWB72240	1B	124.5723142	**
IWB60663	1B	124.8717081	***

Marker	Chromosome	Position	Segregation distortion
IWB72142	1B	125.7338337	**
IWB66973	1B	126.0012082	*
IWB6805	1B	127.3676272	*
IWB57211	1B	127.6393609	*
IWB73698	1B	127.9081729	*
IWB8005	1B	131.0550748	*
IWB36293	1B	131.3268085	*
IWB7686	1B	131.8615728	*
IWB10962	1B	132.6768381	**
Xwmc44	1B	139.6557404	**
IWB31871	1B	139.9783119	*
IWB27085	1B	139.9783119	*
IWB57628	1B	140.2428571	*
IWB4454	1B	141.3240748	*
IWB5732	1B	145.9885632	**
IWB9706	1B	147.0639664	**
IWB35087	1B	150.1403714	ns
IWB9772	1B	150.6722911	ns
IWB64238	1B	151.2128368	*
IWA5758.1	1B	152.0325576	ns
IWB13057	1B	154.5627242	*
IWB68096	1B	154.8300987	ns
IWB31066	1B	156.1890884	*
IWB34435	1B	156.7267278	*
Xwmc728	1B	157.2672734	ns
IWB73657	1B	158.0914987	*

Marker	Chromosome	Position	Segregation distortion
IWB12221	1B	158.3603107	*
IWB5945	2A	0	ns
IWB72720	2A	2.122407085	ns
IWB7792	2A	2.681071918	ns
IWB12342.1	2A	3.24287538	ns
IWB68947	2A	4.076259871	ns
IWB65498	2A	4.625715766	ns
IWB7398	2A	4.900435419	ns
Xbarc124	2A	4.900435419	ns
Xgwm497	2A	6.216471009	ns
IWA8091	2A	9.031831359	ns
IWB6542	2A	9.606550109	ns
IWB60729	2A	10.79720862	ns
IWB15066	2A	27.83908234	ns
IWB6086.1	2A	28.96283116	ns
IWB67305	2A	37.26152661	ns
IWB70098	2A	39.97493096	ns
IWB67791	2A	44.99149857	ns
IWB72462	2A	45.54399019	ns
IWB8363	2A	46.09044354	ns
IWB28073	2A	49.6256107	ns
Xwmc453	2A	59.7617692	ns
IWB73038	2A	60.04266207	*
IWB51951	2A	60.8854116	*
IWB10490	2A	63.17264445	*
IWB56992	2A	65.49982532	*

Marker	Chromosome	Position	Segregation distortion
IWA294	2A	66.62357414	*
IWB10760	2A	68.87220818	*
IWB32310	2A	69.13958268	*
IWA994	2A	75.15626297	**
IWB27678.1	2A	75.69102726	**
IWA581	2A	76.24048315	**
IWB11613	2A	76.51221684	**
IWB59332	2A	80.41218095	ns
IWA3431	2A	80.69150464	ns
Xgwm372	2A	80.69150464	ns
IWA820	2A	81.35376559	ns
IWB68288	2A	81.92195331	ns
IWB7897	2A	82.7840789	ns
Xbarc15	2A	83.64620449	ns
IWA5293	2A	84.53912453	ns
IWB72154	2A	102.4689741	ns
IWB57080	2A	108.5106216	ns
IWA200	2A	118.580063	ns
IWA544	2A	120.6279201	ns
IWB43829.1	2A	122.6638587	ns
IWB58832	2A	123.4835795	ns
IWB11614	2A	124.0300329	ns
IWA8377	2A	124.5735163	ns
IWB12036	2A	126.8348709	ns
IWB26154	2A	130.3700381	ns
IWB70002	2A	130.6447578	ns

Marker	Chromosome	Position	Segregation distortion
IWB7714	2A	130.9209951	ns
IWB11193	2A	139.5005844	*
IWA8385	2A	145.5422319	ns
IWB10182	2A	146.6723313	ns
IWB46244	2A	150.8237094	ns
IWB6121	2A	151.652489	ns
IWB71626	2A	153.5978538	ns
IWB12586	2A	154.6908911	ns
IWB10957	2A	154.9568434	ns
IWB5861	2A	156.8808107	ns
IWB34772	2A	157.9620283	ns
IWB70188	2A	158.2322932	ns
IWB65315	2A	159.0610728	ns
IWB61119	2A	160.435003	ns
IWB45464	2A	160.9755486	ns
IWB3440	2A	161.2458135	ns
IWB56728	2A	169.122523	ns
IWB72840	2A	170.2399921	ns
IWB59980	2A	170.5132107	ns
IWB69132	2A	172.5257238	ns
IWB9488	2A	172.7974575	ns
IWB6431	2A	173.0662694	ns
IWB72117	2A	176.8952358	ns
IWB68598	2A	179.3816583	ns
Xgwm526	2A	179.3816583	ns
IWB14668	2A	180.3751224	ns

Marker	Chromosome	Position	Segregation distortion
IWB32878	2A	180.649842	ns
IWB8941	2A	180.9230606	ns
IWB45239	2A	181.1904351	ns
IWB46343	2A	181.4607	ns
IWB72126	2A	181.7309649	ns
IWB46290.1	2A	186.8382898	ns
Xbarc122	2A	187.6580107	ns
IWB39805.1	2A	188.7510479	ns
IWA4493	2A	190.1402508	ns
IWB33959	2A	190.4105157	ns
IWB52585.1	2A	192.077748	*
IWB47158	2B	0	***
IWB34415	2B	0.810857939	***
IWB29273	2B	1.348497359	***
IWB9207	2B	1.348497359	****
IWB57906	2B	1.623217012	***
IWB6886	2B	3.579460127	*****
IWA7916	2B	4.385958113	*****
IWB46469	2B	5.214737711	*****
IWB59353	2B	5.495630576	*****
IWB69396	2B	6.632152803	*****
IWB21237	2B	7.210193698	*****
IWB32008	2B	8.082345339	*****
IWB71587	2B	8.363238204	*****
IWB73904	2B	8.655629081	*****
IWA8243	2B	9.559308732	*****

Marker	Chromosome	Position	Segregation distortion
IWA4554	2B	9.841788494	*****
IWA6893	2B	10.13417937	****
IWB46988	2B	11.03244699	*****
IWB7072	2B	11.58800807	*****
IWB60831	2B	11.87048783	****
IWB72894	2B	12.74263948	****
IWB72685	2B	13.02834743	****
IWB74844	2B	13.3061194	****
IWB26449	2B	13.58235678	****
IWB60118	2B	13.86324964	****
IWB5684	2B	14.43143737	****
IWB48240	2B	14.98392899	**
IWB62688	2B	16.12694745	***
IWB11285	2B	16.41265541	***
Xbarc55	2B	21.05540391	*
IWB16217	2B	21.92251354	ns
IWB3454	2B	23.05261296	ns
IWB44515	2B	23.92986559	*
IWB26631	2B	26.40091597	*
IWA905	2B	28.76946611	ns
IWA3428	2B	31.51602447	ns
IWB7715	2B	34.21315044	ns
IWB36818	2B	34.80139228	ns
IWB64964	2B	35.09550302	ns
IWB58274	2B	35.38121098	ns
IWA5436	2B	36.26884673	ns

Marker	Chromosome	Position	Segregation distortion
IWB2692	2B	37.16176678	ns
IWB31492	2B	37.44747473	ns
IWB59779	2B	39.48341333	ns
IWB65533	2B	40.0389744	ns
IWB45931	2B	40.62037607	ns
IWA3817	2B	40.90608403	ns
Xbarc18	2B	41.53502283	ns
IWB34576	2B	42.47259562	ns
IWB57577	2B	43.06431825	ns
IWB74647	2B	43.36193014	ns
IWB74518	2B	43.91749122	ns
Xgwm129	2B	45.11528163	ns
IWA5600	2B	46.00291738	ns
IWB56465	2B	47.39212028	ns
IWB62579	2B	47.67144398	ns
IWB2507	2B	47.95076767	ns
IWB67747	2B	52.07761628	*
IWB69363	2B	52.35083479	*
IWB26325	2B	52.62109971	*
IWB63790	2B	54.94828059	**
IWB12137	2B	57.28908959	**
IWB48071	2B	61.2851542	**
IWB43954	2B	61.56447789	***
IWB60374	2B	63.93302804	**
IWA5461	2B	64.50446261	**
IWB50645	2B	64.78378631	**

Marker	Chromosome	Position	Segregation distortion
IWB28721	2B	65.05850596	**
IWB66390	2B	65.62030943	***
IWB11563	2B	65.89808139	***
IWB10410	2B	66.18216608	**
IWB6515	2B	66.46951597	***
IWB52433	2B	66.74423562	***
IWA5413	2B	67.02355932	****
IWA470	2B	67.88075783	**
IWB3537	2B	68.97980236	***
IWB68982	2B	69.81318685	****
IWB11092	2B	70.08492054	****
IWB35393	2B	70.36115792	****
IWB12045	2B	72.9950795	*****
IWB3891	2B	75.295475	****
IWB73114	2B	75.85727846	***
Xwmc175	2B	77.80623365	***
IWB3192	2B	79.76793904	****
IWB72911	2B	79.76793904	*****
IWB67207	2B	81.23029358	*****
IWB4571	2B	81.7827852	*****
IWA6122	2B	83.76115427	****
IWB57922	2B	85.28595966	***
IWB28722	2B	86.20066141	****
IWB8420	2B	86.77209599	****
IWB3588	2B	87.87721418	*****
IWB68952	2B	89.58236471	****

Marker	Chromosome	Position	Segregation distortion
IWB36072	2B	90.1318206	****
IWB73211	2B	90.68431222	***
IWB37873	2B	90.96363592	***
IWB67728	2B	93.01149304	***
IWB71878	2B	93.28926501	***
IWB39394	2B	94.41301382	***
IWB9560	2B	94.6892512	***
IWB5957	2B	94.95951612	***
IWB44694	2B	95.50006175	***
IWB69630	2B	104.0733303	***
IWB6167	2B	104.3421423	***
IWB60041	2B	105.1618631	***
IWB68445	2B	105.4411868	***
IWB57292	2B	106.2983853	**
IWB6323	2B	106.5808651	**
IWB45435	2B	107.7109645	***
IWB11174.1	2B	114.1484994	**
IWB10162	2B	114.4262713	**
IWB66266	2B	114.6994898	**
IWB2341	2B	115.5059878	**
IWB52447	2B	116.5872055	**
IWB11123	2B	116.8560174	**
IWB59226	2B	117.1262823	**
IWB58126	2B	117.3936568	**
IWB2628	2B	117.9431127	**
IWB9088	2B	119.0668615	**

Marker	Chromosome	Position	Segregation distortion
IWB60161	2B	119.3430989	**
IWB34773	2B	119.6163174	**
IWB8894	2B	119.8925548	**
IWB69000	2B	123.427722	*
IWB64039	2B	126.7061041	***
IWA3257	2B	128.7539612	**
IWB39800	2B	129.0271797	**
IWB70683	2B	129.3018994	**
IWB32211	2B	130.7815687	**
IWB7819	2B	131.6486783	**
IWB6618	2B	132.20117	**
Xwmc317	2B	134.4318565	ns
IWB8157	2B	136.3808117	**
IWB36313	2B	136.3808117	**
IWB58205	2B	138.1997279	***
IWB7569	2B	140.6257823	**
IWA5442	2B	140.6257823	***
IWB25347	2B	143.0084512	*****
IWB44797	2B	146.0423595	***
IWB9733	2B	146.9044851	**
IWB8698	2B	147.1762188	**
IWB45312	2B	147.4479525	**
IWB52360	2B	147.7257245	***
IWB58090	2B	151.6973217	**
IWB7893	2B	151.9766454	*
IWB12598	2B	152.5230988	*

Marker	Chromosome	Position	Segregation distortion
IWB8650	2B	152.7948325	*
Xbarc321	3A	0	ns
IWB36703.1	3A	1.282278961	ns
IWB12111.1	3A	2.695038584	ns
IWB5950	3A	3.269757335	ns
IWB7786.1	3A	3.580308203	ns
IWB9278	3A	4.478575827	ns
IWB5333	3A	5.03724066	ns
IWB65471	3A	11.00265033	ns
IWB72257	3A	11.83603482	ns
IWB26667	3A	14.12326768	ns
IWA4804	3A	17.63769443	ns
IWB8714	3A	17.90942812	ns
IWB25484	3A	18.72469341	ns
IWA288.1	3A	20.16182264	ns
IWA6928	3A	31.58022818	ns
IWB45729.1	3A	33.89393879	ns
IWB70095	3A	34.17171076	ns
IWB67571	3A	41.27000506	ns
IWB73247	3A	41.55248483	ns
IWB32591	3A	42.11746238	ns
IWB34845	3A	42.39523435	ns
IWB14340	3A	42.94168769	ns
IWB6837	3A	50.59554447	ns
IWB71479	3A	54.15169869	ns
IWB9991	3A	55.83767685	ns

Marker	Chromosome	Position	Segregation distortion
IWB72544	3A	56.96142567	ns
IWB46342	3A	57.23766305	ns
IWB71974	3A	58.36776247	ns
Xgwm5	3A	61.05478743	ns
IWB67595	3A	64.7034725	ns
IWB72484	3A	65.24111192	ns
IWB39542	3A	65.79056781	ns
IWB39272	3A	66.6239523	ns
IWB72529	3A	67.17040565	ns
IWB37891	3A	67.44362416	ns
IWB65628	3A	67.71535785	ns
IWB4947	3A	67.98562277	ns
IWA538	3A	70.5740531	ns
IWB27964	3A	70.84727162	ns
IWA7012	3A	71.12816448	ns
IWA536	3A	71.40905735	ns
IWB5680	3A	74.57409192	ns
IWB69157	3A	75.10885621	ns
IWB72777	3A	75.9241215	ns
IWB72687	3A	76.47057485	ns
IWB45790	3A	77.64033839	ns
IWA8465	3A	77.92768828	ns
IWB72223	3A	79.33250737	ns
IWB66938	3A	79.60572588	ns
IWB26728	3A	80.15518178	ns
IWA7159	3A	80.98856627	ns

Marker	Chromosome	Position	Segregation distortion
IWB72822	3A	82.97818718	ns
IWB67254	3A	84.66416534	ns
Xwmc428	3A	88.07062702	ns
IWB39719	3A	90.39006712	ns
IWB72995	3A	93.57344478	ns
IWB67653	3A	94.69719359	ns
IWB9778	3A	95.25275467	ns
Xbarc1040	3A	96.72371563	ns
IWB65532	3A	100.3245435	ns
IWB73344	3A	100.3245435	ns
IWB28080	3A	113.5617998	ns
IWB26279	3A	115.8621953	ns
IWA5456	3A	116.1430881	ns
IWA4810	3A	116.430438	ns
IWB58368	3A	116.7097617	ns
IWB10607	3A	117.2715652	ns
IWA7324	3A	118.7600466	ns
IWB17683	3A	119.0473965	ns
IWB4406	3A	122.8557823	ns
IWB8584	3A	124.8567839	ns
IWB7486	3A	128.7334422	ns
IWB11581	3A	129.3016299	ns
IWB6047	3A	130.1588284	ns
IWB72394	3A	136.6889337	ns
IWB10433	3A	139.4188143	ns
IWB8816	3A	140.2809399	ns

Marker	Chromosome	Position	Segregation distortion
IWB25213	3A	140.5733308	ns
IWB31321	3A	144.6703623	ns
IWB50481	3A	145.2321658	ns
IWB7073	3A	145.7846574	ns
Xwmc153	3A	146.0991143	ns
IWB71198	3A	154.2585732	ns
IWB73551	3A	154.8300078	ns
IWB72058	3A	155.9537566	ns
IWB72476.1	3A	172.3009117	ns
IWB52089	3A	174.3487689	ns
Xcfa2076	3A	174.3487689	ns
IWB9606	3A	175.2416889	ns
IWA391	3A	177.9550933	ns
IWA95	3A	186.0903041	ns
IWB8784.1	3A	196.0224078	ns
IWB44666.1	3A	196.2897823	ns
IWB4391	3A	199.3661872	ns
IWB72092	3A	199.9156431	ns
IWB73076	3A	200.465099	ns
IWA7158	3A	202.1323313	ns
IWB73267	3A	202.6787847	ns
Xgwm162	3A	203.7658545	*
IWB63588	3A	204.8689141	ns
IWB36083	3A	206.0251504	ns
IWB29059	3B	0	ns
IWB46537	3B	1.744834327	ns

Marker	Chromosome	Position	Segregation distortion
IWB4668	3B	2.659536076	ns
Xbarc12	3B	3.950090768	ns
IWB58161.1	3B	5.249028725	ns
IWB5600	3B	6.163730475	ns
IWB20761	3B	7.592643597	ns
IWA6038	3B	8.444971043	ns
IWB66471	3B	27.65734883	*****
IWB7693.1	3B	37.58945246	*
IWB58514	3B	41.58551707	ns
Xgwm389	3B	41.58551707	*
IWB69147	3B	41.87962781	ns
IWB8528.1	3B	43.00972723	ns
IWB6475	3B	43.5911289	*
IWB4343	3B	43.88351978	ns
IWB74288	3B	44.16922773	ns
IWB58878	3B	44.45493569	ns
IWA5347	3B	44.73270766	ns
IWB45836	3B	51.69532776	*
IWB6299	3B	52.2417811	ns
IWB9212	3B	55.13508188	ns
IWB39782	3B	55.41756164	ns
IWB8163	3B	59.72248246	ns
IWB7464	3B	60.01149325	ns
Xcfd79	3B	60.90441329	ns
IWB8426	3B	61.19012125	ns
IWB34803	3B	62.04731976	ns

Marker	Chromosome	Position	Segregation distortion
IWB17577	3B	62.33466965	ns
IWB12216	3B	62.8996472	ns
Xbarc131	3B	64.37060817	ns
IWB10462	3B	68.86970437	ns
IWB39127	3B	72.18769752	ns
IWB56689	3B	97.30561307	****
IWB25180	3B	98.14365392	****
Xgwm566	3B	98.76866175	***
Xbarc68	3B	98.76866175	****
IWB56601	3B	99.93162235	***
IWA3390	3B	101.0246596	***
IWB7234	3B	101.8534392	***
IWB44056	3B	101.8534392	***
IWA747	3B	103.2742297	***
IWB26916	3B	104.4043291	***
IWB34239	3B	104.6884138	**
IWB46180	3B	105.2598484	***
IWA3426	3B	106.0978892	****
IWB16995.1	3B	107.1969337	***
IWB32713	3B	108.9118349	***
IWB26261	3B	109.4865537	****
IWB27781	3B	109.4865537	***
IWB7518	3B	111.4990668	***
IWB57107	3B	112.9445072	***
IWB50286	3B	113.2285919	***
IWB34974	3B	114.0573715	****

Marker	Chromosome	Position	Segregation distortion
IWB25473	3B	115.7722727	**
IWB66842	3B	119.3074399	**
IWB72168	3B	120.7282303	**
IWB14775	3B	121.5616148	***
Xwmc625	3B	123.4979846	**
IWA628	3B	125.7429884	***
IWB35464	3B	126.571768	**
IWB72454	3B	127.4240954	*
IWB66740	3B	127.9827603	**
IWB64191	3B	128.8350877	***
IWB3505	3B	129.6972133	**
IWB11389	3B	129.9734507	***
IWB67963	3B	130.2466692	***
IWB7782	3B	130.7961251	***
IWB2766	3B	131.6249047	****
IWA4630	3B	132.1898822	***
IWB63191	3B	132.4676542	***
IWB10691	3B	132.7393879	****
IWB65234	3B	133.2888438	****
IWB69709	3B	133.5605775	***
IWB61144	3B	134.3802983	****
IWB4885	3B	134.6550179	****
IWB27586	3B	135.5073454	*****
IWB5754	3B	136.6374448	****
IWB73183	3B	137.1838982	****
IWB72421	3B	137.4571167	****

Marker	Chromosome	Position	Segregation distortion
IWB8522	3B	138.0065726	****
IWB3526	3B	138.5471182	****
IWB9814	3B	139.105783	*****
IWB65401	3B	140.5346962	*****
IWA7353	3B	140.8064299	*****
IWA8196	3B	141.0752418	*****
IWB12493	3B	142.150645	*****
IWB65220	3B	143.2202959	*****
IWA239	3B	143.7494012	*****
IWB10905	3B	144.0153536	*****
IWB71946	3B	144.862865	*****
IWB71475	3B	145.4246685	*****
IWB32558	3B	145.692043	*****
IWB46996	3B	149.4130603	*****
IWB45792	3B	149.6862788	*****
IWB58033	3B	150.5150584	*****
IWB57562	3B	154.0924508	*****
IWB12466	3B	155.5132412	****
IWB7145	3B	155.7835062	****
IWB25495	3B	156.342171	****
IWB11838	3B	158.3205401	***
IWB8515	3B	158.5879146	**
IWB50187	3B	159.1226789	***
IWB63008	3B	159.9335368	**
IWB35427	3B	160.4799902	**
IWA8287	3B	160.7517238	**

Marker	Chromosome	Position	Segregation distortion
IWB5635	3B	161.2864881	*
IWB27956	3B	162.1017534	**
IWA3669	3B	162.3705654	**
IWB45133	3B	162.6468027	**
IWB64869	3B	165.3933611	*
IWB39561	3B	165.6774458	*
IWB57606	3B	165.9506643	*
IWB60995	3B	166.5093291	*
IWB30796	3B	167.0557825	ns
IWB57820	3B	167.323157	ns
IWB67102	3B	167.5877022	ns
Xgwm108	3B	167.9061648	*
IWB65244	3B	168.8996288	ns
IWB8243	3B	169.7330133	ns
IWB27126	3B	172.26318	ns
IWB31149	3B	172.5349137	ns
IWB63048	3B	174.7835477	ns
IWB59671	3B	175.3240933	ns
IWB58482	3B	189.4832602	ns
IWB6845	3B	195.7658698	ns
IWB10030	3B	196.0390883	ns
IWB31790	3B	206.9215604	*
Xwmc326	3B	213.0118837	ns
IWB12975	3B	213.2896557	ns
IWB9228	3B	215.5768886	ns
IWB26933	3B	221.7366365	ns

Marker	Chromosome	Position	Segregation distortion
IWB59521	3B	222.0239864	ns
IWB10755	3B	222.2927984	ns
IWB2741	3B	224.2711674	ns
IWB73987	3B	228.8290359	ns
IWB15780	3B	229.6624204	ns
IWB8511.1	3B	229.9497703	ns
IWB67339	3B	230.5380122	ns
IWB62853	3B	230.8142495	ns
IWB6446	3B	231.0845145	ns
IWB44760.1	3B	232.1896326	ns
IWB27815	3B	233.0230171	ns
IWB51875	3B	235.9331762	ns
IWB44970	3B	236.4981537	ns
IWB46869	3B	239.7765359	ns
IWB3434	3B	240.3229892	ns
IWB50423	3B	242.6501701	ns
IWB11701	3B	244.0956105	ns
Xgwm181	3B	244.7016782	ns
IWB7537	3B	245.3004875	ns
IWB50139	3B	245.8957324	ns
IWB33098	3B	248.0310957	ns
IWB9651	4A	0	ns
IWA54	4A	0.279323699	ns
IWB21310	4A	5.202965342	ns
IWB8056	4A	5.746448778	ns
IWB67355	4A	8.349867096	ns

