ABSTRACT

| Title of Document: | SCAB RESISTANCE QTLS ARE ASSOCIATED WITH QUALITY AND AGRONOMIC TRAITS OF SOFT RED WINTER WHEAT |
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Fusarium head blight (FHB) is a devastating fungal disease affecting *Triticum aestivum* crops worldwide. While many quantitative trait loci (QTL) responsible for FHB resistance have been reported, some widely used sources are from exotic cultivars that may carry undesirable alleles linked with resistance. Ning 7840, a Chinese hard red spring wheat, contains a major FHB QTL on the 3BS chromosome, along with two minor QTL on the 5A and 2DL chromosomes. Ning 7840 was crossed with Pioneer 2643, a soft red winter wheat, to create 86 recombinant inbred lines. The effect of the Ning 7840 alleles on agronomic traits and milling and baking quality traits was examined over three growing seasons in Maryland. While the 3BS QTL was not associated negatively with other traits, the 2DL and 5A QTL were. This suggests the introduction of FHB resistance QTL on 5A and 2DL into soft red winter wheat may negatively affect agronomic and quality traits.

SCAB RESISTANCE QTLS ARE ASSOCIATED WITH QUALITY AND AGRONOMIC TRAITS OF SOFT RED WINTER WHEAT.

By

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Thesis submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of Master of Science 2011

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Chapter 1: Literature Review

Fusarium Head Blight

Fusarium head blight (FHB) is a devastating fungal disease which occurs in cereals, including wheat (Triticum aestivum), barley (Hordeum vulgare), oats (Avena sativa) and sorghum (Sorghum bicolor). In wheat it is also known as scab, Fusarium blight, ear blight, tombstone scab, pink mold, and white heads. Fusarium head blight occurs throughout the world wherever wheat is grown (Sutton 1982). It was first noted in England in 1884 by W.G. Smith, and in 1891 it was reported in the United States by Arthur and Chester, independently. FHB causes economic losses and grain contamination. Between 1991 and 1996, scab caused yield losses estimated at 378 million bushels to wheat growers in the United States (McMullen et al. 1997). Fusarium Head Blight is caused by a number of species in the genus *Fusarium*, including Fusarium graminearum, teleomorph (Giberella zeae), F. acuminatum, F. avenaceum, (teleomorph G. avenacea), F. crookwellense, F. culmorum, F. nivale (syn. Michrodochium nivale; teleomorph Monographella nivalis, syn. Calonectria nivalis), F. equiseti, F. moniliforme, F. oxysporum, F. poae, F. proliferatum, F. pallidoroseum (syn. F. semitectum), F. sambucinum, F. sporotrichiodes, F. subglutinans, and F. tricinctum. The leading causal species in North America is Fusarium graminearum Schwabe (teleomorph Giberella zeae), while other geographic areas have reported different leading causal fungi (Sutton 1982; Parry et al. 1995; McMullen et al. 1997).

Epidemiology of FHB in wheat

Giberella zeae is a homothallic ascomycete capable of outcrossing. Throughout corn growing regions of the United States, corn debris provides the major source of inoculum (Sutton 1982). Crop residue may contain mycelia and perithecium, while mycelia and spores can overwinter on seed (Khonga and Sutton 1988; Fernandez and Fernandes 1990). The primary inoculum is found in the form of airborne ascospores produced by perithecia and macroconidia produced by mycelia. Rainfall is needed for the maturation of the ascospores and conidia, but it is not needed for dispersal (Paulitz 1996). The ascospores are released due to hydrostatic pressure from increased humidity and are ejected onto the heads of wheat growing in the field. Maximal discharge occurs 6-9 days after the production of perithecia and coincides with high relative humidity. The optimal temperature for infection varies depending on the individual species. Optimal F. graminearum development occurs around 26.5°C (Anderson 1948; Tschanz et al. 1976). Most infection occurs during anthesis, with hyphae penetrating the ovaries, glumes, palea, and lemma (Pugh et al. 1933; Pritsch et al. 2000; Wanyoike et al. 2002; Bushnell et al. 2003). The presence of anthers may prevent infection, but has also been reported to promote growth of the pathogen by providing more tissue for the fungus to colonize (Sutton 1982). Once infected, perithecia and mycelia are produced and spread up and down the head (Pugh et al. 1933; Parry et al. 1995). Seed which has become infected will show the characteristic blight symptoms of FHB.