Marker	Chromosome	Position	Segregation distortion
IWA4232	4A	16.43201749	ns
IWB47589	4A	18.43301901	ns
IWA603	4A	18.70475271	ns
IWB71863	4A	18.9721272	ns
IWB4310	4A	19.78298514	ns
IWB52170	4A	20.05035964	ns
IWB32882	4A	20.86562493	ns
IWB5392	4A	28.14912405	**
IWA7522	4A	28.42536143	**
IWB47937	4A	29.54283062	**
IWB62589	4A	30.08337625	***
IWB3495	4A	30.35364117	**
IWB21081.1	4A	32.06854239	*
IWA3302	4A	32.92086984	**
IWB18200	4A	33.76838126	*
IWA4698	4A	36.31286633	ns
IWB6710	4A	36.58758599	ns
IWB5380	4A	36.87167067	*
IWB73430	4A	38.34263164	ns
IWB48193	4A	38.61436533	ns
IWA568	4A	39.16382123	ns
IWA4785	4A	39.72562469	ns
IWB10618	4A	40.56366553	ns
IWB65999	4A	42.96062271	ns
IWB6369	4A	43.53534146	ns
IWA4199	4A	49.93343531	ns

Marker	Chromosome	Position	Segregation distortion
IWB32858	4A	50.2207852	ns
IWB63835.1	4A	52.98422654	ns
IWB69809	4A	53.26199851	ns
IWA7058	4A	58.73813241	ns
IWB36596	4A	59.00694435	ns
IWB18775.1	4A	61.55142942	*
IWB68318	4A	62.40375687	ns
IWA7118	4A	65.36569177	ns
IWB26773	4A	66.50221399	ns
IWB10788.1	4A	67.07364857	ns
IWB32864	4A	67.63862613	ns
IWB64452	4A	67.91639809	ns
IWA6035	4A	69.34531121	ns
IWB12388	4A	72.27252635	*
IWB20951	4A	74.87594467	ns
IWB68972	4A	76.04570821	ns
IWB27644	4A	79.13593758	ns
IWA3774	4A	80.9013149	ns
IWB2658	4A	81.71658019	*
IWA485	4A	84.57674429	*
IWB8782	4A	85.68186248	ns
IWB27701	4A	93.43540775	*
IWB65650	4A	93.71788751	**
IWA4527	4A	94.00359547	ns
IWB34056	4A	95.77942682	ns
IWB73029	4A	99.07749536	ns

Marker	Chromosome	Position	Segregation distortion
IWB34374	4A	99.92024489	*
IWB28114.1	4A	106.324199	ns
IWB44927	4A	106.6066788	ns
IWB6821	4A	109.2100971	ns
IWB8059	4A	109.7656582	ns
IWA559	4A	111.4611683	ns
Xwmc232	4A	113.3851142	ns
IWB36257	4A	116.745717	ns
IWB52321	4A	117.6178686	ns
IWB73853	4A	117.9019533	ns
IWB68597	4A	119.0581897	ns
IWB71467	4A	119.334427	ns
IWB9701	4A	120.1819385	ns
IWB71844	4A	122.2540565	ns
IWB36617	4A	123.430703	ns
IWB25556	4A	123.7147877	ns
IWB2554	4A	126.0419686	ns
IWB14801	4A	126.0419686	ns
Xbarc78	4A	126.0419686	ns
IWB70620	4A	126.3212923	ns
IWB18869.1	4A	126.603772	ns
IWB3267	4A	127.4512835	ns
IWB3265	4A	129.8627014	ns
IWB34579	4A	132.3185687	ns
IWB57683	4A	132.8966096	ns
IWB8842	4A	135.3374793	ns

Marker	Chromosome	Position	Segregation distortion
IWB52795	4A	138.2646944	ns
IWB8552	4A	138.8202555	ns
IWB39717	4A	139.0995792	ns
IWB65913	4A	139.3836639	ns
IWB64680	4A	146.2896956	ns
IWB18740	4A	146.5721753	ns
IWB26452	4A	146.8578833	ns
IWB39523	4A	148.5926244	ns
IWB70791	4B	0	ns
IWB8794	4B	0.574718751	ns
IWB71989	4B	0.862068635	ns
IWB73905	4B	4.262230993	ns
IWA8107	4B	6.562626488	ns
IWA8108	4B	7.109079834	ns
IWB63893	4B	8.884911188	ns
IWB35920	4B	9.172261072	ns
IWB25162	4B	9.172261072	ns
IWB31302	4B	9.48281194	ns
IWA8178	4B	9.785834686	ns
IWB73117	4B	13.51932051	ns
IWB72527	4B	15.83303112	ns
IWB59992	4B	19.11141324	ns
IWB59993	4B	19.94945409	ns
IWB73302	4B	23.17016413	ns
IWB72764	4B	23.4479361	ns
IWB66414	4B	23.72882896	ns

Marker	Chromosome	Position	Segregation distortion
IWB35969	4B	24.00506634	ns
IWB69815	4B	24.86226486	ns
IWB73258	4B	25.14634955	ns
IWB73832	4B	25.43369943	ns
IWB16360	4B	26.00513401	ns
IWB11928	4B	26.86233252	ns
IWB9610	4B	28.28312297	ns
IWB73411	4B	28.86452464	ns
IWB47531	4B	29.45276648	ns
IWB67487	4B	30.32491812	ns
IWB68116	4B	30.62076908	ns
IWB71418	4B	30.91838097	ns
IWB71386.1	4B	32.6632153	ns
Xbarc1133	4B	33.58352955	ns
IWA8564	4B	35.8142161	ns
IWB36089	4B	37.53898021	ns
IWB25268	4B	38.65644941	ns
IWB31724	4B	40.07723985	ns
IWB36179	4B	40.95449249	ns
Xgwm540	4B	41.26123311	ns
IWB17848	4B	43.42298956	ns
IWB35513	4B	43.96944291	ns
IWB35380	4B	45.94781198	ns
IWB72399	4B	47.0715608	ns
IWB70599	4B	52.24122754	ns
IWB44068	4B	59.24848864	ns

Marker	Chromosome	Position	Segregation distortion
IWB9672.1	4B	60.66927909	ns
IWB7195	4B	61.22484017	ns
IWB28344	4B	62.62180751	ns
IWB34520	4B	64.64596558	*
IWB39624	4B	67.37584617	*
IWB73144	4B	69.47280708	*
IWB69664	4B	70.30158668	ns
IWA3396	4B	70.57630633	ns
IWB70855	4B	70.85102599	ns
IWB32927	4B	71.40969082	ns
IWB73466	4B	72.24773166	ns
IWB17082	4B	72.80953513	ns
IWB44538	4B	75.17808527	**
IWB28273	4B	75.45432265	**
IWB12434	4B	75.45432265	**
IWB71804	4B	75.73209461	**
IWB66294	4B	76.30028233	**
IWB7973	4B	78.3244404	**
IWB45462	4B	78.3244404	*
IWB48267	4B	78.61513141	*
IWB66538	4B	78.88985106	*
IWB60004	4B	79.16608844	*
IWB44585	4B	79.4438604	*
IWB73383	4B	80.28660993	*
IWB71553	4B	82.65516007	*
IWB44750	4B	83.22659465	***

Marker	Chromosome	Position	Segregation distortion
IWB7389	4B	83.77605054	***
IWB47537	4B	84.32854216	***
IWB75280	4B	86.97798524	**
IWB7462	4B	89.59656629	***
IWB60053	4B	89.59656629	***
IWB20754	4B	89.8872573	***
IWB11229	4B	91.01100611	***
IWB75098	4B	98.86689245	*
IWB74054	4B	99.13862614	ns
Xwmc125	4B	100.0880688	ns
IWB48353	4B	100.7209883	ns
IWB3641	4B	103.5811524	ns
IWB74794	4B	104.1398173	ns
IWA27	4B	105.5525769	ns
IWB6896	4B	109.6312278	ns
IWB35942.1	4B	123.5186582	ns
IWB67499	4B	125.195211	ns
IWB70789	5A	0	ns
IWB71134	5A	0.274719653	ns
IWB64323	5A	1.122231079	ns
IWA3567	5A	1.40471084	ns
IWB64781	5A	3.417223994	ns
IWA7361	5A	15.53664536	ns
IWB74361.1	5A	17.93360253	ns
IWB29633	5A	18.81601618	ns
IWB64310	5A	20.03572435	ns

Marker	Chromosome	Position	Segregation distortion
IWB11068	5A	21.7704655	ns
IWA5368	5A	25.28489226	ns
IWB12627	5A	28.54382191	ns
IWB72119	5A	28.82159387	ns
IWB48152	5A	29.10567856	ns
IWB6728	5A	31.81908291	ns
IWB68312	5A	33.5741286	ns
IWB3091	5A	35.00304172	ns
IWB66553	5A	37.93025685	ns
IWA8155	5A	38.20958055	ns
IWB3903	5A	39.33967997	ns
Xbarc186	5A	41.30138536	**
IWA5395	5A	42.29484941	ns
IWB48524	5A	44.0812594	ns
IWB31546	5A	44.65597815	ns
IWB33251	5A	44.94332803	ns
IWA8582	5A	46.67806918	ns
IWA3975	5A	50.50894321	ns
IWB66579	5A	51.0869841	ns
IWB61122	5A	53.54285136	ns
IWB71919	5A	55.54385289	ns
IWB66385	5A	55.81558658	ns
IWB12396	5A	56.92070477	ns
IWB34674	5A	57.46418821	ns
IWB33272	5A	58.01064155	ns
IWB21005	5A	58.28536121	ns

Marker	Chromosome	Position	Segregation distortion
IWA6036	5A	65.66297989	ns
IWB37510	5A	65.95199068	ns
Xgwm186	5A	66.6013501	ns
IWB10677	5A	66.6013501	ns
IWB63767	5A	67.74436856	ns
IWB48382	5A	68.04021952	ns
IWB26864	5A	73.8350165	ns
IWB10384	5A	74.11910119	ns
IWB52863	5A	74.39999405	ns
IWB73963	5A	77.00341237	ns
IWB44434	5A	79.34422138	ns
IWB34371	5A	81.07896253	ns
IWB17918	5A	83.71288411	ns
IWB50162	5A	84.88264765	ns
IWA8588	5A	88.54759607	*
IWB29626	5A	89.1062609	*
IWB61032	5A	90.86130659	**
Xwmc415	5A	90.86130659	*
IWB75269	5A	93.72147069	ns
IWB26027	5A	93.99619034	ns
IWB46709.1	5A	94.27091	ns
IWB47646	5A	94.82036589	ns
IWB34570.1	5A	103.3936345	ns
IWB3340	5A	103.9312739	ns
IWB27298	5A	104.4718195	ns
IWB9503	5A	107.5830732	ns

Marker	Chromosome	Position	Segregation distortion
IWA5668	5A	107.8518851	ns
IWB63299	5A	108.1281225	ns
IWB10966	5A	108.401341	ns
IWB59600	5A	108.6838208	ns
IWB72998	5A	108.9745118	ns
IWB71642	5A	109.2635226	ns
IWB59852	5A	109.2635226	ns
IWB8905	5A	110.6604899	ns
IWA4205	5A	117.62311	**
IWA5624	5A	119.3781557	**
IWB73552	5A	120.2402813	*
IWB6049	5A	123.2198871	*
IWB58257	5A	126.1471023	**
IWB33488	5A	127.2461468	**
IWB73502	5A	128.0888963	***
IWA7256	5A	130.1488124	**
IWB9808	5A	130.9915619	**
IWB59813	5A	132.396381	ns
IWB8258	5A	133.7855839	*
IWB27510	5A	134.0588024	**
IWA4805	5A	134.6174673	*
IWB52008	5A	135.4508517	*
IWB27060.1	5A	136.2888926	ns
IWB72363	5A	137.6937117	*
IWA576	5A	140.9144217	**
IWB44564	5A	145.3004643	*

Marker	Chromosome	Position	Segregation distortion
IWB8292	5A	146.1625899	*
IWB5457	5A	146.9913695	ns
IWB35422	5A	147.264588	ns
IWA582	5A	147.8327757	ns
IWB72888	5A	157.4738741	ns
IWB73761	5A	157.7501115	ns
IWB7685	5A	174.2669636	ns
IWB33102.1	5A	174.5416833	ns
IWB61152	5A	179.7430972	ns
IWB3232	5A	181.1170273	ns
IWB69883	5A	182.5708756	ns
IWB69884	5A	184.4121281	ns
IWB29171	5A	185.5818916	ns
IWB9130	5A	187.2774018	ns
IWA7162	5A	188.6666047	ns
IWB71656	5A	188.9383384	ns
IWB14661	5A	189.2086033	ns
IWB7282	5A	189.4774152	ns
IWB14680	5A	190.5764597	ns
IWB34800	5A	191.1320208	ns
IWB18172	5A	191.4113445	ns
IWB14077	5A	196.2454507	ns
IWB6716	5A	197.6502698	ns
IWB72152	5A	197.9234883	ns
IWB60850	5A	198.4790494	ns
IWB19304	5A	198.753769	ns

Marker	Chromosome	Position	Segregation distortion
IWB9800	5A	202.2074117	ns
IWB3188	5A	202.2074117	ns
XCfb306	5B	0	***
IWB47425	5B	1.724738541	****
IWB11710	5B	2.289716098	****
IWB64829	5B	5.867108473	****
IWB11140	5B	6.984577664	****
IWB73718	5B	7.254842584	****
IWB64286	5B	7.526576275	*****
IWB37583	5B	8.359960766	*****
IWB73786	5B	13.97326903	***
IWB33289	5B	14.25897699	****
IWB26051	5B	18.59060207	***
IWB4841	5B	20.26715488	**
IWB26568	5B	20.54647858	**
IWB25449	5B	21.12788024	**
IWA7181	5B	26.92267722	ns
IWB14163	5B	27.20357009	ns
IWB21416	5B	28.88954825	ns
IWB58311	5B	29.45135171	ns
IWB26650	5B	30.58787394	ns
IWB57734	5B	37.31581073	ns
IWB8792	5B	39.08118805	ns
IWB6617	5B	48.94711034	ns
IWB29025	5B	49.48187463	ns
IWB6012	5B	50.02242027	ns

Marker	Chromosome	Position	Segregation distortion
IWB10925	5B	50.29123221	ns
IWB8397	5B	50.5586067	ns
IWB68299	5B	50.8259812	ns
IWB7200	5B	51.09052645	ns
IWA4158	5B	51.35367941	ns
IWB39718	5B	52.43489706	ns
IWB36090	5B	54.09291192	ns
Xbarc74	5B	54.95503751	ns
IWB11100	5B	56.10462691	ns
IWB70171	5B	56.37343885	ns
Xgwm213	5B	56.69394272	ns
IWB64262	5B	58.00997831	ns
IWA5742	5B	60.87014241	ns
IWB25222	5B	61.13751691	ns
IWB36811	5B	64.87999769	ns
IWB67658	5B	68.00897382	ns
IWB3560	5B	69.66698869	ns
IWB65958	5B	70.47784662	ns
IWB11879	5B	73.58910028	ns
IWB3607	5B	74.41787988	ns
IWB70658	5B	75.53534907	ns
IWB5390	5B	76.0758947	ns
IWB45894	5B	76.3432692	ns
IWB5713	5B	77.43630647	ns
IWB6817	5B	77.70511841	ns
IWB46986	5B	77.97393035	ns

Marker	Chromosome	Position	Segregation distortion
IWB33391	5B	78.25016773	ns
IWB10247	5B	81.47087777	ns
IWB5882	5B	81.73825227	ns
IWB12924	5B	89.5161396	ns
IWB72334	5B	89.7878733	ns
IWB20925	5B	90.33732919	ns
IWB6464	5B	91.16155451	ns
IWA8252	5B	92.00906593	ns
IWA5478	5B	105.2463222	ns
IWB34313	5B	106.3637914	ns
IWB72095	5B	116.9201007	ns
IWB72094	5B	117.2142114	ns
IWB48396	5B	117.7956131	ns
IWA8097	5B	118.0718505	ns
IWB6687	5B	118.3496224	ns
IWB43876	5B	119.5402809	ns
IWB10635	5B	119.8326718	ns
IWB18958	5B	121.7999157	ns
IWB6063	5B	122.0701806	ns
IWB56412	5B	122.3495043	ns
IWB10135	5B	123.1970157	ns
IWB69317	5B	123.7375613	ns
IWB6424	5B	124.0107799	ns
IWB52474	5B	124.2916727	ns
Xwmc75	5B	125.1587824	ns
IWB32852	5B	126.030934	ns

Marker	Chromosome	Position	Segregation distortion
IWB29442	5B	126.3150187	ns
IWB7415	5B	126.5974985	ns
IWB27379	5B	126.8783913	ns
IWB33063	5B	127.7405169	ns
IWB7206	5B	128.0246016	ns
IWB75021	5B	128.2978201	ns
IWB67069	5B	128.5740575	ns
IWB2976	5B	130.0111867	ns
IWB74046	5B	131.4319772	ns
IWB6641	5B	133.7323727	ns
IWB10535	5B	134.556598	ns
IWB68076	5B	134.8359217	ns
IWA4539	5B	135.1216296	ns
IWB29397	5B	135.4041094	ns
IWB71390	5B	135.6865892	ns
IWB71849	5B	136.2515667	ns
IWB73175	5B	136.8010226	ns
Xbarc142	5B	137.3724572	ns
IWB69475	5B	137.9677021	ns
IWB9438	5B	138.8249006	ns
IWB72592	5B	139.6491259	ns
IWB63298	5B	140.4688467	ns
IWA4185	5B	140.7420652	ns
IWB72048	5B	141.8850837	ns
IWB12143	5B	142.4500612	ns
IWB71831	5B	144.5099773	ns

Marker	Chromosome	Position	Segregation distortion
IWB64707	5B	144.7956853	ns
IWB71387	5B	145.0880762	ns
IWB71821	5B	154.3767192	ns
IWB44136	5B	154.6576121	ns
IWB68167	5B	155.5099395	ns
IWB63067	5B	156.0846583	ns
IWB74041	5B	156.652846	ns
IWB27453	5B	156.9353257	ns
IWB29437	5B	158.389174	ns
IWB26828	5B	158.6684977	ns
IWA6211	5B	158.9447351	*
IWB74035	5B	160.0437796	ns
IWA7903	5B	160.8771641	ns
IWB12232	5B	162.3226045	ns
IWB26719	5B	165.8577716	ns
IWB73021	5B	166.1324913	ns
Xbarc243	5B	166.411815	ns
IWB26951	5B	166.411815	*
IWB70634	5B	166.6850335	ns
IWB29509	5B	166.9509859	ns
IWB67752	5B	167.2227195	*
IWB63871	5B	170.1160203	*
IWB7739	5B	175.9346096	ns
IWB46237	5B	176.2139333	ns
IWB70408	5B	176.4917053	ns
IWB7836	5B	177.3297461	ns

Marker	Chromosome	Position	Segregation distortion
Xgwm118	5B	177.6364867	ns
IWB65485	5B	177.6364867	ns
IWB72674	5B	178.4562075	ns
IWB66258	5B	178.7279412	ns
IWB71272	5B	179.2897447	ns
IWA7374	5B	181.9083257	ns
IWB69552	5B	183.0579151	ns
IWB24987	5B	187.5282036	ns
IWB47086	5B	187.8155535	ns
IWB10105	6A	0	ns
IWB7762	6A	1.117469191	ns
IWA5416	6A	1.389202882	ns
IWB12447	6A	1.935656229	ns
IWB60233	6A	2.76904072	ns
IWB11316.1	6A	3.321532341	ns
IWA7913	6A	4.164281868	ns
IWB9075	6A	4.735716444	ns
IWB35466	6A	6.79563253	ns
IWB72510	6A	7.07971722	ns
IWA4552	6A	9.202124305	ns
IWB28201	6A	14.48461823	ns
IWB33750	6A	14.77530924	ns
IWB26040	6A	15.64746088	ns
IWB9567	6A	16.2156486	ns
IWB12224	6A	18.84957018	ns
Xgpw3087	6A	20.78593993	ns

Marker	Chromosome	Position	Segregation distortion
IWB67078	6A	22.42043811	ns
IWB73265	6A	26.466355	ns
IWB66392	6A	26.466355	ns
IWB70731	6A	26.74883477	ns
IWB12439	6A	27.59158429	ns
IWB4117	6A	30.85051394	ns
IWB50336	6A	32.31286848	ns
IWB7500	6A	33.7499977	ns
IWB73817	6A	37.24392638	ns
IWB3692	6A	38.05042437	ns
IWB9036	6A	39.43194867	ns
IWB26966	6A	39.70516719	ns
IWB10234	6A	42.00556268	ns
IWA902	6A	42.28804244	ns
IWB6293	6A	46.81830499	ns
IWB17589	6A	55.79470448	ns
IWA7438	6A	56.08709536	ns
IWA6927	6A	56.37610615	*
IWA8341	6A	57.23823174	ns
IWA3526	6A	58.37475397	*
IWB10038	6A	58.95955572	ns
IWB6717	6A	59.24526368	ns
IWB73642	6A	61.2931208	ns
IWB69886	6A	61.86455537	ns
IWA6962	6A	62.15026333	ns
IWB36081	6A	63.34805374	ns

Marker	Chromosome	Position	Segregation distortion
IWA6033	6A	64.58282496	ns
IWB39473	6A	64.8769357	ns
IWB9844	6A	65.15470767	ns
IWB60244	6A	65.43560054	ns
IWB7281	6A	65.7180803	ns
IWA38	6A	66.28951487	ns
IWB40151	6A	66.88832416	ns
IWB9001	6A	67.49439192	ns
IWB5338	6A	68.63741038	ns
IWB75144	6A	68.91518235	ns
IWB9445	6A	70.60116051	ns
IWB73569	6A	77.74792831	ns
IWB73413	6A	80.35134663	ns
IWB9616	6A	82.04685676	ns
IWB9468	6A	83.76175798	ns
IWB64974	6A	85.4766592	ns
IWB33879	6A	86.59412839	ns
IWB69770	6A	100.4098075	ns
IWB61092	6A	100.6875794	ns
Xgwm169	6A	102.4004966	ns
IWB6825	6A	103.0671727	ns
IWB31101	6A	103.3464964	ns
IWB12203	6A	108.6125933	ns
IWB46146	6A	108.8983013	ns
IWB7048	6A	109.1856512	ns
IWB73296.1	6A	109.4618885	ns

Marker	Chromosome	Position	Segregation distortion
IWB11953	6A	113.6380902	ns
IWB3818	6A	113.927101	ns
IWB73927	6A	114.217792	ns
IWB5971	6A	114.7764568	ns
IWB58802	6A	115.3229102	ns
Xgwm617	6A	117.7439956	*
Xgwm427	6A	119.0485389	ns
IWB56463	6A	119.6978984	ns
IWB14865	6A	119.9937493	ns
IWB71122	6A	120.2746422	ns
IWB57893	6A	122.3591076	ns
IWA8595	6A	122.9405092	ns
IWB71956	6A	122.9405092	ns
IWB21359	6A	123.2182812	ns
IWB73410	6A	123.4945186	ns
CK207347	6A	123.8089755	ns
34398.00	6A	125.036169	**
71956.00	6A	126.9707758	*
BE403950	6A	127.8854776	ns
IWB64114	6A	128.8349203	ns
IWB5885.1	6A	129.1343142	ns
IWB56916	6A	129.1343142	ns
IWB30724.1	6A	129.4200221	ns
IWB33694	6A	129.707372	ns
IWA7908	6A	129.707372	ns
IWB33599	6A	129.9820917	ns