Symptoms

Infection of FHB occurs in the flowers and spreads throughout the head. The symptoms are readily apparent prior to senescence. Beginning at the base of the spreading upwards the spikelet becomes bleached. Pink mycelia or black perithecia may grow on the diseased spikelet. Severely infected heads may be short and dwarfed with closed spikelets. Diseased kernels become shriveled and bleached or pink, weighing much less than healthy kernels (Parry et al. 1995; McMullen et al. 1997).

Effect

Fusarium head blight causes kernel damage, yield loss, and mycotoxin contamination. Between 1991 and 1996, FHB caused yield losses estimated at 378 million bushels to wheat growers in the United States. Infected kernels may become shriveled, bleached, and contaminated with dangerous mycotoxins. These mycotoxins include tricothecenes (deoxynivalenol) and estrogenic mycotoxins (zearalenone) (Neish and Cohen 1981; Desjardins and Proctor 2007). Deoxynivalenol (DON) is a protein biosynthesis inhibitor. Zearalenone (ZEA) is the primary estrogenic mycotoxin responsible for infertility and breeding problems in swine (Forsyth et al. 1977; Vesonder and Hesseltine 1981).

Control

There is no single method of control which is completely effective, so a variety of management methods is necessary (Bai and Shaner 1994; McMullen et al. 2008). Management methods include fungicides, resistant cultivars, and biocontrol. The cultural practices of tillage and avoiding crop rotations of corn (*Zea mays*) before

wheat are suggested methods for controlling inoculum source and spread (Dill-Macky and Jones 2000). In Maryland a corn-wheat-soybean (*Glycine max*) rotation is popular, as it allows three crops, instead of two, to be grown in two years. No-till methods of planting these crops have become more popular in recent years, as they keep the soil intact and prevent erosion and run-off. Unfortunately, no-till methods may leave corn and wheat residue behind, providing a habitat for the fungus to overwinter. While research has been done which shows promise concerning biocontrol methods to combat FHB, no method has yet been produced commercially (Leonard and Bushnell 2003).

Triazole fungicides are effective against FHB. These fungicides work by inhibiting C14-demethylase, a chemical that functions in the production of sterols, which are necessary in the proper development of cell walls in the fungus. Triazoles currently approved by the Environmental Protection Agency (EPA) are prothioconazole, metconazole, and tebuconazole (McMullen et al. 2008). These are available in Proline (prothioconazole), Caramba (metconazole), Folicur (tebuconazole), Prosar-o (prothioconazole + tebuconazole), as well as other commercial forms. Fungicides must be applied just before infection or during early infection in order to be most effective. The recommended application time for Proline is at 50% flowering (Feekes growth stage 10.5.2). All of the triazoles have preharvest application restrictions of 30 days.

Wheat Genome

Wheat has a complex genome. It is comprised of over 16,000 Mb, 80% of which is redundant. It is a hexaploid which behaves as a diploid (2n=6x=42). Because of this complexity, less is known about the wheat genome as a whole when compared to other plant species' genomes. The wheat genome is comprised of three diploid genomes- designated as A, B, and D (Smith 1995).

Quantitative Trait Loci (QTL)

Genetic resistance to FHB is one of the strongest methods of control at present, although no cultivar exists which is 100% resistant. FHB resistance presents itself as a quantitative trait. The term quantitative trait locus refers to an area of a genome associated with a continuous trait- one that varies in degrees of expression, as opposed to Mendelian traits, which are qualitative. Zhou et al. (2003) showed the distribution of the percentage of scabbed spikelets of an F2 population derived from a cross between an FHB resistant cultivar, Ning7840, and a susceptible cultivar, Wheaton, showed a normal distribution.

Sources of Resistance

A number of quantitative trait loci (QTL) have been identified which provide resistance to FHB. Three widely used QTL have been identified from the cultivar Sumai 3. They are located on the 3BS, 5A, and 2DL chromosomes (Gupta et al. 2000; Mardi et al. 2005). Anderson et al. (2001) found that the QTL located on 3BS was responsible for 41.6% of the FHB resistance in Sumai 3. They also showed that the 3BS QTL was responsible for resistance to fungal spread, while the 5A QTL controlled initial fungal infection. Sumai 3 is a widely used source of resistance with many derived lines being used in wheat breeding programs (Liu 1984; Wilcoxson 1993). One of those derived lines is Ning 7840, a Chinese hard red spring wheat. Ning 7840 contains all three of the FHB resistance QTL from Sumai 3 (Buerstmayr et al. 2009).