Marker	Chromosome	Position	Segregation distortion
IWB27573	6A	130.5738143	*
IWB2835	6A	131.2148484	ns
IWB59051	6A	131.7895671	ns
IWB47141	6A	132.3610017	ns
IWA3644	6A	141.935354	*****
IWA3641	6A	143.0107572	*****
IWB3172	6B	0	ns
IWB7728	6B	1.105118192	ns
IWB67429	6B	2.781671	ns
IWB6572	6B	3.89293037	*
IWB6212	6B	3.89293037	*
IWB59377	6B	4.448491448	*
IWB9057	6B	5.286532293	*
IWB71329	6B	6.106253112	*
IWB74087	6B	6.379471626	*
IWB28633	6B	10.16563222	ns
IWB47396	6B	10.43444416	ns
IWB65787	6B	11.57096638	*
IWB64815	6B	19.24624574	ns
IWB26083	6B	19.52556944	ns
IWB60019	6B	20.40282207	*
IWB7937	6B	20.69017196	ns
IWB7935	6B	21.50989278	ns
IWB73576	6B	21.7801577	ns
IWB33652	6B	23.4567105	ns
Xwmc487	6B	27.82813053	ns

Marker	Chromosome	Position	Segregation distortion
IWB11642	6B	28.36867616	ns
IWB26775	6B	28.63894108	ns
IWB58963	6B	29.19760591	ns
IWB62877	6B	29.47692961	ns
IWB59118	6B	31.2319753	ns
IWA8228	6B	32.74753446	ns
IWB69190	6B	37.18938273	ns
Xwmc494	6B	40.66703217	*
IWB63807	6B	42.32319314	ns
IWB9609	6B	42.60096511	ns
IWB72401	6B	43.42974471	ns
IWB71937	6B	43.71063757	ns
IWA862	6B	45.73479564	ns
IWA7239	6B	45.73479564	ns
IWB45612	6B	46.59692123	ns
IWB45887	6B	47.16189878	ns
IWB3473	6B	48.30491725	ns
IWB71635	6B	49.48156381	ns
IWB26716	6B	50.63780015	ns
IWB71284	6B	52.07492938	*
IWB64914	6B	52.35270134	*
IWB33858	6B	52.9145048	*
IWA6032	6B	53.19074218	**
IWB73968	6B	53.47322194	*
IWB65137	6B	53.75411481	**
IWB72416	6B	55.18302793	**

Marker	Chromosome	Position	Segregation distortion
IWA3676	6B	56.60381838	**
IWB29373	6B	57.74034061	**
IWB59925	6B	58.02769049	***
IWB47211	6B	58.30858336	***
IWB10393	6B	59.43868278	**
IWB34946	6B	62.10383154	***
Xwmc397	6B	63.39438624	****
IWA6153	6B	63.72770949	***
IWB47049	6B	64.33012615	*****
IWB11783	6B	64.61583411	****
IWA3459	6B	65.72709348	*****
IWB35737	6B	66.00798634	*****
IWB31833	6B	66.29046611	*****
IWA1251	6B	67.1525917	*****
IWB68061	6B	67.74431433	*****
IWA5625	6B	68.32911608	*****
IWB35946	6B	69.4528649	*****
IWB45959	6B	69.74187569	*****
IWB72677	6B	72.73936482	*****
IWB57801	6B	73.01868852	*****
IWB50214	6B	73.29958139	*****
IWB73860	6B	73.57735335	*****
IWB75290	6B	77.07128203	*****
IWB63539	6B	77.35060573	*****
IWB26622	6B	77.6314986	*****
IWB73387	6B	78.17795194	*****

Marker	Chromosome	Position	Segregation distortion
Xbarc79	6B	79.43602862	*****
IWB71734	6B	80.36202468	*****
IWB71780	6B	80.63524319	*****
IWB72209	6B	80.91148057	*****
IWA1263	6B	81.19080427	*****
IWB61166	6B	82.61159472	*****
IWB33834	6B	82.88936669	*****
IWB72305	6B	83.16408634	*****
IWB14152	6B	85.10945112	*****
IWB65825	6B	87.93722974	*****
IWB60027	6B	88.47777538	*****
IWB9394	6B	90.42314016	*****
IWB9393	6B	91.54060935	*****
IWA8383	6B	93.53023026	*****
Xbarc24	6B	96.0964771	*****
IWB58636	6B	102.1109333	*****
IWB71618	6B	103.5647815	*****
IWA404	6B	104.6885303	*****
IWB46771	6B	104.9694232	*****
IWA8064	6B	110.1708371	**
IWB45036	6B	114.9470457	*
IWB26890	6B	115.2248177	ns
IWB48236	6B	115.5041414	*
IWB73204	6B	117.7783615	*
IWB34340	6B	118.8896208	ns
IWB27763	6B	133.5266964	ns

Marker	Chromosome	Position	Segregation distortion
Xbarc134	6B	144.0799891	ns
IWB74863	6B	152.3009726	***
IWB70316	6B	152.5834523	**
IWB26627	6B	152.8659321	**
IWA7098	6B	155.193113	**
IWB31091	6B	158.3581475	ns
IWB8341	6B	158.631366	ns
IWB65437	6B	160.4284815	ns
IWB47825	6B	161.3267491	ns
IWB66055	6B	161.8949368	ns
IWA3947	6B	164.5288584	*
IWB72523	6B	165.4010101	**
IWB34745	6B	166.8218005	***
IWB74864	6B	167.66455	**
IWA4919	6B	168.4887754	**
IWA4920	6B	169.29096	***
IWB8425	6B	169.8315057	***
IWB70734	6B	170.3809616	**
IWB12610	7A	0	ns
IWB25834	7A	0.558664833	ns
IWB20752	7A	1.136705727	ns
IWB73683	7A	2.56561885	ns
IWB11001	7A	6.692467454	ns
IWB3124	7A	11.46867607	ns
IWB29333	7A	13.82327388	ns
IWB31010	7A	16.89449838	ns

Marker	Chromosome	Position	Segregation distortion
IWB7400	7A	17.17539124	ns
IWB74024	7A	18.31840971	ns
IWA954	7A	18.59618168	ns
IWB27944	7A	22.33866246	ns
IWB73570	7A	22.33866246	ns
IWB59817	7A	23.75142208	ns
Xbarc127	7A	27.60505199	ns
IWB44791	7A	29.30056212	ns
IWB47321	7A	29.86553968	ns
IWB12197	7A	30.14331164	ns
IWB34499	7A	33.30834621	ns
IWB59294	7A	34.13257153	ns
IWB39676	7A	34.70075925	ns
IWB33919	7A	34.97853121	ns
IWA3760	7A	35.24879613	ns
IWB73665	7A	39.4249978	ns
IWB8251	7A	39.9744537	ns
IWB11091	7A	40.25069108	ns
IWB26398	7A	42.27484914	ns
IWB48426	7A	43.13697473	ns
Xwmc83	7A	45.45641483	ns
IWB25760	7A	47.05946126	ns
IWB63867	7A	47.33569864	ns
IWB60588	7A	47.61502234	ns
IWA8492	7A	48.44840683	ns
IWA4181	7A	50.43802774	ns

Marker	Chromosome	Position	Segregation distortion
IWB70597	7A	50.71735144	ns
IWB60067	7A	51.00143613	ns
IWB4724.1	7A	52.74627045	ns
Xbarc174	7A	54.21723142	ns
IWB12628	7A	55.42223969	ns
IWA5258	7A	55.99367426	ns
IWB27867	7A	56.55547772	ns
IWB11841	7A	57.11414256	ns
IWB8372	7A	57.38886221	ns
IWB8703	7A	57.65912713	ns
IWB28629	7A	58.75817166	ns
IWB12533	7A	59.02554616	ns
IWB7752	7A	59.56031045	ns
IWB11234	7A	60.09507474	ns
IWB60270	7A	60.90157272	ns
IWB72739	7A	61.44802607	ns
IWB9633	7A	63.72224616	ns
IWB45830	7A	65.11144906	ns
IWB8555	7A	65.380261	ns
IWA305	7A	65.91790042	ns
IWB48549	7A	67.04799984	ns
IWB35738	7A	67.32121835	ns
IWB34110	7A	68.95218266	ns
IWB33920	7A	69.23150636	ns
IWB8620	7A	69.23150636	ns
IWB72694	7A	69.49888086	ns

Marker	Chromosome	Position	Segregation distortion
IWB35503	7A	71.7475149	ns
IWA208	7A	73.44302503	ns
IWB59123	7A	74.27180463	ns
IWA4638	7A	74.54061657	ns
IWB11124	7A	74.81088149	ns
IWB9558	7A	76.20784883	ns
IWB8935	7A	76.76651367	ns
IWA4601	7A	78.80245226	ns
IWA8073.1	7A	81.74692481	ns
IWB46770	7A	82.85204301	ns
IWB45735	7A	83.1237767	ns
IWB29555	7A	84.24124589	ns
IWB68969	7A	84.79680697	ns
IWB10959	7A	85.07457893	ns
IWB44085	7A	88.22326269	ns
IWB14692	7A	89.4210531	ns
Xwmc607	7A	93.48383748	ns
IWB4809	7A	96.40912369	ns
IWB72494	7A	96.67938861	ns
IWB9063	7A	98.06859151	ns
IWB25280	7A	99.1737097	ns
IWB8305	7A	99.71134912	ns
IWB47653	7A	99.97730147	ns
IWB6963	7A	100.2432538	ns
IWB3803	7A	100.7780181	ns
IWB70469	7A	101.5932834	ns

Marker	Chromosome	Position	Segregation distortion
IWB73704	7A	103.5386482	ns
IWB52378	7A	108.3436306	ns
IWB57246	7A	108.6229543	ns
IWB46635	7A	108.897674	ns
IWB46703	7A	113.3470944	ns
IWB7632	7A	114.1851352	ns
IWB74845	7A	115.2902534	ns
IWB45179	7A	115.5619871	ns
IWB58863	7A	115.8397591	ns
IWB36250	7A	116.3953201	ns
IWB35048	7A	117.8001392	ns
IWB69898	7A	118.3557003	ns
IWA4621	7A	118.6259652	ns
IWB36680	7A	119.4412305	ns
IWB6983	7A	126.7714852	ns
IWB44281	7A	127.0477225	ns
IWB57321	7A	127.3165345	ns
IWB26081	7A	128.1317998	ns
Xcfa2019	7A	134.767383	*
IWB36108	7A	144.1341853	ns
IWB12038	7A	144.6776687	ns
IWB71398.1	7A	146.344901	ns
IWA6115	7A	157.2524645	ns
IWA866	7A	158.095214	ns
IWB33997.1	7A	158.3745377	ns
IWB63209	7A	158.9332025	ns

Marker	Chromosome	Position	Segregation distortion
IWB12246	7A	161.4921691	ns
IWA4434	7A	161.4921691	ns
IWB27807	7A	162.041625	ns
IWB73997	7A	162.3209487	ns
IWB11121	7A	162.9091906	*
IWB73864	7A	166.9551075	ns
IWB25307	7A	168.3443104	*
IWB64099	7A	168.8907637	*
IWB34223	7A	169.4525672	*
IWA501	7A	169.7288046	*
IWB6675	7A	169.9976165	*
IWB36793	7A	171.6556314	*
IWB6037	7A	171.6556314	*
IWB33121	7B	0	ns
IWB46416	7B	0.26881194	ns
IWB6919	7B	9.991763966	ns
IWB10879	7B	10.26953593	ns
IWB27107	7B	11.3625732	ns
Xwmc323	7B	11.3625732	ns
IWA1181	7B	11.68307707	ns
IWB6455	7B	14.33252015	ns
IWB3164	7B	14.89432361	ns
IWB40019	7B	19.5084287	ns
IWB74056	7B	23.02285545	ns
Xgwm537	7B	31.74284001	ns
IWA1220	7B	35.01533722	ns

Marker	Chromosome	Position	Segregation distortion
IWA4977	7B	36.38926737	ns
IWA4967	7B	39.78419596	ns
IWB44432	7B	40.61297556	ns
IWB39492	7B	41.73044475	ns
IWA3572	7B	41.99925669	ns
IWB34204	7B	42.54274012	ns
IWB7646	7B	43.08622356	ns
IWB11703	7B	44.4831909	ns
IWB5875	7B	44.75492459	ns
IWB68850	7B	46.12134363	ns
IWB67435	7B	46.38729598	ns
IWB35361	7B	48.33266076	ns
IWB25649	7B	49.72186366	ns
IWB5739	7B	50.26831701	ns
IWB59024	7B	51.39206582	ns
IWB3531	7B	53.10696704	ns
IWB72147	7B	53.38320442	ns
IWB63035	7B	56.2765052	ns
IWA7846	7B	56.84469292	ns
IWA5210	7B	56.84469292	ns
IWB59735	7B	58.28182215	ns
IWB51978	7B	58.85325673	ns
IWB34369	7B	59.13258042	ns
IWB4857	7B	62.61909172	ns
Xgwm46	7B	63.23259606	ns
IWB34169	7B	64.6949506	ns

Marker	Chromosome	Position	Segregation distortion
IWB56734	7B	64.96967025	ns
IWB68177	7B	65.80771109	ns
IWB33246	7B	66.36327217	ns
IWB16218.1	7B	67.46839036	ns
IWB35172	7B	71.99865291	ns
IWB67917	7B	76.89208197	ns
IWB21203	7B	77.4507468	ns
IWB69818	7B	78.92170777	ns
IWB69817	7B	79.49314235	ns
IWB69816	7B	80.05180718	ns
IWB60403	7B	82.04142809	ns
IWB71925	7B	82.33381896	ns
IWB34102	7B	83.23208659	*
IWB56488	7B	83.51943647	*
IWB35736	7B	83.80678636	*
IWB33623	7B	84.38150511	*
IWB66304	7B	84.6705159	**
IWB72925	7B	85.25191757	**
IWB69740	7B	85.81372103	ns
IWB73840	7B	87.25916141	*
IWB43821	7B	89.0455714	**
IWB69447	7B	92.1167959	*
IWB60324	7B	92.39927567	**
IWB46260	7B	94.78194459	*
IWA436	7B	96.49684581	ns
IWB69178	7B	100.6981704	ns

Marker	Chromosome	Position	Segregation distortion
IWB75195	7B	100.9940213	ns
IWB46046	7B	101.2898723	ns
IWB9018	7B	103.0047735	ns
IWB47178	7B	104.4419027	ns
IWB7711	7B	104.7166224	ns
IWB9687	7B	105.8037177	ns
IWB25633	7B	106.6234385	ns
IWB28760	7B	107.1884161	ns
IWA3928	7B	110.1859052	ns
IWB69542	7B	110.7508828	ns
IWB64750	7B	112.8478437	ns
IWB31227	7B	115.611285	ns
IWB10895	7B	115.8875224	ns
IWB3092	7B	116.1577873	ns
IWB6608	7B	116.1577873	ns
Xwmc517	7B	119.3534581	ns
IWA836	7B	122.6694222	ns
IWB8151	7B	123.2219138	ns
IWB25319	7B	126.8208	ns
IWB9384	7B	128.5259505	ns
IWB26359	7B	129.0784421	ns
IWB9261	7B	129.6466298	ns
IWB72319	7B	130.2180644	ns
IWB72939	7B	131.090216	ns
IWA4306	7B	131.6682569	ns
IWB13010.1	7B	132.5254555	ns

Marker	Chromosome	Position	Segregation distortion
IWB60959	7B	134.2114336	ns
IWB59225	7B	139.7898054	ns
IWA4309	7B	142.4392485	ns
IWB34900.1	7B	143.8930967	ns
IWB68676	7B	147.8166491	ns
IWB34981	7B	148.103999	ns
IWB47992	7B	148.39469	ns
IWB7456	7B	148.6837008	ns
IWB60879	7B	149.8814912	ns
IWA3387	7B	152.8970799	ns
IWB72683	7B	153.4751208	ns
IWB72830	7B	153.7658118	ns
IWB68215	7B	154.0548226	ns
IWB74670	7B	154.9530902	ns
IWB60899	7B	155.5448128	ns
IWB8577	7B	156.6813351	ns
IWB25083	7B	157.5742551	ns
IWA7072	7B	159.4155076	ns
IWB47204	7B	162.178949	ns

* P< 0.05
** P< 0.01
*** P< 0.001
**** P< 0.0001
***** P< 0.00001
ns indicates non-significant markers

APPENDIX B. THE LIST OF SNP MARKERS THAT CO-LOCATED TO MARKERS SHOWN IN THE GENETIC MAPS BASED ON THE RIL MAPPING POPULATION DERIVED FROM RUSTY/PI 367696

Chromosome	Marker shown in the maps	Co-located markers
1A		
	IWB12616	IWB65373 IWB6058 IWB7208IWB7944IWB9222IWB2454IWB9223 IWB8776 IWB34801 IWB12147 IWB25590 IWB16675 IWB6234 IWB6476 IWB74213 IWB71565 IWB57868 IWB47522 IWB29495.1 IWB7943 IWB74011.1 IWB13141 IWB8777 IWB34707
	IWB71424.1	IWB29206
	IWB57448	IWB8696
	IWB6172	IWB29039 IWB29562 IWB35349 IWB33789 IWB44057 IWB3087IWA8622 IWB17894 IWB44655 IWB8796 IWB28577 IWB11117 IWB31866 IWB31867.1IWA4351 IWB11098
	IWB71687.1	IWB59361.1 IWB11162 IWB71688.1
	IWB61182	IWB12612 IWB7008 IWB10730.1 IWB46642
	IWB10922	IWB10921 IWA4644IWB11203 IWB12166 IWB13009 IWB9667 IWB11301IWA4678 IWB12206IWB11053IWB71172.1IWB73271IWB71173IWB7089IWB36389IWB73615IWB59865.1
	IWB36053	IWB72128IWB5896 IWB10192.1 IWB72794 IWB7627IWB12126 IWB7351 IWB72127 IWB10932 IWB72258 IWB35266.1
	IWA414	IWB19101 IWB69805 IWB68393
	IWB7233	IWB31746 IWB67281 IWB67282 IWB7640 IWB35007.1
	IWB3519	IWB50401 IWB57361 IWB31764.1 IWB59245 IWB9029 IWB31763.1 IWB9329 IWB51995.1 IWB57360.1 IWB12172.1 IWB9541 IWB31415 IWB8188 IWB31414.1 IWB59888.1
	IWB3334.1	IWB28549 IWA6217 IWB3682 IWB31933.1
	IWB47933	IWB68107 IWB68106 IWB73417
	IWB72800	IWB66889 IWB26996 IWB72799 IWB66891

Chromosome	Marker shown in the maps	Co-located markers
	IWB47241	IWB72042 IWB6583 IWB73155 IWB10025 IWB12486IWB7300 IWB59951IWB72041 IWB7075.1 IWB43982
	IWB52279	IWB57837 IWB57838
	IWB57257.1	IWA8307 IWB34853
	IWB6962	IWB14948 IWB12189.1 IWB28360 IWB45313 IWB6784 IWB8519 IWB31787 IWB6744IWB65085 IWB50585 IWB65677 IWB25221 IWB44535 IWB44534 IWB6380IWB31380IWB27755IWB72311 IWB36350 IWB65824 IWB57485 IWB43938IWB6966IWB59609
	IWB71416	IWB71415IWB65334IWB8098IWB6933
	IWA3883	IWB11427IWB6128IWB36287IWB31862IWB7828 IWA4302 IWA7922 IWB57739 IWB65010 IWB57895IWA3884 IWB36224 IWA6887IWA7879 IWB57676IWA8520IWB9258 IWB44145 IWB73513 IWB39261 IWA4301 IWA7505 IWB34735 IWB59957 IWB35639 IWB3618 IWB46887 IWA3499 IWA3882 IWA8394 IWB9345 IWB25829 IWB25830 IWB58586
	IWB8898	IWB11660
	IWB13492	IWB64861IWA3536 IWB3507 IWB4472 IWB35080 IWB31366 IWA6985 IWB56828 IWB35436 IWB45374 IWB59094 IWA4852 IWA3538 IWB60215 IWB65705 IWB59768 IWB65314 IWB20955 IWB31652 IWB31690 IWB32307 IWA8198
	IWB15064	IWB27064 IWB15302 IWB57405 IWB14005 IWB57483 IWB45811 IWA3665 IWA8026 IWB27889 IWB12984 IWA3806 IWB14772 IWB57546 IWA498 IWB57547.1 IWB60796
	IWB8273	IWB66135 IWA4576 IWA6971IWB11893 IWB10292 IWB12595 IWA5268IWA3528 IWB10807.1 IWB12529 IWB65452 IWB17431 IWB9465 IWB16658IWA3695 IWA7945 IWA4265 IWA6972 IWB35410 IWB72825 IWB10918 IWB46963 IWB35945 IWB3707 IWB25621IWA7104 IWB56573 IWB26574 IWB35883 IWB31760 IWA42
	IWB66378	IWA490 IWA3957IWB72418 IWB6779 IWB11190 IWB31640 IWB57290IWA3955 IWA3956 IWB35364 IWB47404

Chromosome	Marker shown in the maps	Co-located markers
	IWB20695	IWB60037 IWB72053 IWB2927 IWB35117 IWB52241 IWB20671 IWB35842
	IWB35308	IWA4326 IWA4328
	IWA8070	IWB34341
	IWB11515	IWB11516
	IWB5406	IWB34656 IWB35023 IWB40078 IWA7018 IWB7921 IWB46302 IWA3820 IWB70213
	IWB25487	IWB6733
	IWB34337	IWB35039 IWB35897
	IWB11628	IWB70352IWB6769IWA4283
	IWB65763	IWB12119
	IWA7871	IWB7079 IWB11063
	IWB46385	IWA3496IWB25493IWB9588
	IWB11543	IWA3406IWB65398 IWB46448
	IWB58118	IWB28402 IWB27332 IWB58119 IWB34331
	IWB8167	IWB7965 IWB8166 IWB9545 IWB13379 IWB6354 IWB47390 IWB60784IWA3405 IWB9631IWA5493 IWA7144IWB64795IWA5534 IWB31849 IWB29087IWA3859
	IWB35531	IWB47990
	IWB6517	IWB45538
	IWB12579	IWB20654
	IWB29580	IWB29579
	IWB4075	IWB68917
	IWB35025	IWB4042 IWA145 IWA3805 IWA8482 IWB65422 IWA6042 IWA3434 IWB36087 IWA3435
	IWB11406	IWB72493IWB36711.1IWB50094
	IWB64554	IWB64553

Chromosome	Marker shown in the maps	Co-located markers
	IWB66930	IWB66931
	IWB31445	IWB60380
	IWB2751	IWA6253 IWB11057 IWB74107 IWB28698 IWB65681IWA4713 IWB26250 IWB31696 IWB59427
	IWB13639	IWB58474 IWB13551 IWB73690IWA6191
	IWB4244	IWA3409 IWB73557 IWB13385 IWB35045 IWB47703 IWB2902
	IWB61091	IWB64453 IWB33223 IWA7893IWB29244
	IWB12293	IWB7275 IWB7430
	IWA4898	IWB58979 IWA4897
	IWB6426	IWB60174
	IWB43929	IWB12340.1 IWB70021 IWB58886
	IWB30871	IWB67027 IWB45183 IWB59763.1 IWB31959 IWB31956 IWB31955 IWB31958.1 IWB26766.1 IWB26765 IWB45182 IWB58726
	IWB3413	IWB7489 IWB7490 IWB36094 IWB8643 IWB37412 IWB27546 IWB34683 IWB34872IWB7532 IWB35476 IWA8523 IWB65748 IWB9191.1 IWA7289
	IWB65294	IWB73764 IWB71744 IWB63140IWB16568 IWB60807 IWB12954.1 IWB44295 IWB45352 IWB60808 IWB28413.1 IWB7260 IWB52266 IWB39912IWA5734 IWB11979
1B		
	IWB15041	IWB10856
	IWB44730	IWB25090 IWB13538 IWB27585 IWB11290
	IWB44816	IWB52019 IWB47985 IWB47978 IWB7419.1 IWB44448.1 IWB40116 IWB66045 IWB12256 IWB73733 IWB12354 IWB59696
	IWB57219	IWB66722 IWB39279 IWB39278
	IWB12603	IWB71754 IWB10492 IWB29450.1 IWB26731 IWB68307 IWB31615 IWB6008 IWB12284 IWB52473 IWB73112 IWB10312 IWB65827 IWB35936 IWB59785 IWB17979 IWB72908 IWB12602

Chromosome	Marker shown in the maps	Co-located markers
	IWB14010	IWB12346 IWB47908.1 IWB72085 IWB65667 IWB73358 IWB72083IWB12347 IWB64131 IWB9270
	IWB65685	IWB65159 IWB65156 IWB65155 IWB2622.1
	IWB13124.1	IWB59981
	IWB58765	IWB32639
	IWB62647.1	IWB57679 IWB25424 IWB34093 IWB28467
	IWB8310.1	IWA63 IWB71166 IWB67669 IWB67670 IWB71165 IWB9977 IWB73612 IWB18010 IWB9664 IWB69778 IWB17273
	IWB72704	IWB35211 IWB33689 IWB7923 IWB7922
	IWB9932	IWB12279
	IWB9627	IWB31874 IWB47951 IWB10080 IWB31875 IWB72466 IWB6522 IWB34356
	IWB29515	IWB46853
	IWB72487	IWB9109 IWB9236 IWB73942.1 IWB63847 IWB60993 IWB33204 IWB9942 IWB9421 IWB11695
	IWB69962	IWB7840 IWB35982 IWB9645
	IWB8665	IWB68666
	IWB10753	IWB73550 IWB69254 IWB8845 IWB69668 IWB10754 IWB7660 IWB45383 IWB63556 IWB72419 IWB60713 IWB60711 IWB67163 IWB35406 IWB12252 IWB73332 IWB35128 IWB35375
	IWB63352	IWB60710 IWB28269
	IWB67741	IWB48048 IWB7314 IWB46756
	IWB14738	IWB58936 IWB10660 IWB8585 IWB47264 IWB8473 IWB8041 IWB58569 IWB28335 IWB8588 IWB10923 IWB9464 IWB63258 IWB9700 IWB7485 IWB36303 IWB11553 IWB11720 IWB7228
	7IWB205	IWB45947
	IWA6965	IWB57824

Chromosome	Marker shown in the maps	Co-located markers
	IWB39745	IWB31722 IWB63613 IWB47026 IWB51784 IWB67218 IWB63614 IWB35740 IWB58640 IWB72968 IWB34998 IWB71062 IWA580 IWB65882 IWB47024 IWB31723 IWB47025 IWB70190 IWB71413 IWB70189 IWB49800 IWB35515 IWB68271 IWB72967 IWB67968 IWB74187 IWB68771 IWB20536 IWB26169 IWB39145 IWB4322 IWA7219 IWB72756 IWB65426 IWB8100 IWB63062 IWB27146 IWB21152 IWB17346 IWB73650 IWB70284 IWB5596 IWB71064 IWB72741 IWB65799 IWB64056 IWB59775 IWB72966 IWB72742 IWB67237 IWB47585 IWB60596 IWB2664 IWB74186 IWB73256 IWA5592 IWB72755 IWB71887 IWB69022 IWB60665 IWB63945 IWB8141 IWB31721 IWB9573 IWB60860 IWB60859 IWB45552 IWB27242 IWB69882 IWB47788
	IWB73157	IWB72174 IWB6409 IWB72789 IWB7114 IWB73504 IWB9281
	IWB67338	IWB67336 IWB50463 IWB25098 IWB31677 IWB14452 IWB50530 IWA7234 IWB73015 IWB32306 IWB67337 IWB51878
	IWB40109	IWB70974 IWB46989 IWB50050 IWB71800 IWB58817 IWA3295 IWA5546 IWA5673 IWB72330 IWB69041 IWB6103 IWB8612 IWB8257 IWB72329 IWA139 IWB73662 IWB73373 IWB71717 IWB5843 IWB71369 IWB68893
	IWB65744	IWB8296 IWB71872 IWB50261 IWB6519 IWA4849
	IWB40146	IWB56493 IWB9703 IWA8081 IWB74145 IWB65091 IWA6063 IWA792 IWB10646 IWA7119 IWB6921
	Xbarc302	IWB51889
	IWB5590	IWA128
	IWB5511	IWB58266 IWB72533
	IWB10551	IWB68429 IWA4197 IWB12316 IWA188 IWB7443 IWB71512 IWB65360 IWB31711 IWB47412 IWB69496 IWB69495 IWB7992 IWB59187 IWA189 IWB47330 IWB60937 IWB31478 IWA890 IWB69494 IWB14999 IWB14021 IWA4198 IWB72532 IWB27169
	IWB46080	IWB63932

Chromosome	Marker shown in the maps	Co-located markers
	IWB2788	IWB35028 IWB35412 IWB47134 IWB47132 IWB52443 IWB27767 IWB47135 IWB61058 IWB72645 IWB27097 IWB47136 IWB5590 IWB28554 IWB11607 IWA3307 IWA5278 IWA4987 IWB44100 IWB71511 IWB69973 IWB35581 IWB67838 IWB59128 IWB45235 IWB10445 IWB17725 IWB30875 IWB34661 IWB69772 IWB11284 IWB11168 IWB62738 IWB29292 IWB35864 IWB27095 IWA7017 IWB60913
	IWB7183	IWB51971 IWB34504 IWB35239 IWA3945 IWB7324 IWB35577 IWB73484 IWB37331 IWB65731 IWB27300 IWA491
	IWB65754	IWB27762 IWB46465 IWB7180
	IWA270	IWA554 IWA4316 IWB72738 IWB59481 IWA460
	IWB66204	IWB7286 IWB72498
	IWB68866	IWB72962 IWB68864 IWB35635 IWB68865 IWB72619 IWB6521 IWB70777 IWB68867 IWB70519
	IWA4203	IWA7982 IWB72078 IWA6917
	IWB6215	IWB26949 IWB52353 IWB64848 IWB44429
	IWA1231	IWA4823
	IWB31909	IWB29159 IWA540
	IWB39291	IWB34737 IWB39290 IWA6018 IWB10066 IWB32500
	IWB73745	IWB35192 IWB71351 IWB40176 IWB20648 IWB26560 IWB73004 IWB72079 IWB34917 IWB71355 IWA7275 IWB39932 IWB68968 IWB40124 IWB73005
	IWB57391	IWB10226 IWB71530 IWB3191 IWB35474 IWB39431 IWB40125 IWB71352 IWB11968 IWB31680
	IWB73964	IWB71350 IWB3677 IWB71348 IWB71349
	IWB28518	IWB56758 IWB11261 IWB4734 IWB31653 IWB73024 IWA8474 IWB5184 IWB73016 IWB11372 IWA7002.1 IWB12327 IWB31807
	IWB71902	IWB45575 IWB71596 IWB57213 IWB27998 IWB9175 IWB71904 IWB66244 IWB47923.1 IWA7317

Chromosome	Marker shown in the maps	Co-located markers
	IWB8999	IWB10880
	IWB72552	IWB59152 IWB72551 IWB72549 IWB72550
	IWB71822	IWB75197 IWB73694 IWB35689 IWB47726 IWB72730
	IWB70038	IWB70037 IWB70039 IWB29348 IWB29347
	IWB61202	IWB64025 IWA4703IWA4939 IWB50027 IWB34848 IWB40167 IWB2681 IWB67259
	IWB7534	IWB9016 IWB64027 IWB11437 IWA4090 IWB65886 IWB7846 IWB48254 IWB48255 IWA4091 IWB7533 IWB39199 IWB51921
	IWB60916	IWB63960 IWB11589 IWB10104 IWB67865
	IWB67348	IWB73156 IWB48469
	IWB8066	IWB46336 IWB10982
	IWB35875	IWA5382 IWB5761 IWA5383
	IWB59663	IWB56771 IWB7446 IWB9781 IWB12322 IWB45213
	IWB3067	IWA4488 IWB40197 IWA8313 IWB44036 IWB8245 IWB7579
	IWB63855	IWB63853 IWB7410 IWB9208 IWB73681 IWB63852 IWB26591 IWB58887
	IWB60525	IWB66483
	IWB9764	IWB29430
	IWB64093	IWB12356 IWB2667 IWB64037 IWB64094 IWB35479 IWA3341 IWB59930 IWB10243 IWB64091 IWB64092 IWB35726 IWB7290 IWB6709 IWA255
	IWB31201	IWA5186 IWB10050 IWB11283 IWB11211 IWB12497 IWB26166 IWB45740 IWB58378 IWB3260 IWB26168 IWB26167 IWB31454 IWB65180 IWB58356 IWB4407 IWB58355
	IWB2607	IWB7976 IWB73033 IWB73032 IWB6989 IWB10621
	IWB35890	IWB11958
	IWB5074	IWB3330 IWB35958

Chromosome	Marker shown in the maps	Co-located markers
	IWB29141	IWB13447 IWB57827 IWB74776 IWB27691 IWB56525
	IWB37326	IWB13458 IWB10068
	IWB66919	IWB5855 IWB66920
	IWB12325	IWB60344 IWB12536 IWB46553.1 IWB6947 IWB46187
	IWB66189	IWB29144 IWB34335 IWB43818 IWA5448 IWB31486 IWB36598 IWB70380 IWB73882 IWB34402 IWB66196 IWA3497 IWB66195 IWB66192 IWB25498 IWB25499 IWB66198 IWB44899 IWB66191.1 IWB70151 IWB66185 IWB65905 IWB66186
	IWB60663	IWA4031 IWA7141IWB9116 IWB7872 IWB36125 IWB6213 IWB7871 IWB11390 IWB13106 IWB35340 IWB65867 IWB6777
	IWB66973	IWB63739 IWB36563 IWB29151 IWB29150 IWB12399
	IWB6805	IWB5810 IWB10454 IWB66900
	IWB57211	IWB69649
	IWB73698	IWB46397
	IWB8005	IWB64154
	IWB36293	IWB11855 IWB15640 IWB73738 IWB73736 IWB73737 IWB8840 IWA8542
	IWB7686	IWB7459 IWB8409 IWB73299IWB9182
	IWB31871	IWA7992 IWA8332 IWB73284 IWB11006 IWB11007 IWB72444 IWB35847 IWB72443 IWB36371 IWB27960 IWB69702
	IWB27085	IWB69701 IWB13473 IWB31174 IWB35119 IWB36268 IWB39347 IWB44883 IWB72561 IWB6507 IWB6619 IWB7869 IWB7870 IWB28819IWA3783 IWB7868 IWB50473 IWA2558IWA3998
	IWB57628	IWB7694 IWB31676 IWB43860 IWB59155 IWB71943 IWB57627 IWB29684
	IWB4454	IWB8096 IWB72031 IWB72029 IWB72030 IWB8097 IWB65512 IWB71885 IWB20729 IWB72033 IWB47986 IWB34935 IWA848 IWB14703 IWB71884 IWB71886 IWA3892

Chromosome	Marker shown in the maps	Co-located markers
2A	IWB9706	IWB8053 IWB4839 IWB5678 IWB7427 IWB11634 IWB34471
	IWB9772	IWB6488
	IWA5758.1	IWB2673 IWB9040
	IWB13057	IWB70716 IWB7523 IWB36253 IWB72244 IWB74944 IWB72243 IWB9931 IWB72247 IWB72245 IWB70717
	IWB68096	IWB71657 IWB15244 IWB46804.1 IWB9077 IWB27845 IWB46805IWB9079 IWB9110 IWB35151 IWB68093.1 IWB27844 IWB65272 IWB6700 IWB46800 IWB26024 IWB68094.1 IWB6721.1 IWB3405
	IWB31066	IWB35036 IWB11265 IWB70859 IWB71898 IWB20993 IWB71971.1
	IWB73657	IWB73820 IWB7641
	IWB12221	IWB72218 IWB63988 IWB72626 IWB72625
	IWB72720	IWB73487 IWB14009 IWB73151
	IWB7792	IWB11669
	IWB68947	IWB16988.1
	IWB65498	IWB52199 IWA3468 IWB7056 IWB65522 IWA3469
	IWB7398	IWB25480 IWB30883 IWB72492.1 IWB25949 IWB72490 IWB27886 IWB6671.1 IWB27885 IWB72491 IWA5340 IWB30801.1 IWB30800.1 IWA5423 IWB31328.1 IWB64569
	IWB6542	IWB35651 IWB10983 IWB64927.1
	IWB60729	IWB60728.1 IWB7706.1 IWA965
	IWB15066	IWB4006 IWB5525 IWB13159 IWB17580.1 IWA1242
	IWB6086	IWB31703 IWB7112 IWB10238 IWB36297 IWB7053.1 IWB44249 IWB31705 IWB10837 IWB6164 IWB4418 IWB48508 IWB44250
	IWB67305	IWB67308 IWB67304 IWB67306 IWB67307
	IWB67791.1	IWB67790
	IWB72462	IWB72463 IWB10811

Chromosome	Marker shown in the maps	Co-located markers
	IWB8363	IWB8362
	IWA294	IWB45777 IWA293 IWB73758 IWB25061 IWB9926 IWB71526 IWB73981.1IWB27013IWA5495 IWB50486 IWB44985 IWB71880 IWB71879 IWB8160.1 IWB8937
	IWB10760	IWB27190 IWA3569 IWB8331.1 IWB20811 IWB26960 IWB34544
	IWB32310	IWB4047.1 IWB12320 IWB28709 IWB68419IWB68420 IWB45265 IWB36149 IWA8491 IWB65847
	IWA994	IWB45445
	IWB27678.1	IWB45406
	IWA581	IWB69369
	IWA820	IWB2990 IWA336 IWB34501 IWB67490 IWA5305 IWB28385 IWB39681 IWB68556 IWB34366 IWB46662 IWB61262 IWB69340 IWB30726 IWA5273 IWB46663 IWB72435 IWA3368 IWB14023 IWB34874 IWB52548 IWA588 IWA5744 IWA4793 IWB51841 IWB65453 IWA3653 IWB34999 IWA5303 IWB35580 IWB57773 IWB72292 IWA5219 IWB45843 IWA5307 IWB73280 IWA5188 IWB74893 IWA3294 IWB57685 IWA5550 IWA7969 IWB35068 IWB46970 IWA309 IWA7464 IWB65363 IWB32405 IWB21103 IWA5272
	IWB57080	IWB62635 IWA5449 IWB11139 IWB7051 IWB10432 IWB32664 IWB64479 IWB11175
	IWB58832	IWA542 IWB35296.1
	IWA8377	IWB61299
	IWB12036	IWB33700 IWB68084
	IWB11193	IWB11796 IWB2843 IWB8088 IWB48026 IWB30740 IWB28504 IWB63995 IWB60759.1
	IWB10182	IWB8707 IWB8706 IWB32717
	IWB46244	IWA3752 IWB62594 IWA6931 IWB62592
	IWB10957	IWB72716 IWB72723 IWB73878 IWA3920 IWB10956 IWB72722 IWB6997 IWB44731 IWB72718 IWA3919 IWB73879 IWB44394.1 IWB11146

Chromosome	Marker shown in the maps	Co-located markers
	IWB5861	IWB36028
	IWB34772	IWB71497 IWB26553 IWB64480
	IWB65315	IWB35910 IWB5740 IWB73568 IWB73663
	IWB45464	IWB3601 IWB39577 IWB36400
	IWB3440	IWB7597
	IWB9488	IWB29388 IWB35139 IWB39958 IWB26483
	IWB6431	IWB34766
	IWB32878	IWB5752
	IWB45239	IWB35319
	IWB46343	IWB46050
	IWB72126	IWB72976 IWB6807 IWB44629 IWB72125 IWB10627
	IWB46290.1	IWB60386.1
	IWB39805.1	IWB7757 IWB6685.1 IWB34582.1
	IWA4493	IWA4491
	IWB33959	IWB75252 IWB70684.1 IWB13647.1 IWB62573.1 IWB32029 IWB71298.1 IWA7327 IWB27789.1 IWB10465.1 IWA6963 IWB57850.1 IWB70340.1 IWB14834 IWB44619 IWB25355.1 IWA4463 IWB44005 IWB70730 IWB44454.1 IWB9316 IWB32909
2B		
	IWB46469	IWB71940IWA3868 IWA546 IWB37705 IWB73253IWB44373 IWB2702IWA1093IWB26451
	IWB59353	IWB44381
	IWB2008	IWB70087 IWB71313 IWB39654
	IWB71587	IWB49945 IWB21394 IWB59021 IWB71586 IWB59678 IWB35359
	IWA8243	IWA4652 IWB6159 IWB36310

Chromosome	Marker shown in the maps	Co-located markers
	IWA4554	IWB71895 IWB45339 IWB35392 IWB60907 IWB69854 IWB28588 IWB45338 IWB67532 IWB13632 IWB13631 IWB68807
	IWA6893	IWB65417 IWB28589 IWA6943 IWB16695 IWB73263 IWB73250 IWB72776 IWB74618 IWB47405 IWB68761 IWB73251 IWB35421 IWB31983 IWB66020 IWB69852 IWB27354 IWB67029 IWB31982 IWB69853 IWB27355 IWA6026 IWB73252 IWB36769 IWB68808 IWB45337
	IWB46988	IWB60107 IWB45403 IWB45402 IWB63381 IWB47187 IWB65311
	IWB7072	IWB45731 IWB50337 IWB31002 IWB39832 IWB70041 IWB36124 IWB7781 IWB72307 IWB31001 IWB34324 IWB7346 IWB65326 IWB71775
	IWB72894	IWB7481IWB72760 IWB44618 IWB57346 IWB2380 IWB10024 IWB36550 IWB2338 IWB3877
	IWB74844	IWB8125 IWB74841 IWA4673 IWB7738 IWB8126 IWB8332
	IWB60118	IWB28282 IWB70581 IWB70580
	IWB5684	IWB50438 IWB6075 IWB58252
	IWB62688	IWB58252 IWB65460 IWA7030.1 IWB39369 IWB35350 IWB36727 IWB10430IWA7029 IWB4951IWB73426 IWA5560
	IWB16217	IWB32006 IWA8221 IWB32007 IWB60585 IWB32005 IWB11568
	IWB44515	IWB44605 IWB28514 IWB34871 IWB12056 IWB28515 IWB63624 IWA7076 IWB46789 IWB74180 IWB25795 IWB34613 IWB27957 IWB73197 IWB60825 IWB56586 IWB33921 IWB39220 IWB74064 IWB26224 IWB35295 IWB47398 IWB44975 IWB7335 IWB65565 IWB17890 IWB58343 IWB48351 IWB73834 IWB63655 IWB47512 IWB56587 IWB34771 IWB34545 IWB63625 IWB32296 IWA1204 IWB47399 IWB7331 IWB48352 IWB11527 IWB10670 IWB74443 IWB56514 IWB63682 IWB11184 IWB45082 IWB33642 IWB7069 IWB64803 IWB35158 IWB9540 IWB7825 IWB73030 IWB35020 IWB12063 IWB57695 IWB12041 IWB10408 IWB7334 IWB46325
	IWB26631	IWB29391
	IWA905	IWA6308 IWB74209

Chromosome	Marker shown in the maps	Co-located markers
	IWA3428	IWA6075 IWB65378 IWB45219 IWB26859 IWB35009 IWB4614 IWB3996 IWA4102
	IWB36818	IWB14689
	IWB58274	IWB9584 IWA169 IWB65623 IWB8102 IWA4606 IWB59913 IWA4605 IWB4425
	IWA5436	IWA4100 IWB4546
	IWB2692	IWA7520 IWB2691 IWB34732 IWB3357 IWB65990
	IWA3817	IWB43921 IWB74656.1 IWB25870 IWB64603.1
	IWB34576	IWB49966 IWA3995
	IWB74647	IWB60896 IWB47381 IWB39777 IWB21312 IWB21074
	IWB74518	IWB59508 IWA5256
	IWA5600	IWB71012 IWB61024 IWA7146 IWA4106 IWA6000 IWA5659 IWA7524 IWA4107 IWA4136 IWA7499 IWA5653
	IWB62579	IWA6016 IWB48056 IWB48057 IWA586 IWA587 IWA1215 IWA772 IWB2679 IWB9833 IWB69314 IWA1216
	IWB2507	IWB30844 IWA6921 IWB65488 IWA6240 IWA6948 IWA7015 IWB2458 IWA4517 IWB57693 IWB3491 IWA7195 IWA3840 IWB39200 IWB11319 IWB4321 IWB34486 IWB62651
	IWB67747	IWB34793
	IWB69363	IWA7019 IWB72986 IWB47895 IWB69329 IWB69362 IWB71212
	IWB26325	IWB51844 IWB68278 IWB39834 IWB32588
	IWB48071	IWB52584 IWB50067
	IWB60374	IWB21139 IWB48280 IWB49862 IWB21199 IWB21140 IWA4256 IWB28486 IWB30854 IWB47243 IWB35867 IWA5397 IWB48279 IWB46616 IWB70825 IWB34696 IWB73022 IWA5513 IWB30933 IWB48278 IWB27165 IWB60373 IWB27166 IWB49783 IWB47244 IWB45631 IWB59086 IWB73040 IWB62675 IWB28487 IWA5512 IWB25132 IWB70826 IWB60039
	IWB28721	IWB21466
	IWB66390	IWB6859

Chromosome	Marker shown in the maps	Co-located markers
	IWB11563	IWB12239 IWB72407 IWB32250 IWB9310 IWB64322 IWB10411 IWB65589 IWB72411 IWB32140 IWB14419 IWB45046 IWB64321 IWB52020
	IWB6515	IWB70307
	IWB52433	IWB65526 IWB6383 IWB32028 IWB67744 IWB62910 IWB32027
	IWA5413	IWB28591
	IWB68982	IWB69070 IWB62876 IWB44765
	IWB11092	IWA8478
	IWB3891	IWB47664 IWA3395 IWA4358
	IWB3192	IWB73172 IWB25798
	IWB67207	IWB31274 IWB67208
	IWB4571	IWB12298 IWB11177 IWB26189 IWB26191 IWB2982 IWB4443 IWB9247 IWB10915 IWB11451 IWB36062 IWB6270 IWB6631 IWB12230 IWB63030 IWB32165 IWB60670 IWB48248 IWB5436 IWA6453IWB15068 IWA4294 IWB2985 IWB6150 IWB8789 IWB34949 IWB63235 IWB74910 IWB49117 IWA3742 IWB28807 IWB68671 IWA3741
	IWA6122	IWB5627 IWB56896 IWB64172 IWB65989 IWB73178 IWB73960 IWB36126 IWB36140 IWB60406 IWB6567 IWB57723 IWA7371 IWA4095 IWA4096 IWB9873 IWB35840 IWB68283 IWB35839 IWB32189 IWB43934 IWB46242 IWB40156 IWB52451 IWB64245 IWB64246 IWB4424
		IWB43935IWB48012 IWB28363 IWB32190 IWB26742 IWA8295 IWB66366 IWB73961 IWB66367 IWA4098 IWA4097
	IWB8420	IWB34633 IWB8419 IWB25695
	IWB3588	IWB34658 IWB58059 IWB58061 IWB11942 IWB63970 IWB58060 IWB47959 IWB3648
	IWB36072	IWB67760

Chromosome	Marker shown in the maps	Co-located markers
	IWB67728	IWB46174.1 IWB9044.1 IWB27775 IWB73441 IWB34377 IWB67729 IWB8054 IWB72385 IWB70765 IWB61305 IWB60671 IWA7955
	IWB71878	IWA7909 IWB56915 IWA3564
	IWB39394	IWB68692
	IWB5957	IWB49828 IWB73567 IWB49827.1 IWB69430 IWB73566 IWB69431.1 IWB49829
	IWB44694	IWB48386.1 IWB58646.1 IWB29532 IWB9328
	IWB69630	IWB57664 IWB57663 IWB69628 IWB49829 IWB69631 IWB4648 IWB7050 IWA8534 IWB25868 IWB25869 IWB58747.1 IWA8449 IWB63201.1
	IWB6167	IWB72654
	IWB57292	IWB59956.1 IWB35179
	IWB6323	IWB29332 IWB11888 IWB14959 IWB57313 IWB14677.1 IWB32119 IWB26011
	IWB66266	IWB12574
	IWB2341	IWB2482 IWB7671
	IWB52447	IWB71976 IWB4865 IWB71975
	IWB11123	IWB28651
	IWB59226	IWB35156 IWB36286 IWB39104
	IWB58126	IWB8813 IWB36279 IWB10706 IWB5864 IWB56526 IWB6113 IWB46445.1
	IWB2628	IWB13680
	IWB34773	IWB26482 IWB32262 IWB50096 IWB47010 IWB46560
	IWB8894	IWB5976 IWB33668 IWB33669 IWB24984
	IWB69000	IWB68998 IWB68997
	IWB32211	IWB4318 IWB66206 IWB72277 IWB4319 IWB72278 IWB66207
	IWB7819	IWA8055 IWA4422

Chromosome	Marker shown in the maps	Co-located markers
	IWB6618	IWA3982
	IWB8157	IWB10173 IWB62759 IWB65625 IWB56582 IWB5978 IWB7106 IWB21105 IWB32143 IWB36136 IWB73565 IWB62757 IWB62763 IWB11295
	IWB7569	IWB7625 IWB12117 IWB48388 IWB32245 IWB12415 IWB66438 IWB59762 IWB69343 IWA4658 IWB7580 IWB29461 IWB34450 IWB46858 IWB31257 IWB7624 IWB14135 IWB70778 IWB65734
	IWB9733	IWB28691
	IWB8698	IWB7605 IWA3315 IWB74736 IWB11333 IWB24927.1 IWB65020 IWA988
	IWB45312	IWB68447 IWB6341 IWB15636
	IWB12598	IWB48199 IWB35507 IWB35005
	IWB8650	IWB11314 IWB11856.1 IWB13375.1 IWB6563 IWB57127 IWA5192.1 IWB60398 IWB10841 IWB11171 IWB63909 IWB46025.1 IWB8633
3A		
	Xbarc321	IWB74975 IWB60480 IWB11846 IWB29214 IWB11362 IWB3127.1 IWB10398.1 IWB67382 IWB28209 IWB27973 IWB8502 IWA447 IWB75018 IWB73895 IWB60417 IWB35638 IWB10820 IWB8501 IWB60283 IWB3850 IWB7136.1 IWB7261 IWB4691 IWB10973.1 IWB18431 IWB49840 IWB4690 IWB3128 IWB2820
	IWB36703.1	IWB11852
	IWB5950	IWB48009.1 IWB29389 IWB65500 IWB50684 IWB50683 IWB50548 IWB12993 IWB60531 IWA8280 IWB46438 IWB28726 IWB44955 IWB11084 IWB7037 IWB7003 IWB12606 IWA8587 IWB12994 IWB12170 IWB5952 IWB34333 IWB11377 IWB8658 IWB12968 IWB12607 IWB10638 IWB60530 IWB12967 IWB12225
	IWB9278	IWB29131
	IWB26667	IWA8106 IWB26668 IWA3939 IWB34361 IWA8105
	IWB8714	IWB8715 IWB14876 IWA4781.1 IWB29612
	IWB25484	IWB58561

Chromosome	Marker shown in the maps	Co-located markers
	IWB70095	IWB25465 IWB70096 IWB44091 IWB44089
	IWB73247	IWB72638
	IWB32591	IWB44601 IWB15006 IWB47000
	IWB34845	IWB44372
	IWB6837	IWA4675 IWB73640
	IWB71479	IWB63578 IWB71480 IWB71477
	IWB9991	IWB9990 IWB73757 IWB50038
	IWB46342	IWB73868
	IWB72484	IWB9076 IWB68071
	IWB39542	IWA5616 IWB20642 IWB67553
	IWB39272	IWB67857 IWB39273
	IWB37891	IWB29267 IWA6204 IWA6229 IWB48393 IWB14697
	IWB4947	IWB6891.1 IWB48477
	IWA538	IWB8262 IWB16112 IWA8590 IWB31065 IWA5617 IWB35157 IWB27368 IWA6108 IWB71668 IWB58686 IWA143 IWA4912 IWA8283 IWB29336IWB37650 IWB2801 IWA4172 IWA3498 IWA3535 IWA4913 IWB20753
	IWB27964	IWB58191 IWB71028
	IWA536	IWB66604 IWB45727 IWB68422
	IWB69157	IWB67654
	IWB72777	IWB74968 IWB74967 IWA3376
	IWB72687	IWB9725 IWB3645 IWB65798 IWA5632 IWB57248 IWA7355 IWA1279 IWB14015 IWB35097 IWB60253 IWB72560 IWA7476 IWA4917 IWB70313 IWB73850 IWA1019 IWB50023 IWB50071 IWA4883 IWB36660 IWA3929 IWB35463 IWB3210 IWB20961 IWB69595 IWB62575 IWA8061 IWA3836 IWB72686 IWB2704 IWB72075 IWA6170 IWB63064 IWB72621 IWB65564 IWB9982 IWB72652 IWA4075 IWB72763 IWA234 IWB56927 IWB67049 IWB25115 IWB8196 IWB9012 IWB72653 IWB73647 IWB65513 IWB10592

Chromosome	Marker shown in the maps	Co-located markers
	IWA8465	IWB62796.1 IWB70411 IWB72139 IWB70165 IWB10508 IWB32801
	IWB72223	IWB72224 IWA8272
	IWB66938	IWB66939
	IWB26728	IWB11027 IWB7381 IWB52157.1 IWB34172 IWB12173 IWA6914 IWA6913 IWB35534 IWB21475 IWB34552 IWB35184 IWB33344
	IWA7159	IWA7877 IWB12317 IWA5286 IWB52500
	IWB72822	IWB35578
	IWB67254	IWA8435
	IWB39719	IWB52753 IWB6177 IWB5446 IWB39720
	IWB72995	IWB72994 IWB72993
	IWB73344	IWB73345
	IWB28080	IWA4298 IWB36101 IWA4296
	IWB26279	IWB13444 IWB27647 IWB49970 IWB65934 IWB27648
	IWB10607	IWB8806
	IWB17683	IWB26056 IWB35794 IWA5596 IWA7169 IWA5419 IWB6655 IWB12852 IWB60875 IWB57435 IWB63185 IWB74979 IWB36056 IWB47989 IWA623 IWB35440 IWB35470
	IWB8584	IWB58868 IWB35917
	IWB7486	IWB68483 IWB2973
	IWB11581	IWB11580 IWB73103 IWB72897 IWB18010 IWB73102 IWB35125 IWB63055 IWB73101 IWB3798
	IWB10433	IWB6993 IWB12566
	IWB25213	IWB5927 IWB11738 IWB8645 IWB20737 IWB4110 IWB26085 IWB46039 IWB31324 IWB39922.1 IWB47680 IWB20736 IWB36105 IWB57733
	IWB31321	IWB63323 IWB52569 IWB7623
	IWB7073	IWB39724 IWB7543 IWB39723 IWB49995

Chromosome	Marker shown in the maps	Co-located markers
	IWB72058	IWB58806
	IWB72476.1	IWB70483 IWB33546
	IWB8784.1	IWB12017
	IWB44666.1	IWB29489 IWB35582 IWB35035 IWB66063.1
	IWB4391	IWB14312 IWB67246.1 IWB28841
	IWB72092	IWB67819 IWB2753 IWB11436 IWA5755IWB70196 IWB12268 IWB35872 IWB11435 IWB10770 IWB65706 IWB28780 IWB67817
	IWB73076	IWB72045 IWB73079 IWB73080 IWB7722.1 IWB73078 IWB73081.1 IWB73077.1 IWB73075.1 IWB72043 IWB72044
	IWB73267	IWA4407 IWB73266 IWB3584 IWB73716 IWB72446 IWB9186 IWB63934 IWB66168 IWB69167 IWB73715 IWB73851 IWB69399 IWB72216 IWB72217 IWB63935
3B		
	IWB46537	IWB63795 IWB8962
	IWA6038	IWB14081.1 IWB58562.1 IWB66968
	IWB66471	IWB11617 IWB7204 IWB6979
	IWB58514	IWB74350 IWB70524 IWB47239.1 IWB28481 IWB71522.1 IWB26544.1 IWB13387.1IWB72064IWB11873 IWB65347 IWB73423
	IWB69147	IWB32711 IWB47165.1 IWB69146 IWB35950 IWB6062 IWB7355 IWB73424 IWB34636 IWB56684.1 IWB71225 IWB35226 IWB8756 IWB72020IWB5790 IWB3843 IWB67769 IWB14676 IWB12193 IWB6573 IWB8745 IWB8755 IWB71813 IWB71814 IWB64176 IWB64989IWA4796 IWB67388 IWB56857 IWB12194 IWB50465 IWB3027 IWB24980 IWB25867 IWB63733 IWA4654 IWB2828 IWB73916 IWB26152 IWB62893 IWB68698 IWB3026 IWB11923 IWB75112 IWB74599 IWB6491
	IWB8528	IWB31170.1 IWB67389 IWB67771.1 IWB36021 IWB6145
	IWB4343	IWB64968
	IWB58878	IWB34624 IWB72959
	IWA5347	IWB50547 IWB70625 IWB67376 IWB60533IWB19201 IWB18164 IWB6054 IWB12253 IWB7919 IWB24979

Chromosome	Marker shown in the maps	Co-located markers
	IWB45836	IWB64166 IWB52743 IWB57156 IWB74456
	IWB6299	IWB6673
	IWB9212	IWB9415
	IWB39782	IWA3260
	IWB464	IWB8751 IWB52159
	Xcfd79	IWB74008 IWB74007 IWB45078
	IWB17577	IWB67002
	IWB25180	IWB62638 IWA7860.1 IWB2481 IWB7068 IWB37541 IWA6201 IWB48161 IWB64951 IWA6202 IWB29321 IWB59419 IWA8326 IWB64517 IWB25051 IWA6200 IWB3565 IWB13605 IWB60996 IWB26756 IWB47168 IWA186 IWB44919 IWA6185 IWB48116 IWB46612 IWB64601 IWA1266 IWB50676 IWB58793 IWB66203
	IWA3390	IWB52841 IWB52842 IWB26447 IWB52840 IWB29116 IWB6813
	IWB7234	IWB72222 IWB8803 IWB10783 IWB57061 IWB8986 IWA4838 IWB8802 IWB4907 IWB45902 IWB48217 IWB59313 IWB73520 IWB57066 IWB57065 IWB48218 IWB45903
	IWB44056	IWB47348
	IWB26916	IWB71972 IWB60598
	IWB34239	IWB34238.1 IWB35437 IWB35458 IWB39511 IWB5120 IWB6626
	IWB16995.1	IWB58218
	IWB26261	IWB28825
	IWB27781	IWB6079 IWB34153 IWB62905 IWB7439 IWB65864 IWB65924 IWA6238 IWB63252 IWB35832 IWA6920
	IWB7518	IWB12551 IWB60844 IWB67915 IWB67918 IWB9544 IWB67916
	IWB50286	IWB34161 IWA4054 IWB71531 IWB25874 IWB47020 IWB34160 IWB69999 IWA3788
	IWB34974	IWB35616 IWA4755 IWA6165 IWB9734 IWB14946 IWB71405 IWB8111 IWA4310 IWB7412 IWB36039 IWB11463 IWA7294 IWB71608 IWA4040 IWA4226 IWA1496 IWB66513 IWB43862 IWB65260

Chromosome	Marker shown in the maps	Co-located markers
	IWA628	IWB73922 IWA629 IWB27206 IWB56471 IWB73051 IWB37878
	IWB35464	IWA211 IWA210 IWB65362
	IWB72454	IWB72057 IWB72456 IWB72453
	IWB66740	IWB35493
	IWB11389	IWB74433 IWB74434
	IWB67963	IWB11913
	IWB7782	IWB45103 IWB59103 IWB45058 IWB11270 IWB35074 IWB66016 IWB35272 IWB35331 IWB45059 IWB58687 IWB36387 IWB40103 IWB45112 IWB60017
	IWB63191	IWB34827 IWB3264
	IWB10691	IWB65116 IWB67789 IWA537 IWB58223
	IWB65234	IWB26723
	IWB61144	IWB65080 IWB8616
	IWB4885	IWA898 IWB32129
	IWB27586	IWB12061 IWB9888 IWB12062 IWB56431 IWB52028
	IWB5754	IWB44228
	IWB73183	IWB73591 IWB67009 IWB3106 IWB56881 IWB73357 IWB73181 IWB73182 IWB72928
	IWB526	IWB60623 IWB3723 IWB26579 IWB11632 IWB35908 IWB11633 IWB60906 IWB10992 IWB8797 IWB9815 IWB44593 IWB8347 IWB27395 IWB25775.1
	IWB65401	IWA7035
	IWA8196	IWA7519 IWB32489
	IWB12493	IWB28943 IWB27863 IWB59348 IWB27759
	IWA239	IWB3480 IWB27905 IWB27904 IWB36172 IWB27903 IWB7903 IWB29033 IWB57595 IWA5626 IWB36679 IWB65344 IWB27902 IWB27903 IWB59708

Chromosome	Marker shown in the maps	Co-located markers
	IWB10905	IWB28150
	IWB71946	IWB71968 IWB72987 IWB73084 IWB7999 IWB34786 IWB36059 IWB14043 IWB36652 IWB46341 IWB71969 IWB72040 IWA3306 IWB60466 IWB25044 IWA3305 IWB6001 IWB28853 IWA4721 IWB58666 IWB47499 IWB31045 IWB71945 IWB28184 IWB69438 IWB64938 IWB25739
	IWB71475	IWB66519 IWB71476
	IWB46996	IWB73162
	IWB45792	IWB58358 IWB73553 IWB74409 IWA1196 IWB57136 IWB73554 IWA7225 IWB58359 IWB72037
	IWB58033	IWA773
	IWB57562	IWB11501
	IWB12466	IWA3601 IWA4457 IWB6101 IWB58890 IWA3402
	IWB7145	IWB51803 IWB74795
	IWB11838	IWB34730 IWB25787 IWB69866 IWB7838 IWB65507
	IWB63008	IWB39488 IWB46503 IWB8984 IWA81 IWB11298 IWA5209 IWB65948 IWB65726
	IWA8287	IWB9522 IWB9529 IWB35497 IWB12430 IWB16140 IWB59356
	IWB5635	IWB5637 IWB29288
	IWA3669	IWB5030 IWB18842 IWB74683 IWB12192 IWB63106 IWB68946 IWB34833
	IWB45133	IWB25336
	IWB57820	IWA3332 IWB35213 IWA8053 IWB60235 IWB60236 IWA8054 IWB52444
	IWB67102	IWB73060 IWB73061 IWB25321
	IWB65244	IWB65245
	IWB8243	IWB3832 IWB73140 IWA8354 IWB51903 IWB62764 IWA6057 IWB72472 IWB71427 IWB72473
	IWB27126	IWB8291 IWB9005
	IWB59671	IWB71096 IWB71098 IWB71097 IWB73555 IWB11997 IWB7789

Chromosome	Marker shown in the maps	Co-located markers
	IWB31790	IWB9502 IWB20636
	IWB12975	IWA785 IWB35557 IWB14720 IWB63997 IWA787 IWA786 IWB48304 IWA3454 IWB8700 IWA784
	IWB9228	IWB34424 IWB10390
	IWB73987	IWB72945 IWB72294
	IWB6446	IWB2932
	IWB27815	IWB44195 IWB48528 IWB66222
	IWB44970	IWB28240 IWB45539 IWB48183 IWB9387 IWB9386 IWB10672 IWB29374 IWB67268 IWB32795 IWB28241 IWB44969 IWB45212 IWB36533
	IWB46869	IWB10839
	IWB3434	IWB66535 IWB19046
	IWB7537	IWB10304 IWB10530 IWB74099 IWA8203 IWB9011 IWB10667 IWB34409 IWB65776 IWB74101 IWB35514 IWB44061 IWB5917 IWB10528 IWB20447 IWB28522 IWB45892 IWB58481 IWB64375.1 IWB8058 IWB4890.1
4A		
	IWA54	IWA8389
	IWB21310	IWB21402 IWB40004 IWB52625 IWB21309 IWA3993 IWB72314
	IWB67355	IWB26155
	IWB71863	IWA5363 IWB3922 IWB5591 IWB71865 IWB34759
	IWB4310	IWB4316 IWA4260 IWA4261 IWB6362 IWB47864
	IWB52170	IWB5953 IWB39302
	IWB5392	IWA115 IWB35812 IWB37681 IWB62767 IWB2614 IWA172 IWB35055 IWB14818 IWB25927 IWA3326 IWA109 IWA5652 IWB65690 IWA110 IWB50522 IWA3565
	IWA7522	IWB45447 IWA3582 IWB35538 IWB74553 IWA5498 IWB32815 IWB32816 IWA5729 IWB56922 IWA3581

Chromosome	Marker shown in the maps	Co-located markers
	IWB62589	IWB25952 IWA232 IWB75118 IWB64521 IWB70360 IWA126 IWA8416
	IWB3495	IWB72073
	IWA3302	IWA4359 IWA4253 IWB51756 IWA4254 IWA4768 IWB34384 IWB58994 IWB31312 IWA4921 IWA7107
	IWA4698	IWA4867 IWB7960 IWA7448 IWB31143
	IWB6710	IWA402
	IWB5380	IWB5379
	IWB73430	IWB71275 IWB73431 IWB71278 IWB71279
	IWA568	IWA4431 IWA4657 IWA483
	IWA4785	IWB3706 IWA4512 IWA4787.1 IWA4786 IWB36333 IWB3123 IWB21367 IWA4784 IWA8269.1 IWB3142 IWB6208 IWB28352 IWB3705
	IWB10618	IWB6880
	IWB65999	IWB59982 IWB35567 IWB58950 IWA7077
	IWB6369	IWA6193 IWB63874 IWB6533 IWB44533
	IWA4199	IWB58408
	IWB32858	IWB58650 IWB5911 IWB20842 IWB48433 IWB34445 IWB20843
	IWB63835.1	IWB9799
	IWB69809	IWB11902 IWB40107.1 IWB7283
	IWB68318	IWB34721 IWB29177 IWB26115 IWB34669 IWB7798
	IWB26773	IWB74450.1
	IWB10788.1	IWB72724 IWB2776 IWB25931
	IWB64452	IWB35289 IWB15484 IWB5865
	IWA6035	IWA4425
	IWB20951	IWB47072 IWB46985
	IWB27644	IWB59205 IWB74494 IWA7066.1 IWB44327 IWB52747.1 IWB70060 IWB44077.1 IWB27645 IWB27643 IWB60773

Chromosome	Marker shown in the maps	Co-located markers
	IWB2658	IWB28717
	IWB27701	IWB60582IWB51902 IWB28330 IWB48305 IWB48306 IWB27429 IWB73262 IWB60503 IWA811 IWB44902 IWB60583
	IWB65650	IWB31476 IWB57074
	IWA4527	IWB66725 IWA3698 IWB26405 IWB3509 IWB74680 IWB46033 IWB35078
	IWB34056	IWB11890 IWB18371 IWB27365 IWB27364 IWB8697 IWB34057 IWB61041 IWB28552 IWB9927 IWB68839 IWB34058 IWB65979 IWB11891 IWB10035
	IWB73029	IWB57119
	IWB44927	IWB65221 IWB66033 IWB65900
	IWB8059	IWB60459 IWB19112 IWB7057 IWB44391
	IWB36257	IWB11041 IWB69901 IWB6276 IWB28894 IWB45076 IWB73461 IWB7327 IWB73459 IWB73460
	IWB52321	IWB46927 IWB52323 IWB10131
	IWB73853	IWB8487 IWB60429 IWB73854 IWB10456
	IWB36617	IWB64352 IWB73328
	IWB25556	IWB64511 IWB64509 IWB11654.1 IWB73322 IWB64508 IWB73321 IWB64510 IWB73320 IWB73329 IWB34547 IWB64513 IWB73323 IWB73324 IWB8406 IWB8408 IWB7445 IWB58337 IWB37657 IWB11799 IWB10781 IWB66546 IWB64507 IWB10488 IWB71843 IWB8407 IWB16921 IWB11714 IWB73845 IWB73842 IWB70641 IWB6439 IWB32051 IWB73843.1 IWB4506.1 IWB59715 IWB11715 IWB73844 IWB11713 IWB5706 IWB4507 IWB9122
	IWB14801	IWB34028 IWB25400 IWB60304 IWB34029 IWB68682
	IWB70620	IWB63966 IWB6832 IWB9431 IWB66663 IWB68352 IWB63757 IWB13152 IWB57765 IWB7370 IWB73505 IWB59018 IWB5798
	IWB3267	IWB16109 IWB73660 IWB69029 IWB69030 IWB48471 IWB12490 IWB62597 IWB3268 IWB12459 IWB10945
	IWB57683	IWB63976 IWB27971 IWB47401 IWB63975 IWB10519 IWB52207 IWB63979 IWB34733 IWB3571 IWB26020 IWB3570 IWA7305 IWB3572 IWB3569
	IWB8552	IWB74014 IWB36777 IWB58087 IWB8778

Chromosome	Marker shown in the maps	Co-located markers
	IWB39717	IWB71808 IWB39716 IWB71809 IWB60692 IWB12593 IWB5608 IWB71810
	IWB18740	IWB68148 IWB59099 IWB57528 IWB19424 IWB25415
	IWB65913	IWB73721 IWB70769 IWB45417 IWB69888.1 IWB73203 IWB71700 IWB71978 IWB71764 IWB58574 IWB14910 IWB71319 IWA178.1 IWB57367 IWB71699 IWB59774.1 IWB65772 IWB21471 IWB26822 IWB11466 IWB57392 IWB60881 IWB34249 IWB34226 IWB59345 IWB71765 IWB31447 IWB31040 IWB71768 IWB27194 IWB12146 IWB71979 IWB31039 IWB68322 IWB34224 IWB27358 IWB6928 IWB31512 IWB34246 IWB58396 IWB8062 IWB69889.1 IWB71767 IWB34594 IWB4517 IWB26246 IWB66436 IWB71697 IWB73723 IWA4946 IWB4478 IWB71698 IWB59346
4B		
	IWB70791	IWB70795 IWB74960 IWB70793 IWB70794 IWB74226 IWB74227 IWB70790
	IWA8107	IWB32911
	IWB63893	IWB63894 IWB71830
	IWA8178	IWB62755 IWB28772 IWB39916 IWB28771 IWB73384
	IWB73117	IWB73118 IWB2333
	IWB72527	IWB44350 IWB69708 IWB30977 IWB46249
	IWB72764	IWB72765 IWB69587 IWB73835
	IWB66414	IWB72203 IWB66413
	IWB35969	IWB58052 IWB33162 IWB12150 IWB7508 IWB12149
	IWB69815	IWB66138 IWA566 IWB14853 IWB44602
	IWB73258	IWB71276 IWB71281 IWB65937 IWB72949 IWB73919 IWB4719 IWB71024 IWB70449 IWB73563 IWB11340 IWB47162 IWB7255 IWA4916 IWB70450 IWB73564 IWB66679 IWB71022.1 IWB71280 IWB70187 IWB4721 IWB73918 IWB73561 IWB47988 IWB5676 IWB4720
	IWB73832	IWB73831 IWB6877 IWB12982 IWB7934 IWB73830
	IWB9610	IWB72801

Chromosome	Marker shown in the maps	Co-located markers
	IWB73411	IWB73589 IWB73588 IWB71634 IWB72936 IWB71407
	IWB67487	IWB73915 IWB67483 IWB67485 IWB72792 IWB67486
	IWB68116	IWB6658 IWB35533 IWB17788 IWB65865 IWB30893 IWB73026 IWB46581.1 IWB73027 IWB66308 IWB72187
	IWB71418	IWB67854 IWB33116 IWB67738 IWB57527 IWB33115 IWB73701 IWB28112.1 IWB69165 IWB73300 IWB10265 IWB10821 IWB70250 IWB74042 IWB45275 IWB9492 IWB73207 IWB72884 IWB74043
	IWB36089	IWB10740 IWB11611 IWB58174
	IWB31724	IWB69182 IWB69236 IWB67330 IWB59727 IWB34149 IWB70047 IWB33140 IWB35802 IWB69559 IWB69560 IWB58216 IWB47287 IWB70063 IWB45500 IWB57889 IWB68468 IWB35870 IWB47113 IWB32941 IWB68259 IWB69181 IWB31053 IWB69705 IWB61136 IWB69938 IWB65875 IWB58977 IWB44029 IWB71186 IWB45221 IWB50249 IWB56796 IWB43967 IWB27331 IWB26492 IWB3197 IWB68348 IWB12519.1 IWB44467 IWB73930 IWB72225 IWB47430 IWB5508 IWB46169 IWB70484 IWB36179 IWB72265 IWB72288 IWB33131 IWB66082 IWB58952 IWB45794 IWB72287 IWB58933 IWB63293
	IWB36179	IWB72265 IWB72288 IWB33131 IWB66082 IWB58952 IWB45794 IWB72287 IWB58933 IWB63293
	IWB17848	IWB9392 IWB21302
	IWB35513	IWB61000 IWB15003
	IWB35380	IWB33082 IWB34629 IWB74037 IWB28989 IWB34873 IWB47207 IWA5679 IWB35352 IWB3636
	IWB70599	IWB73146
	IWB28344	IWB64316
	IWB34520	IWB36336 IWB7850 IWB9697 IWB27710 IWA3846 IWB7849 IWB20947 IWB6952
	IWB3144	IWB9230 IWB73143 IWB6948 IWB73462
	IWB69664	IWB69695 IWB71669
	IWA3396	IWB70299 IWB72778 IWB61304

Chromosome	Marker shown in the maps	Co-located markers
	IWB32927	IWA4640 IWA3609 IWA3608 IWA3611 IWB71858 IWB71859 IWB60954
	IWB73466	IWB73473
	IWB28273	IWB12276 IWB8168
	IWB71804	IWB68421
	IWB66294	IWB69711 IWB35851 IWB32903 IWB71402 IWB47175
	IWB7973	IWB3117 IWB25056 IWB73999
	IWB48267	IWB65375
	IWB66538	IWB73113 IWB7278 IWB72310 IWB36159 IWB66539 IWB47105
	IWB60004	IWB70938 IWB71666 IWB71667
	IWB73383	IWB73629 IWB17020 IWB73630
	IWB44750	IWB56768 IWB66095
	IWB7389	IWB44155 IWB39351
	IWB47537.0	IWB6506 IWB72121IWB72120 IWB71883 IWB32976 IWB45303
	IWB11229	IWB72883 IWB29648 IWB34604 IWB6828.1 IWB29649 IWB4426
	IWB75098	IWB5989
	IWB74054	IWB11859 IWB58739 IWB72184 IWA5408 IWB7266 IWB35505
	IWB3641	IWB8229 IWB57254 IWA5358 IWB50138
	IWB74794	IWB4448 IWB7044 IWB4447 IWB12222 IWA3781 IWB3246 IWA564 IWB17522
	IWA27	IWB35335
	IWB6896	IWB73485 IWB12144 IWB73486
	IWB74316135942.1	IWB3256 IWB5799 IWB6596 IWB37519 IWB6635 IWB9483
5A		
	IWB71134	IWB71133 IWB71135 IWB25755

Chromosome	Marker shown in the maps	Co-located markers
	IWB64323	IWA4445
	IWA3567	IWA3566
	IWA7361	IWA7360 IWB7817
	IWB74361.1	IWB50392 IWA8268 IWA6226.1 IWB11440 IWB5245 IWB4171 IWA6227 IWB29632
	IWB11068	IWA4970
	IWA5368	IWB35357
	IWB48152	IWB48151 IWB40035 IWB12085 IWA5615 IWA4069 IWA3811 IWA3365
	IWB68312	IWB9025
	IWA8155	IWA6287 IWB7826 IWA8154
	IWA5395	IWB47210
	IWB48524	IWB35024 IWA5295
	IWB31546	IWB17850 IWB73385 IWA3349
	IWB33251	IWB49889 IWB46277
	IWA3975	IWB65837 IWB9723 IWA5539 IWA5538 IWB65885 IWB74436 IWB45248 IWB9139 IWB9138
	IWB66579	IWB27439 IWB51874 IWB7967 IWB68868 IWB12830 IWB11474 IWB10513 IWB44194
	IWB61122	IWB47676 IWB34727 IWB35587
	IWA6036	IWB33227 IWA850 IWB71455 IWB73141 IWB52403 IWB60328 IWB26857IWA8012 IWB72698 IWA8013 IWB69498 IWB64699 IWB35711 IWA5326 IWB12120 IWB63769 IWB11110 IWB71628 IWB71630 IWB49769 IWB7558 IWB2714 IWB11700 IWB11586 IWB71627 IWB2713 IWB10451 IWB73545 IWB27684 IWB71631 IWA5327 IWB46440 IWB60329 IWB36666 IWB10452 IWB31223 IWA5330 IWB69450 IWB19015 IWB5955 IWB51790 IWB12121 IWB6585 IWB7040 IWB46074
	IWB10677	IWB46680

Chromosome	Marker shown in the maps	Co-located markers
	IWB48382	IWB9533 IWA6126 IWB33393 IWB7271 IWB74982 IWB46350 IWB60075 IWB52429 IWB20824 IWA4050 IWB36569 IWB36130 IWB5443 IWB75149 IWB3965 IWB4699 IWB59045
	IWB26864	IWB5849 IWB33444 IWA4667 IWA3313 IWB12115IWA4669 IWB34540 IWB12116
	IWB10384	IWB36264 IWB36245 IWB6074
	IWB52863	IWB52864
	IWB44434	IWB33346 IWA6949 IWB11865 IWB35355 IWB33345
	IWB17918	IWB35000 IWB9118 IWB8807 IWB65371 IWB39532 IWB66091 IWB50640 IWB75097 IWB58598 IWB3848
	IWB50162	IWA7529 IWA4299
	IWA8588	IWA7135
	IWB61032	IWB6762 IWB73631
	IWB75269	IWB72978 IWB72977
	IWB26027	IWB6273
	IWB47646	IWB33329 IWB36671 IWB10250
	IWB27298	IWB6702 IWB26710 IWB6708 IWB12467
	IWA5668	IWA3996 IWA12
	IWB63299	IWB72387 IWB72386
	IWB10966	IWB10965 IWB6184
	IWB59600	IWB62557 IWB35938 IWB9988
	IWB72998	IWB71983 IWB71984 IWB73294 IWB69159 IWB73295
	IWB59852	IWB50059 IWB71643 IWB59853 IWB71641
	IWA4205	IWB66355
	IWA5624	IWA5623 IWB52187 IWB10766IWB7746 IWB26647 IWB73200 IWB70567
	IWB6049	IWB72992 IWB73058 IWB66717

Chromosome	Marker shown in the maps	Co-located markers
	IWB33488	IWB72283 IWB72327
	IWB73502	IWB36340 IWB72425 IWB56489
	IWA7256	IWA7255 IWB11585
	IWB27510	IWB26265
	IWB72363	IWB72362 IWB72361
	IWB3232	IWB67141 IWB8349 IWB66080 IWB65128 IWB11676 IWB10909 IWB28898
	IWB14661	IWB45943 IWB6827 IWB5368
	IWB14680	IWB4543 IWB71385 IWB4836
	IWB14077	IWB9855
	IWB72152	IWB72151
	IWB60850	IWB73574 IWB60644
	IWB9800	IWB6768
5B		
	IWB47425	IWB3560 IWB33430 IWB46248
	IWB11710	IWA3436
	IWB64829	IWA5486 IWB65483 IWA7507 IWA8343 IWB28346 IWB44555 IWA5485 IWA5621
	IWB11140	IWB3561
	IWB73718	IWB34844 IWA5331
	IWB64286	IWB56529 IWB34553
	IWB37583	IWB72268
	IWB73786	IWB33287
	IWB26051	IWB46856 IWA3514
	IWB4841	IWB4020 IWB8869 IWA421 IWA332IWB33515IWA420 IWB66134
	IWB14163	IWB14332
	IWB21416	IWA4856 IWB58056 IWB5907

Chromosome	Marker shown in the maps	Co-located markers
	IWB58311	IWB7932 IWA6947 IWB47615 IWA6946
	IWB8792	IWB10350
	IWB29025	IWB58992
	IWB6012	IWA8604 IWB33248 IWB58528IWA5439 IWB3400 IWB39846 IWB65840 IWB47295 IWA5440 IWB52869 IWA8378 IWA8569 IWB43890 IWA4016 IWB21107 IWB12549 IWB44326 IWB66116 IWB49857 IWA5438
	IWB6617	IWB8358 IWB27923 IWB33409 IWB34691 IWB49864 IWB67262 IWA6987 IWB3389 IWB4368 IWB46762 IWA4400 IWA6967 IWB10779 IWB34442 IWB74739 IWB29582 IWB64498 IWB66057 IWA5281 IWA7307 IWB34843 IWB35059 IWA271 IWA4547 IWA5604 IWB8594 IWB11231 IWB35390 IWA4839 IWA5517 IWB20683 IWB48001 IWB44376 IWB59222 IWA4127 IWB60973 IWB34808 IWB45165 IWA4540 IWA7186IWB9030 IWA7096 IWB36654 IWB48052 IWB65246 IWB65912 IWA7515 IWB5537 IWB33490 IWB8593 IWA7079 IWB9094 IWB60145 IWB20682 IWA7882 IWA5730IWB34924 IWA6968 IWB39139 IWA5519 IWB39138 IWB25908 IWB39140 IWA5412 IWA4060 IWB45167 IWA5603 IWA4756 IWB15223
	IWB8397	IWB9536 IWB64551IWA396
	IWB68299	IWB71274
	IWB7200	IWB35584 IWA3707 IWB58307 IWB4516 IWA7272 IWB26887 IWB6899 IWB34781 IWB44691 IWA3706 IWB10495 IWB20936 IWB20644
	IWA4158	IWA4414 IWB70531 IWB47892 IWB21305 IWB26138 IWA8005 IWB27987 IWB29478 IWB33377
	IWB39718	IWB73671 IWB65517 IWB7194 IWB9881 IWB33255 IWB5705 IWB33437 IWB35796 IWB5806 IWB24957 IWB27185
	IWB36090	IWB36619 IWA5280 IWB64495 IWB70100IWA5279 IWB69519 IWB74026
	IWB11100	IWB67284 IWA5289 IWA4422 IWB71914 IWB11638 IWB62611 IWB71912 IWB45956IWA123 IWB33454

Chromosome	Marker shown in the maps	Co-located markers
	IWB64262	IWB33231 IWA8603
	IWA5742	IWB35030
	IWB36811	IWB9324
	IWB3560	IWB33430 IWB46248 IWA3436 IWA5486IWB65483 IWA7507 IWA8343 IWB28346 IWB44555 IWA5485 IWA5621 IWB3561 IWB34844 IWA5331 IWB56529 IWB34553 IWB72268
	IWB11879	IWB63206 IWB47848
	IWB70658	IWB65972 IWB33293 IWB65268 IWB70492
	IWB45894	IWB32971 IWB73106 IWB57415 IWB70679.1 IWB35878 IWB52780 IWB65086 IWA3985 IWA4074IWB37690 IWA5283 IWB69455
	IWB6817	IWB57484 IWB72579 IWB45663 IWB66469 IWB73111 IWA265 IWB28823 IWB44183 IWB65241 IWB45559 IWB73110 IWB57882 IWB72578 IWB9767 IWB45662
	IWB46986	IWA4222 IWB13598 IWB48223 IWB48132 IWB9038 IWA4571 IWB73416 IWB6346 IWB8758 IWB4727 IWB66311 IWB39314 IWB28625 IWB46563 IWB6188
	IWB33391	IWB33316 IWB66934 IWB36579 IWB33390
	IWB10247	IWB27412
	IWB5882	IWB29181 IWA4641
	IWB12924	IWB11179 IWB35598 IWB4569 IWB33263 IWB52612 IWA5672 IWA8187 IWB44588
	IWB20925	IWB27613 IWB7132 IWB20967 IWB6302 IWB10415 IWB6211 IWB66391 IWB10904 IWB58357 IWB10903 IWB64820 IWB7809 IWB35898 IWB58072 IWB59471 IWB65583 IWB8298 IWB33814 IWB11306 IWB6612 IWB9523 IWB34284 IWB16701 IWB28901 IWB48375 IWB34489 IWB43973 IWB33476 IWB65697 IWB60951 IWB61075 IWB26666 IWB31745 IWB69283 IWB20927
	IWA8252	IWB63264 IWB63265 IWB63263
	IWA5478	IWB11817 IWB30911 IWB35467 IWB3593 IWB25540
	IWB34313	IWA6905 IWB33507 IWB36661 IWB33509

Chromosome	Marker shown in the maps	Co-located markers
	IWB48396	IWB57214
	IWA8097	IWB46363
	IWB6687	IWB56720 IWB70159 IWB5758 IWB11074IWA6915 IWB11477 IWB13523 IWB66356 IWB8368 IWB11522 IWB27688 IWB44719 IWB35873 IWB33371 IWB61049 IWB60182 IWB12092 IWB57669 IWB36772 IWB27651 IWB33372
	IWB10635	IWB61245 IWB71533 IWB9783
	IWB18958	IWB10018 IWB46125
	IWB6063	IWB6407 IWB70387 IWB35127 IWB6852 IWB8052 IWB29205 IWB34530 IWB34918 IWA3479 IWB35621 IWB36098 IWB11813 IWB39412 IWB70720IWA6024 IWB48019 IWB47298 IWB34332 IWB6023 IWB25936 IWB52446
	IWB10135	IWB8906
	IWB69317	IWB75248
	IWB6424	IWA8395
	IWB32852	IWB21097 IWB66067 IWB56628 IWB11341 IWB36002 IWB58682 IWB35480 IWB34518 IWB2787 IWB34511 IWB2786
	IWB7415	IWB65012 IWB31717
	IWB33063	IWA5552 IWB60268 IWB46235 IWB11984 IWB9459 IWA5551
	IWB7206	IWB7441
	IWB75021	IWB33023
	IWB74046	IWB74045
	IWB6641	IWB7213
	IWB68076	IWB7405 IWB45473
	IWA4539	IWB7930 IWB48107 IWB59550 IWB36107 IWB59549 IWB47857 IWB21390 IWB7634 IWB7633 IWB34578 IWB25600 IWB44945 IWB7931 IWB73702 IWB72281 IWB8537IWA7478

Chromosome	Marker shown in the maps	Co-located markers
	IWB29397	IWB50044 IWA7872IWB36568
	IWB69475	IWB8035 IWB64502 IWB64503 IWB68202 IWB29637 IWB69510 IWB64501 IWB28146 IWB47520
	IWB72592	IWB73678 IWB73572
	IWA4185	IWB3699 IWA4184 IWA4182 IWB69025 IWA4183 IWB8581
	IWB72048	IWB72049 IWB34592
	IWB12143	IWB5765 IWB50686 IWB74826 IWB63422 IWB12142 IWA3394 IWB7080 IWB37513 IWB7359 IWB7593 IWB70782

Chromosome	Marker shown in the maps	Co-located markers
	IWB64707	IWB35993 IWB71938 IWB72667 IWB7744 IWB73816 IWB72681 IWB73814 IWB72666 IWB72503 IWB71437 IWB47069 IWB7105 IWB72680 IWB71439 IWB71438 IWB73815 IWB69972
	IWB71387	IWB75132 IWB6980 IWB64600 IWB73499 IWB5199
	IWB71821	IWB71819 IWB32973 IWB65531 IWB71818 IWB71820
	IWB44136	IWB33119 IWB44993 IWB7672 IWB12043 IWB71749 IWB45090 IWB50470 IWB26748 IWB46501 IWB10888.1 IWB34447IWA3972 IWB8173 IWB2823 IWB46655 IWB34550 IWB9382 IWB30997 IWB71748 IWB11032 IWB61247 IWB58120 IWB36006 IWB73180 IWB5837
	IWB68167	IWB64466 IWB11919
	IWB63067	IWB9424 IWB9901.1 IWB63068 IWB48112 IWB34960 IWB12106 IWB12107
	IWB74041	IWB72617 IWB72615 IWB72618 IWB72616
	IWB27453	IWB26458 IWB27369 IWB4834 IWB63462 IWB29239 IWB5599 IWB4441 IWB5663
	IWB26828	IWB26827
	IWA6211	IWA4748 IWB29675 IWB34210 IWA5454 IWA4635 IWB7719 IWB11035 IWB25892
	IWB12232	IWA22 IWB36204 IWB34704 IWB13050 IWB18951 IWB9279
	IWB67752	IWB65591

Chromosome	Marker shown in the maps	Co-located markers
	IWB7739	IWB65055 IWB73941
	IWB70408	IWB34482 IWB11661IWA3358
	IWB7836	IWB74021 IWB7835 IWB74020
	IWB65485	IWB8808 IWB7302.1 IWB68170.1 IWB5688 IWB59928 IWB52723 IWB72711 IWB65484 IWB36771 IWB73046 IWB48153 IWB65802 IWB72714 IWB36621 IWB28207 IWB27150 IWB72712 IWB10360 IWB10359 IWB18224
	IWB66258	IWB66257
	IWB71272	IWA8006 IWB63348 IWB47639 IWB64061 IWB4410 IWA8391 IWB65926 IWB47640 IWB25477 IWB73352 IWB39994 IWB28158 IWB71271 IWA4329 IWB4412
	IWB69552	IWB73829 IWB69551 IWB4803
	IWB24987	IWB47090 IWB74919 IWB28598 IWB47087 IWB20541 IWB26850 IWB46556 IWB29548 IWB45643 IWB28597 IWB44680 IWB44679 IWB29164 IWB59314
6A		
	IWB7762	IWB10814 IWB39292 IWB11785 IWB7353 IWB10458 IWB59591 IWB71875 IWB10558 IWB47842 IWB10557 IWB60891
	IWB12447	IWB11910 IWB26592 IWB33855IWB5029 IWB12448 IWB44965 IWB65570 IWB2598
	IWB9075	IWB72428 IWB6902.1 IWB37515
	IWB35466	IWB11242
	IWB72510	IWB8452
	IWA4552	IWB72905 IWB10743 IWB65474 IWB31824 IWB9288 IWB20946 IWB14410 IWB74738 IWB29603 IWB9150IWA6999.2IWB34573 IWB9287 IWB65918 IWB17902 IWB48174 IWB25242 IWB65379 IWB47076 IWB9439 IWB5854 IWB47077 IWB13112 IWB65350 IWB8061 IWB36781 IWB6871.1 IWB9985 IWA4962 IWB11711 IWA7287 IWB63698 IWB9898 IWB59995.1 IWB50019 IWA4551 IWB25243.1
	IWB28201	IWB44960 IWB7337 IWB67933 IWB29014 IWB28559 IWA51IWB13400IWA770IWB28199
	IWB33750	IWB61273 IWB10958 IWB75134 IWB71485 IWB33749 IWB27480IWA4961 IWB10710

Chromosome	Marker shown in the maps	Co-located markers
	IWB26040	IWB58142 IWB36543 IWB66218 IWB29622 IWB66602IWA8608 IWB73285 IWB44659 IWB11433 IWB10776 IWB50402 IWB59681 IWB10775 IWB66603 IWB36242 IWB6044 IWB6401 IWB66606 IWB66601 IWB66600 IWB10227
	IWB12224	IWB72039
	IWB67078	IWB63758 IWB67079 IWB58031
	IWB73265	IWA3320 IWA3319 IWA7444 IWB32523 IWB25326 IWB7442 IWB64837 IWB32524 IWB65633IWA3322 IWB56969IWA621 IWB66393 IWB71378 IWB73939 IWB73937 IWB32522 IWB72866 IWB72868 IWB44471 IWB72869 IWB65434 IWB65923 IWB72867 IWB65862 IWB35338 IWB32525 IWA5402 IWB70421 IWB73938 IWB39835 IWB10887 IWA5401
	IWB70731	IWB6111 IWB71802 IWB36291 IWB34830 IWB72983IWB74901 IWB69176 IWB27926 IWA8510 IWB2984IWB72839 IWB12513 IWB73008 IWB48232IWB69175 IWB14461 IWB72985 IWB74194 IWB11723 IWB9857 IWB58326 IWB70424
	IWB3692	IWB34957
	IWB9036	IWB10644 IWB13025
	IWB10234	IWA6311
	IWB6293	IWB72208
	IWB17589	IWB52347 IWB59351 IWB52665 IWB35130 IWB34635 IWB52666 IWB35228
	IWA7438	IWB52712 IWB39921 IWB21378 IWB29660 IWB35121 IWB25812 IWB51879 IWB49990 IWB52050 IWB39414 IWA6095 IWA5656 IWA7492 IWB65577 IWB28056IWA3782 IWB20844 IWB52222 IWA5421 IWB26704 IWA7847 IWB9334 IWB9221 IWB10857 IWA6928 IWB43905 IWB63144 IWB10774 IWA7354 IWB65773 IWB9705 IWA5376 IWB11029 IWB35256 IWB11434 IWB44856 IWB9704 IWB8871 IWB27029 IWB12060 IWB74895 IWB7152 IWB78518 IWB7175 IWA3879 IWB9144 IWA7349 IWB11484 IWA28 IWA7940 IWA4371 IWB59409 IWB10629 IWB7319 IWB59349 IWB52786 IWB36276 IWA3356 IWB27992 IWB52105 IWB7951 IWB26877 IWB9444 IWB59543 IWB21080 IWB39584 IWB35212 IWB34757 IWA4029 IWB63073 IWB59402 IWB37679 IWB34375 IWB6555 IWB65393

Chromosome	Marker shown in the maps	Co-located markers
	IWA3526	IWA3527 IWB3738
	IWB10038	IWA428 IWB74380 IWB60499 IWB62878 IWB35526 IWB57264 IWB65965 IWA8348 IWB25702
	IWB69886	IWB30925 IWB67403 IWB31234
	IWA6962	IWA3463 IWB33567 IWB39171 IWB74244 IWB52504 IWA3482 IWA8306 IWA3483 IWB35169 IWB31050
	IWB36081	IWB75285 IWB62830 IWB6191 IWB5848 IWB36195 IWB36012 IWB8206
	IWA6033	IWA6012 IWA4842 IWB8036 IWB34964 IWB62858
	IWB39473	IWB5996
	IWB9844	IWB33751 IWB33872 IWB35485
	IWB60244	IWB27445 IWB6511 IWB6286
	IWB7281	IWB10739
	IWA38	IWB36100 IWB35929 IWB65994 IWB36365
	IWB9001	IWB34914 IWA5757 IWA4036 IWB74549 IWB69855 IWB10600IWA8264 IWB10995 IWB44050 IWB39623 IWB36794IWA4035 IWB71373 IWB71372 IWB75106 IWB47270
	IWB73413	IWB73414 IWB13073 IWB58127
	IWB9468	IWB60449
	IWB33879	IWB35971 IWB14335 IWB69370
	IWB69770	IWB64875
	IWB61092	IWB45292 IWB71441
	IWB12203	IWB65198 IWB65197 IWB69637 IWB63000 IWB50538
	IWB3818	IWA504 IWB28546 IWB35685 IWA4603 IWA4602
	IWB73927	IWB58641 IWA6116 IWB57644 IWB37899 IWB35343 IWB29652
	IWB5971	IWB5419
	IWB14865	IWB64255

Chromosome	Marker shown in the maps	Co-located markers
	IWB71122	IWB35245 IWB57413 IWB71119 IWB10261
	IWB57893	IWB75127 IWB31096 IWA4691IWB35122
	IWB71956	IWB6085 IWB72197 IWB47393.1 IWB36618 IWA4918.1 IWB8923.1 IWB69846 IWB33717.1 IWB69845
	IWB73410	IWB73398 IWB32665.1
	IWA7908	IWB33695 IWB65649 IWB45430 IWB26059.1 IWB6359 IWB58370 IWB44753.1 IWB44475IWA7496.1 IWB60184 IWB57517 IWB47593 IWB72070 IWB72068 IWB59857 IWB46593.1 IWB45980IWA4699 IWB45431 IWB12277 IWB60185 IWB52129 IWB10833.1 IWB72067IWB72069 IWB48235 IWB47317 IWB14997.1 IWB25780.1 IWB10767.1 IWB8763.1 IWB73365 IWB27179.1 IWB3554.1 IWB6503 IWB74644IWA7495 IWB46592 IWB6725 IWB73478 IWB57726 IWB50034 IWB12066 IWB3463 IWB34589 IWB57516.1 IWB45981 IWB8736.1 IWB11446 IWB45429 IWB45106 IWB35026 IWB12553 IWB73750.1 IWB73686 IWB10911 IWB46594 IWB39591 IWB26640 IWB8735.1 IWA7497 IWB50130 IWB50129 IWB34398 IWB70113 IWB26613 IWB11258 IWB33552.1 IWB9067.1 IWB9319.1 IWA4697IWB48492 IWB10832.1 IWB25644 IWB8323IWB57070.1
6B		
	IWB3172	IWB10604IWB45119 IWB45121.1
	IWB6572	IWB36361 IWB6463 IWB39540 IWB8078 IWB39541 IWB73020IWB56606 IWB68662 IWB56604
	IWB6212	IWB25142.1 IWB3282 IWB56605 IWB63423 IWB71552 IWB14443 IWB71436 IWB2946 IWB57350 IWB73489 IWB3564 IWB2693 IWB10358 IWB65546 IWB63938 IWB57351 IWB59320 IWB71434 IWA3297 IWB29542 IWB71433 IWB67427 IWB29541 IWB3563 IWB71431 IWB71432 IWA3298 IWB71435 IWB67428
	IWB59377	IWB21062 IWB58008 IWB60101 IWB58009IWA7070 IWB59378 IWA8477
	IWB9057	IWB46708

Chromosome	Marker shown in the maps	Co-located markers
	IWB71329	IWB71331 IWB65148 IWB18280 IWB72322 IWB4662 IWB25035
	IWB74087	IWB28262 IWB13056
	IWB28633	IWB28634
	IWB65787	IWB52738 IWB7119 IWB57421 IWB57334 IWB52739 IWA4610 IWB6216 IWB6353 IWB69722 IWB45870
	IWB26083	IWB10163
	IWB7937	IWB60219 IWB65635 IWA4290
	IWB33652	IWA4010 IWA4011 IWB34432 IWA52 IWB32767 IWB32769 IWB63285 IWB7723 IWB59637.1 IWB59107
	IWB11642	IWB11641 IWB11643
	IWB26775	IWB37846 IWB65084 IWB36341 IWB73955
	IWB62877	IWB36095 IWB46957
	IWB59118	IWB3182 IWB12568 IWB52064 IWB57839 IWB7074 IWB11192 IWB59119 IWB57840 IWB75076 IWB72594 IWB44180 IWB59120 IWB10742
	IWB69190	IWB10716 IWB25627 IWB10351
	IWB63807	IWB43931 IWB44083 IWB33797 IWB65961 IWB33796 IWB10087 IWB33795 IWB63808
	IWB9609	IWB9354
	IWA7239	IWA1243 IWB31535 IWB5533 IWA842 IWB60404 IWA861
	IWB45612	IWA4408 IWB35555 IWB39117 IWB44230
	IWB45887	IWB69518
	IWB3473	IWA3300 IWB34422 IWB11556 IWB10625
	IWB71635	IWB43853 IWB43852 IWB7680 IWB71636 IWB73728 IWB73303 IWB68621
	IWB26716	IWB68256 IWB68254 IWB68255
	IWB71284	IWB25823 IWB10704 IWB33273 IWB74027 IWB26976 IWB35654

Chromosome	Marker shown in the maps	Co-located markers
	IWB33858	IWA4730 IWB28975
	IWB73968	IWB33618 IWB70635 IWB68130 IWA7937 IWA3501
	IWB72416	IWB72202 IWB58313
	IWA3676	IWB25217 IWB56415
	IWB29373	IWB8809 IWB29372 IWB3465 IWB35384
	IWB59925	IWB59055 IWB5941 IWB59737 IWB3608 IWB6452IWA6064
	IWB34946	IWB14722 IWB70530 IWB57022 IWB66131 IWB63057 IWB60265 IWB47313
	IWA6153	IWB28873 IWB70979 IWB36648 IWB56968IWA5504 IWB48185 IWB66246 IWB31348IWB52110.1 IWB18183 IWB48400 IWB46486 IWB60984IWA4170 IWB60288 IWB45266 IWB34780 IWA4848 IWA5225 IWA3917 IWB50447 IWB56703
	IWB47049	IWB28268 IWB33747 IWB67439 IWB25027 IWB65914 IWB69753 IWB33826 IWB71605 IWB32014 IWB71603
	IWB35737	IWB47634 IWA8165 IWA5346 IWA5345 IWB31411 IWB6932 IWB68769 IWB73415
	IWB31833	IWB12289 IWB58440 IWB35826
	IWA1251	IWB36146
	IWB68061	IWB21249 IWA971 IWA4502 IWA4501 IWB46344 IWB8492IWA755 IWB12855 IWA7962 IWA4500
	IWA5625	IWB65680 IWB31076 IWA4435 IWB65195 IWB74159 IWB34321
	IWB35946	IWB17986 IWA3289 IWB13603
	IWB45959	IWA7084 IWA3679 IWB35399 IWB57949IWA3354 IWB47281 IWB56906 IWB34839 IWB20733 IWB45958 IWB34510 IWB30825 IWA1017 IWB35401 IWB68902
	IWB50214	IWB72870 IWB25440 IWB14861IWB57917 IWB64884 IWB44917
	IWB5290	IWB71501 IWB73456

Chromosome	Marker shown in the maps	Co-located markers
	IWB63539	IWB63538 IWB13090 IWB73501 IWB74611
	IWB26622	IWB73599 IWB70007
	IWB73387	IWB73386
	IWB71780	IWB73374 IWB61094IWA283
	IWB72209	IWB71113
	IWA1263	IWB25654
	IWB33834	IWB71546 IWB35377IWA3735
	IWB72305	IWB73224 IWB73225
	IWB14152	IWB32217
	IWB5825	IWB43845
	IWA8383	IWB46624
	IWB58636	IWB25254 IWB59482 IWB58733
	IWB71618	IWB70643
	IWA404	IWB71722 IWB58494 IWB29386 IWB72325 IWA405
	IWA8064	IWB36530
	IWB26890	IWB39172 IWB47632
	IWB73204	IWB60708 IWB52227 IWB50537 IWB65276
	IWB34340	IWB7417 IWB68655
	IWB27763	IWB63554 IWB69466 IWB56963 IWB50278 IWB45524IWA7116 IWB27200
	IWB70316	IWB72471
	IWB26627	IWB31443 IWB67504 IWB3121 IWB59005 IWB57728 IWA3880 IWB73836 IWB20749 IWB26626 IWB26624 IWB69375 IWB57727IWA4244 IWB59116 IWB6219 IWB45263 IWB59006
	IWB8341	IWB68750 IWB10824
	IWB47825	IWB64004 IWB19435

Chromosome	Marker shown in the maps	Co-located markers
	IWB72523	IWB58199 IWB34443
	IWB74864	IWB4183 IWB3696 IWB68721 IWB34507 IWB44253 IWB74861 IWB44252 IWB13511 IWB74865 IWB74862 IWB13510
	IWB8425	IWB71412 IWB70379
7A		
	IWB12610	IWB26552
	IWB25834	IWB7458 IWB75056 IWB73433 IWB12369
	IWB74024	IWB9904 IWB9397 IWB67721 IWB9078 IWB65110 IWB19485 IWB71683 IWB65111 IWB58667 IWB74161.1 IWB18185
	IWA954	IWB74238
	IWB73570	IWB73571 IWB9383
	IWB47321	IWB8374
	IWB12197	IWB12020 IWB73688 IWB12198 IWB6718 IWB68545 IWB68544
	IWB59294	IWB57059 IWB64911
	IWB39676	IWB57737 IWB6198 IWB7484
	IWA3760	IWB56953 IWB52818
	IWB73665	IWB11441 IWB62921
	IWB26398	IWB74061 IWB36370
	IWB48426	IWA4386
	IWB25760	IWB32666
	IWB63867	IWB21011 IWB17515.1 IWB72710 IWB8241 IWB28082 IWB58671
	IWB60588	IWB34025 IWB7985
	IWA8492	IWB66777
	IWA4181	IWA4180 IWB6339 IWB14901
	IWB60067	IWB60068 IWA7205

Chromosome	Marker shown in the maps	Co-located markers
	IWA5258	IWB3129 IWB62609 IWB34932 IWB45866 IWB46130 IWB7104 IWB8471
	IWB12533	IWB29169 IWB65530
	IWB7752	IWB3676
	IWB60270	IWB34318 IWB43994 IWB60651 IWB43995 IWB34967 IWB34718 IWB11693 IWB60652 IWB43993 IWB50318IWA7500 IWB50319 IWB34968 IWB26683 IWB43996
	IWB8555	IWB72148
	IWA305	IWB70592
	IWB48549	IWB32122
	IWB35738	IWB48383 IWB46718 IWB49814 IWB66115
	IWB8620	IWB14782 IWA796 IWB35092 IWB50013 IWB35799IWA797
	IWB72694	IWB4178 IWB36190
	IWB35503	IWB56070.1 IWB9983 IWB9702 IWB59583 IWB62936 IWA6183 IWB34519 IWB45583 IWB39122 IWB34519 IWB45583 IWB39122IWA7472 IWB69646 IWB9049 IWB10939 IWB28701 IWB50244 IWB8022 IWB52438 IWB9602 IWB52549 IWB69937 IWB6806 IWB51943 IWB60298 IWB20679 IWB52367 IWB68081 IWB9156IWA788 IWB72880 IWB39180 IWB65015 IWB59874 IWB11089 IWA8171
	IWA208	IWB6006 IWB8231 IWB11537 IWB36528 IWB12101 IWB35659 IWB12129 IWB50557IWA4277 IWB35894 IWB21459
	IWB59123	IWA7293 IWB34725 IWB14967 IWB10876
	IWA4638	IWA4639 IWA4637 IWB11698 IWB61040
	IWB11124	IWB36186
	IWB9558	IWB4194 IWB8563 IWB7607
	IWB8935	IWB9490

Chromosome	Marker shown in the maps	Co-located markers
	IWB46770	IWB71702 IWB71703 IWB72620 IWB52135 IWB58341IWA4996 IWB72486 IWA448 IWB27404
	IWB45735	IWA4062 IWB51810 IWA4672 IWB5811 IWB11559 IWB34535 IWB8790 IWA3662 IWB65986 IWA7917 IWA8248 IWB35881 IWB21281 IWA4411 IWB29543 IWA5526 IWB33880 IWB45736 IWB21282 IWB34290 IWA4735 IWA3925 IWB26548.1 IWB31301 IWA4817 IWA4037IWB6695
	IWB29555	IWB29556 IWB7146 IWB7238IWA808
	IWB68969	IWB72890 IWB71633IWA6940 IWB68970 IWB34700 IWB68971
	IWB14692	IWB34090 IWB64111 IWB49799
	IWB4809	IWB8359
	IWB9063	IWB9062 IWB14235 IWB3470 IWB4764
	IWB8305	IWB69294 IWB52737
	IWB3803	IWB73653 IWB10968
	IWB52378	IWB74326 IWB11584 IWB57762 IWB59224 IWB10093
		IWB10552
	IWB74845	IWB61074
	IWB45179	IWB58299
	IWB69898	IWB35597
	IWA4621	IWA4620
	IWB6983	IWB25011 IWB25012.1 IWB9574 IWB17825
	IWB26081	IWB47016
	IWB71398.1	IWB72397
	IWA6115	IWB2539 IWB12588 IWB35278 IWB7189 IWB14178.1 IWB12587IWA4594 IWB48035 IWB65614 IWB46622 IWA7185 IWA4595 IWB35137 IWB48036 IWB12618

Chromosome	Marker shown in the maps	Co-located markers
	IWA866	IWA865 IWB8800 IWB34754 IWB14331 IWB14426
	IWB33997.1	IWB9343
	IWB63209	IWB72691
	IWB12246	IWA4173
	IWB73864	IWB6268 IWB72673 IWB26780
	IWB34223	IWA179 IWB5828
	IWA501	IWB3406 IWA6923IWB10682 IWB7367 IWB29001 IWB60813 IWB58668 IWB58344 IWB9146
	IWB6675	IWA7005
	IWB36793	IWB36289 IWB6132 IWB8915 IWB65289 IWB17924 IWB67930 IWB10183.1 IWB7006 IWB65291 IWB71625 IWB25497 IWB57412.1 IWA7904 IWB60246
	IWB6037	IWB52831
7B		
	IWB33121	IWB33120
	IWB46416	IWB65211 IWB65212
	IWB6919	IWB29117 IWB29118
	IWB10879	IWB66787 IWB17787 IWB65277 IWB72316 IWB45102 IWB69416 IWB69202IWB74022
	IWB27107	IWB68516 IWB57207 IWB73685 IWB27109 IWB27108
	IWA1181	IWB25434 IWB70085
	IWA4977	IWB11322 IWB58277 IWB11323
	IWA4967	IWA4966
	IWA3572	IWB3402 IWB70551 IWB27459 IWB71980 IWA7232 IWA7233 IWB49859 IWB72146 IWA3508 IWA3507 IWB3050
	IWB34204	IWB65888 IWB34206 IWB34205 IWB26214 IWB34035 IWB60479IWA518 IWB3251 IWB34207
	IWB7646	IWB66826 IWB8603 IWB33909 IWB56817

Chromosome	Marker shown in the maps	Co-located markers
	IWB11703	IWB31792
	IWB5875	IWB36566 IWB65114 IWB65115
	IWB68850	IWB34211
	IWB67435	IWB71513 IWB71514 IWB70399
	IWB35361	IWB7118
	IWB25649	IWB3173 IWA8456 IWB57670 IWB27525
	IWB5739	IWB67979
	IWB3531	IWB73107 IWA4873 IWB59235 IWB45667
	IWB72147	IWB5043 IWB46912
	IWB63035	IWB57007
	IWA7846	IWA5210 IWA5663 IWB33982 IWB33983 IWA5662 IWA3663 IWA5661.1
	IWB59735	IWA8233
	IWB51978	IWB31169 IWB21151 IWB57449
	IWB34369	IWB62994 IWB34748
	IWB4857	IWB5264 IWA881 IWB69619 IWB69305 IWB68814 IWB28367 IWB65104 IWB30874 IWB65103 IWB12878 IWB73957 IWB73956
	IWB56734	IWB63670 IWB74638 IWB61270 IWB63688 IWB34131IWA8418 IWB63369 IWB35064IWA3886 IWB5634 IWB5632
	IWB68177	IWB45035 IWB8566 IWB73858 IWB65764 IWB71523 IWB63985 IWB71357 IWB71359 IWB60430 IWB58211 IWB66868 IWB12526 IWB14836 IWB7824 IWB62732 IWA8300 IWB34768IWA7105 IWB73123 IWB10628 IWB7697 IWB4395
	IWB16218.1	IWB48336 IWB59968 IWB65369IWA632 IWB26248 IWB69152IWA8345 IWB14262
	IWB21203	IWB33961 IWB3003 IWB46739 IWB46738 IWB4352 IWB45752 IWB31460 IWB34033 IWB45718 IWB25156

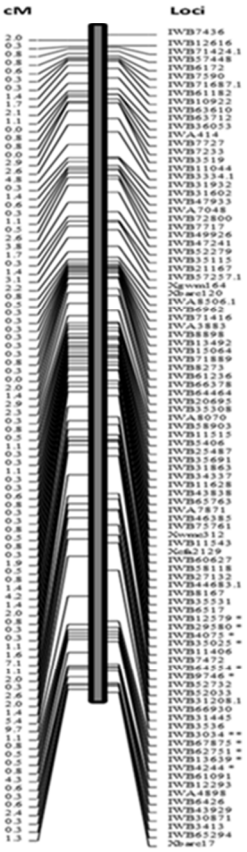
Chromosome	Marker shown in the maps	Co-located markers
	IWB60403	IWB71916
	IWB71925	IWB69052 IWB75309 IWB71838 IWB51895 IWB73909 IWB71924 IWB71926 IWB68015 IWB26171 IWB69050 IWB58270
	IWB34102	IWB45912 IWB3274 IWB4812 IWB4816
	IWB56488	IWB26679 IWB62673 IWB72331 IWB2834 IWB62671 IWB71496 IWB36651 IWB71733 IWB71582 IWB26677 IWB57075 IWB72641 IWB73338 IWB73339 IWB73340 IWB73341 IWB72960 IWB72961
	IWB35736	IWB69881 IWA354 IWB13066 IWB33945 IWB61022 IWB13479 IWA355
	IWB33623	IWB73892 IWB33622 IWB73891 IWB73890 IWB73395 IWB59338
	IWB69740	IWB8765 IWB3161 IWB72254 IWB72504 IWB8766.1 IWB72505 IWB69741IWA3987 IWB72979 IWB7521 IWB44319 IWB69449 IWB73035
	IWB73840	IWB8805 IWB12371 IWB11767 IWB71827 IWB5830
	IWB43821	IWB70890 IWB44978 IWB68837 IWB47614 IWB57668 IWB47700 IWB26969IWA8030 IWB45709 IWB68838 IWB26968 IWB68451
	IWB69447	IWB69446 IWB69758 IWB69445 IWB59199 IWB59197
	IWB60324	IWB28473 IWB56832 IWB35732 IWB45276 IWB34138 IWB45277 IWB59506 IWB75085 IWB48219 IWB34139 IWB59887IWA594 IWB34141 IWB48044 IWB34202
	IWB46260	IWB27692 IWB27833 IWB66025 IWB27696
	IWA436	IWA437 IWB5025 IWB58428 IWB58429
	IWB69178	IWB69177
	IWB75195	IWB34042 IWB46134
	IWB46046	IWB57705 IWB2717
	IWB9018	IWB7572 IWB7573
	IWB47178	IWB33975 IWB7710

Chromosome	Marker shown in the maps	Co-located markers
	IWB28760	IWB36066 IWB28758 IWB6881 IWB15590 IWB28757 IWB28759 IWB57362 IWB9899
	IWA3928	IWB27012 IWA3927 IWB29268 IWB2638 IWB9120
	IWB69542	IWB56849 IWB56847 IWB56848 IWB66049 IWB57298 IWB58468 IWB73542 IWB28513 IWB63754
	IWB31227	IWB7642
	IWB3092	IWB58112 IWB17756.1
	IWA836	IWB13136 IWB9204
	IWB25319	IWB73350 IWB73349 IWB72357
	IWA9261	IWB12159
	IWB72319	IWB60960 IWB72317 IWB72320 IWB72318 IWB35230.1 IWB20616 IWB69205
	IWA4306	IWB12171 IWB9373 IWB7845
	IWB13010.1	IWB8451
	IWB34900.1	IWB7099.1
	IWB34981	IWB31241 IWB6594 IWB59453 IWB68494 IWB52637 IWB31273 IWB63339 IWB60654 IWB43871 IWB27142 IWB34928 IWB59454 IWB68493 IWB35300 IWB27294 IWB37730 IWB71573 IWB59455 IWB48453 IWB35376 IWB48454IWA130 IWB71571 IWB71575 IWB71574 IWB71572 IWB37731
	IWB47992	IWB36230.1 IWA432.1 IWB35813 IWB35787 IWB9818 IWA431.1 IWB17743 IWB49960 IWB72479 IWB47991
	IWB7456	IWB68171 IWB47495 IWB58295 IWB7329.1 IWB63121 IWB71465 IWB20849IWA4750 IWB57797 IWB36376 IWB34699 IWA4864 IWB68612 IWB71622 IWB35653 IWB2670 IWB28666 IWB5869 IWB6544 IWB75191 IWB7134 IWB35704
	IWA3387	IWA4393 IWB56681 IWA3386
	IWB72830	IWB51787 IWA1091 IWB10844 IWB72829 IWB73725 IWB52641 IWB20596 IWB52567 IWB12168 IWB39684 IWB10477 IWB3163 IWB65152IWA3513 IWB71559

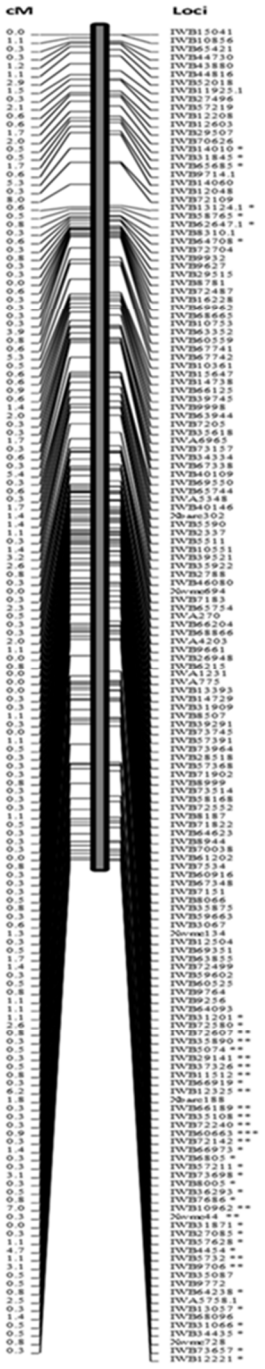
Chromosome	Marker shown in the maps	Co-located markers
	IWB68215	IWB57979.1 IWB72834 IWB7268 IWB74566 IWB47563 IWB8911 IWB8215 IWB27056 IWB27055 IWB73659 IWB45400 IWB71977 IWB33998 IWB73658 IWB35547 IWB33999 IWB12068 IWB6574 IWB68214 IWB5105 IWB3581
	IWB74670	IWB73261 IWB31089 IWB63220 IWB56659 IWB47876 IWB26595IWA3675 IWB74818 IWB57016 IWB68321 IWB64301 IWB64172 IWB71996 IWA4522 IWA4897 IWB13534 IWB64162 IWB5954 IWB73667 IWB44608 IWB58997 IWB31410 IWB14033 IWB64859 IWB8761 IWB57013 IWB60900 IWB27877 IWB69905 IWB11144 IWB6321 IWB58998 IWB11145 IWB8571 IWB27818 IWB13417 IWB7408 IWB3236 IWB12377.1 IWB5969 IWB64173 IWB64077 IWB44744 IWB64015 IWB75239 IWB74817 IWB57443 IWB27881 IWB58601 IWB50374 IWB11951 IWB11225 IWB49806 IWB29008 IWB71288 IWB59570 IWB9064 IWB27876 IWB75237 IWB39904 IWB59150 IWB48518 IWB66158 IWB34196 IWB47549 IWB28483 IWB45629 IWB62917 IWB8587 IWB31292 IWB7586 IWB68521 IWB11950 IWB45871 IWB57444 IWB12006 IWB8724 IWB64303 IWB10816 IWB10676 IWB70127 IWB64302 IWB58460 IWB13462 IWB65255 IWB8824 IWB10533 IWB58600 IWB71506 IWB31408 IWB12638 IWB34193 IWB13463 IWB74819 IWB71671 IWB56661 IWB29360 IWB25320 IWB69562 IWB46381 IWB14072IWA4888 IWB6736 IWB56660 IWB56658 IWB56657 IWB47461 IWB44297 IWB34230 IWB27414 IWB9405 IWB69904 IWB44298 IWB28121IWA7003 IWB56656 IWB65365 IWB10818 IWB9782 IWB57859 IWB50136 IWB6089 IWB7512 IWB34231 IWB13363 IWB13384 IWB4835 IWB66980 IWB59072 IWB58836 IWB26682 IWB3312 IWB12007 IWB34886 IWB10815 IWB63221 IWB48282 IWB9137 IWB8586 IWB8613 IWB58861.1 IWB8725 IWB64414 IWB13461 IWB8762 IWB39301 IWB21268 IWB28543 IWB31485IWA8312 IWB10917 IWB8469IWA7190 IWB50373 IWB25962
	IWB8577	IWB34117 IWB12557 IWB10240

APPENDIX C. GENETIC LINKAGE MAPS OF CHROMOSOMES 1A, 1B, 2A, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6B, 7A, AND 7B IN THE RUSTY×*T. CARTHLICUM* (PI 387696) POPULATION DEVELOPED USING SIMPLE SEQUENCE REPEAT (SSR) MARKERS, SINGLE NUCLEOTIDE POLYMORPHISM (SNP) MARKERS, EXPRESSED SEQUENCE TAGGED (EST), AND SEMI-THERMAL ASYMMETRIC REVERSE PCR (STRAP).THE CENTIMORGEN (CM) DISTANCES BETWEEN THE MARKERS LOCI INDICATED TO THE LEFT SIDE AND MARKERS LOCI ARE PRESENT ON THE RIGHT SIDE OF THE LINKAGE MAP.MARKERS WITH DISTORTED SEGREGATION INDICATED AS ASTERISK (*)

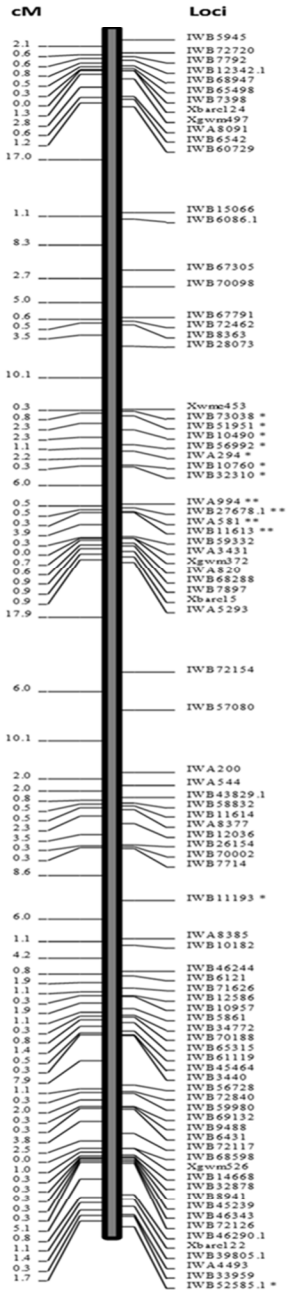
1A



1B



2A


cM
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IWB7398
Xbarc124
Xgwm497
IWA8091
IWB6542
IWB60729
IWB15066
IWB6086.1
IWB67305
IWB70098
IWB67791
IWB72462
IWB8363
IWB28073
Xwmc453
IWB73038 *
IWB51951 *
IWB10490 *
IWB56992 *
IWA294 *
IWB10760 *
IWB32310 *
IWA994 **
IWB27678.1 **
IWA581 **
IWB11613 **
IWB59332
IWA3431
Xgwm372
IWA829
IWB68288
IWB7897
Xbarc15
IWA5293
IWB72154
IWB57080
IWA200
IWA544
IWB43829.1
IWB58832
IWB11614
IWA8377
IWB12036
IWB26154
IWB70002
IWB7714
IWB11193 *
IWA8385
IWB10182
IWB46244
IWB6121
IWB71626
IWB12586
IWB10957
IWB5861
IWB34772
IWB70188
IWB65315
IWB61119
IWB45464
IWB3440
IWB56728
IWB72840
IWB59980
IWB69132
IWB9488
IWB6431
IWB72117
IWB68598
Xgwm526
IWB14668
IWB32878
IWB8941
IWB45239
IWB46343
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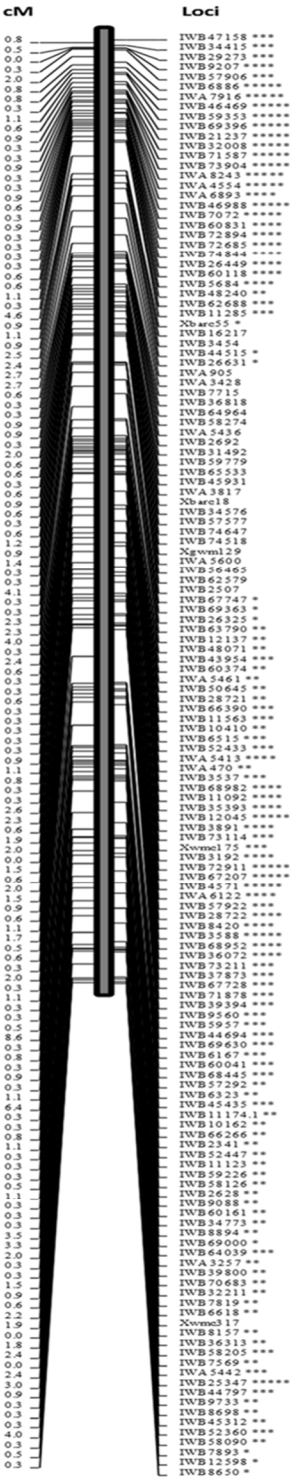
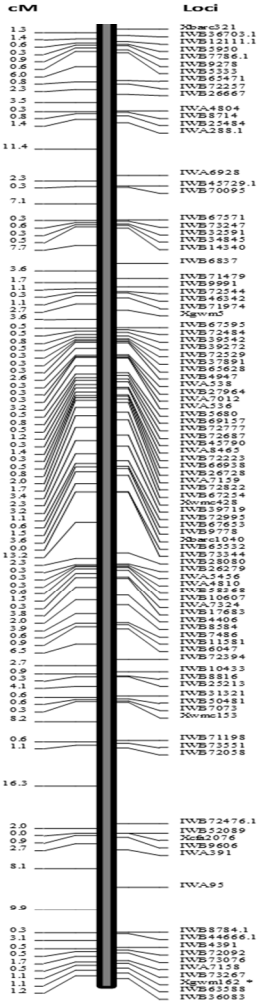
IWB39805.1
IWA4493
IWB33959
IWB52585.1 *

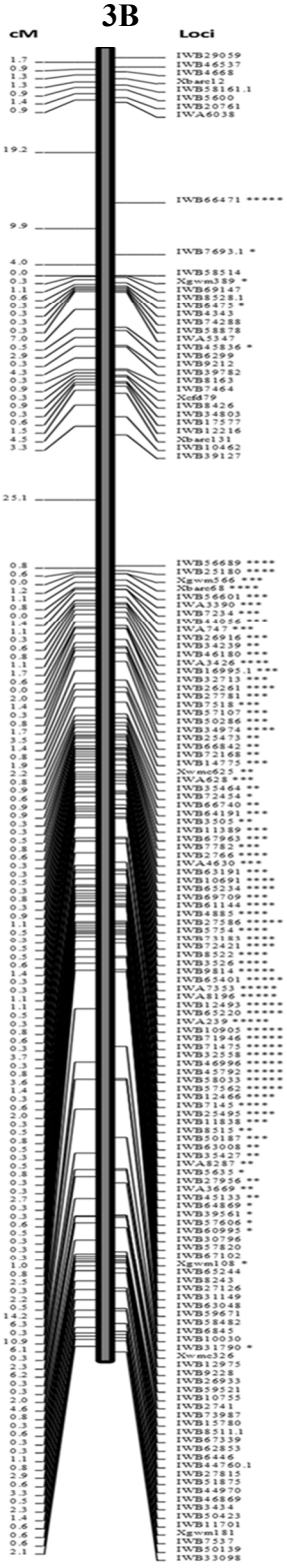
2B


cM
Loci

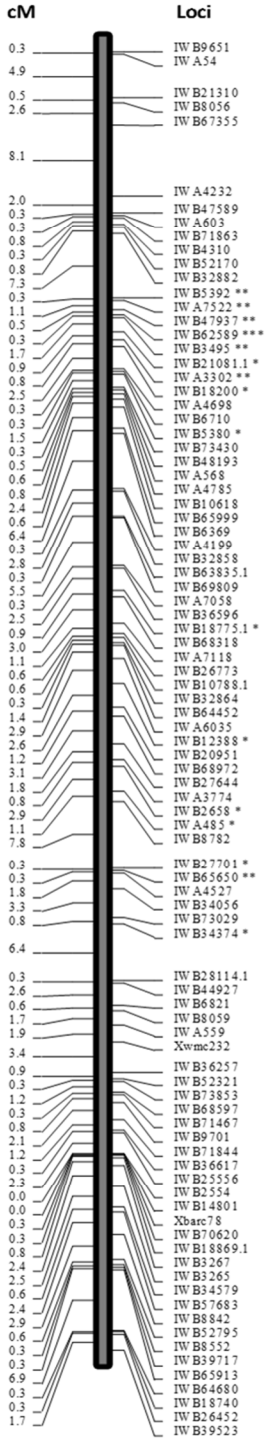
3A



3B



4A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Loci
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IWA54
4.9
0.5 IWB21310
2.6 IWB8056
IWB67355
8.1
IWA4232
2.0
0.3 IWB47589
0.3 IWA603
0.8 IWB71863
0.3 IWB4310
0.8 IWB52170
7.3 IWB32882
0.3 IWB5392 **
1.1 IWA7522 **
0.5 IWB47937 **
0.3 IWB62589 ***
1.7 IWB3495 **
0.9 IWB21081.1 *
0.8 IWA3302 **
2.5 IWB18200 *
0.3 IWA4698
0.3 IWB6710
1.5 IWB5380 *
0.3 IWB73430
0.5 IWB48193
0.6 IWA568
0.8 IWA4785
2.4 IWB10618
0.6 IWB65999
6.4 IWB6369
0.3 IWA4199
2.8 IWB32858
0.3 IWB63835.1
5.5 IWB69809
0.3 IWA7058
2.5 IWB36596
0.9 IWB18775.1 *
3.0 IWB68318
1.1 IWA7118
0.6 IWB26773
0.6 IWB10788.1
0.3 IWB32864
1.4 IWB64452
2.9 IWA6035
2.6 IWB12388 *
1.2 IWB20951
3.1 IWB68972
1.8 IWB27644
0.8 IWA3774
2.9 IWB2658 *
1.1 IWA485 *
7.8 IWB8782
0.3 IWB27701 *
0.3 IWB65650 **
1.8 IWA4527
3.3 IWB34056
0.8 IWB73029
IWB34374 *
6.4
0.3 IWB28114.1
2.6 IWB44927
0.6 IWB6821
1.7 IWB8059
1.9 IWA559
Xwmc232
3.4
0.9 IWB36257
0.3 IWB52321
1.2 IWB73853
0.3 IWB68597
0.8 IWB71467
2.1 IWB9701
1.2 IWB71844
0.3 IWB36617
2.3 IWB25556
0.0 IWB2554
0.0 IWB14801
0.3 Xbarc78
0.3 IWB70620
0.8 IWB18869.1
2.4 IWB3267
2.5 IWB3265
0.6 IWB34579
2.4 IWB57683
2.9 IWB8842
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0.3 IWB8552
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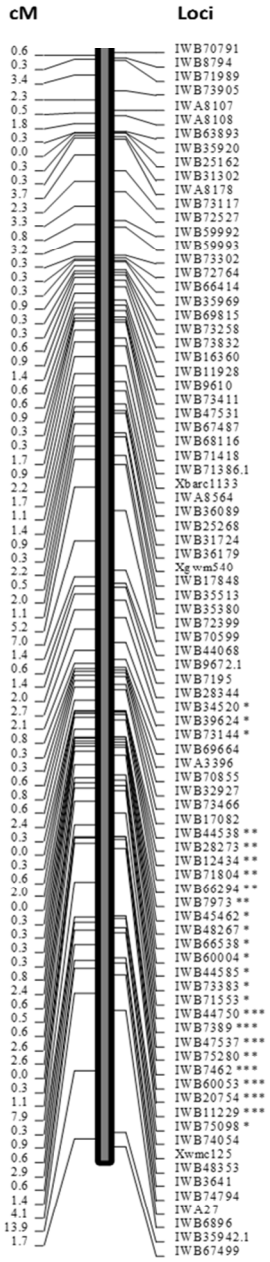
IWB39523

4B


cM
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3.4 IWB71989
2.3 IWB73905
0.5 IWA8107
1.8 IWA8108
0.3 IWB63893
0.0 IWB35920
0.3 IWB25162
0.3 IWB31302
3.7 IWA8178
2.3 IWB73117
3.3 IWB72527
0.8 IWB59992
3.2 IWB59993
0.3 IWB73302
0.3 IWB72764
0.3 IWB66414
0.9 IWB35969
0.3 IWB69815
0.3 IWB73258
0.6 IWB73832
0.9 IWB16360
1.4 IWB11928
0.6 IWB9610
0.6 IWB73411
0.9 IWB47531
0.3 IWB67487
0.3 IWB68116
1.7 IWB71418
0.9 IWB71386.1
2.2 Xbarc1133
1.7 IWA8564
1.1 IWB36089
1.4 IWB25268
0.9 IWB31724
0.3 IWB36179
2.2 Xgwm540
0.5 IWB17848
2.0 IWB35513
1.1 IWB35380
5.2 IWB72399
7.0 IWB70599
1.4 IWB44068
0.6 IWB9672.1
1.4 IWB7195
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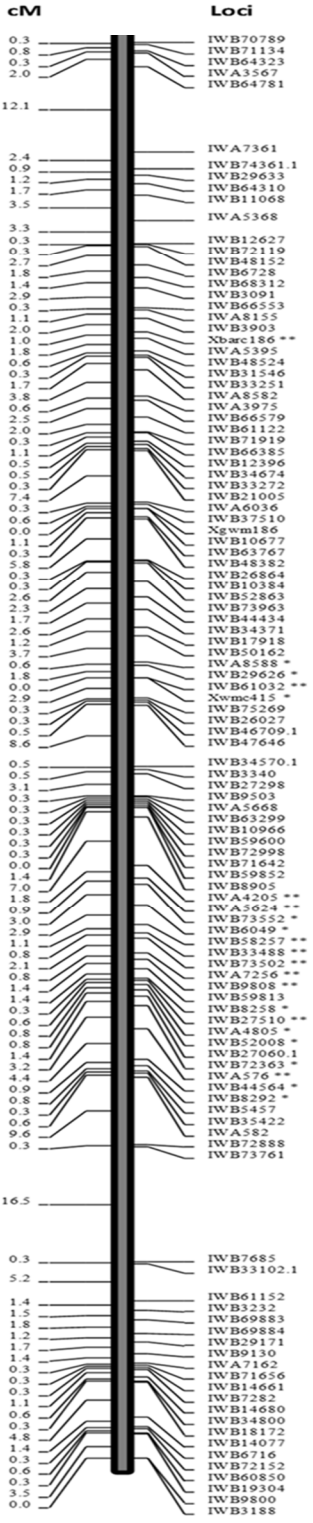
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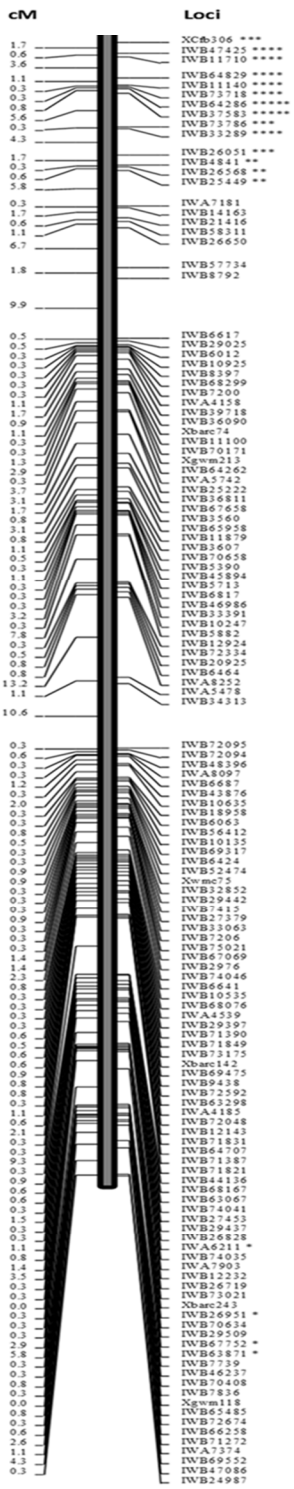
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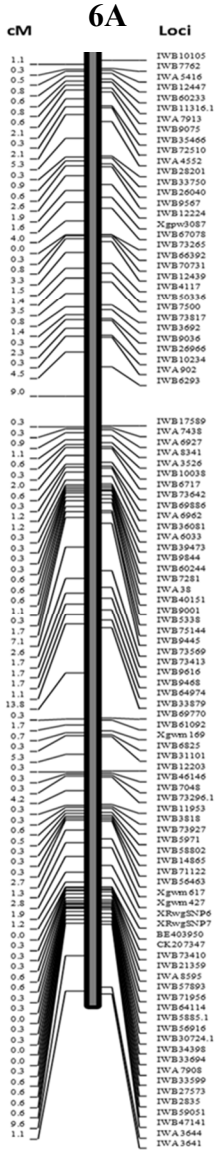

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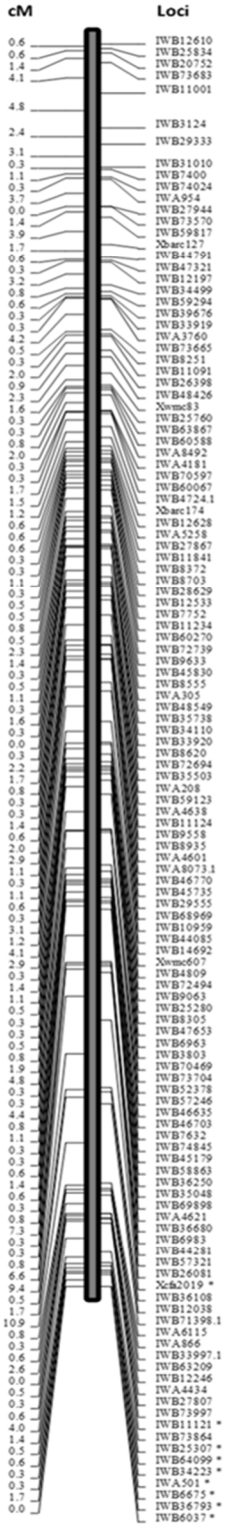
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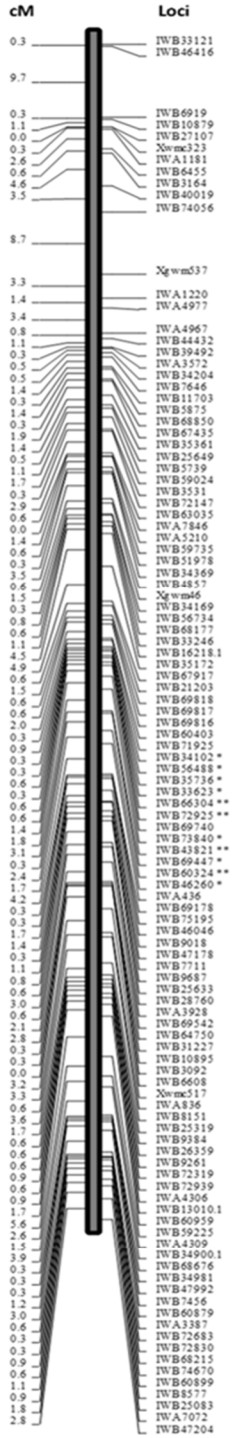
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