Genetic Markers

Genetic markers have been extremely useful in wheat breeding. Using traditional breeding methods to select traits in wheat breeding requires a lot of time and resources. Wheat goes through one growth cycle each year. It is costly to grow many different breeding lines only to select a few to advance to the next generation. Using markers, it is possible to screen many lines quickly. This is done by sowing many seeds (obtained from different breeding lines) in trays and performing DNA testing on the leaves to select which lines to advance. Markers make it possible to detect differences in DNA between cultivars that otherwise may or may not be visible. Phenotypic markers are physical differences in the organism that correspond to the underlying responsible DNA. Molecular markers, on the other hand, have the ability to detect DNA differences between organisms which are not phenotypically expressed or easily identifiable. Phenotypic evaluation requires time and resources that could be conserved using genetic marker assessment techniques (Bai and Shaner 1994, Rudd et al. 2001). There are a number of different marker associated techniques available in wheat breeding, including single nucleotide polymorphisms (SNPs),

restriction fragment length polymorphism (RFLPs), simple sequence repeats (SSRs), and diversity arrays technology (DArTs).

Simple Sequence Repeat Markers (SSRs)

Simple sequence repeats (SSRs), or microsatellites, are a type of genetic marker comprised of sequences of repeating DNA base pairs. The number of times the sequence is repeated may vary between alleles. This characteristic makes it possible to determine which parent supplied the SSR. Using SSRs located near the significant QTL makes it possible to determine whether or not the QTL has been passed on to the progeny. SSR markers developed for wheat (Song et al. 2005, Kolb et al. 2001) have previously been used successfully for FHB resistance breeding.

Wheat Classes

The USDA recognizes six distinct classes of wheat: durum, soft white, hard white winter, hard red winter, hard red spring, and soft red winter (Wheat Foods Council 2010). Wheat from each class is suited to a different end use or uses. Hard red spring wheat, named for its hard endosperm, red bran color, and its growing season, is used primarily for bread, due to its high protein and strong gluten. On the other hand, soft red winter wheat, which has a soft endosperm, red bran, and requisite vernalization in order to express its reproductive growth stages, is used for making products that require low protein content, such as cookies, pretzels, and crackers. The end uses for the flour from different classes of wheat often result in the different classes of wheat having very different ideal traits. Even within a class, two cultivars

may have different end uses. For example, gluten quality is a determinant in whether a particular soft red winter wheat may be used for pastries or crackers. Crackers need strong gluten, while pastries use flour with weak gluten. (Wheat Foods Council 2010)

Agronomic traits

Test weight

Test weight is correlated with milling quality (Schuler et al. 1995). It is measured in pounds per bushel in the United States. Lower test weight may indicate shriveled or sprouted kernels. However, according to the US grading system for wheat, hard red spring wheat must be at least 58 pounds per bushel to meet grade 1, while soft red spring must be at least 60 lbs per bushel. This is because hard red spring wheat tends to have lower test weight than most of the other classes.

Plant Height

Some traits are advantageous to all classes. For instance, height is a very important trait for wheat breeders. Shorter plants typically results in less lodging. Lodging, or the plants falling over, can be the result of either plants that are too tall or as frequently is the case, it can occur when too much nitrogen is supplied to the crop It is often exacerbated when heavy rains or winds occur. It ultimately results in lowered yield because it is much hard to harvest wheat with a combine when its heads are inches off the ground. Wheat cultivars used to be much taller than they are today. This is because Norman Borlaug, during the mid-twentieth century, developed semidwarf wheat cultivars. Because of the increased yield from his research and its global

impact, Dr. Borlaug is credited with saving over a billion lives worldwide (Easterbrook 1997).

Heading date

Heading date is another important trait, which may vary widely between classes of wheat. Flowering is controlled by vernalization, photoperiod, and earliness *per se* genes (Lewis et al. 2008). Spring wheat usually heads much earlier from the date of planting, because it does not undergo vernalization. Winter wheat must be planted before the winter, but is not harvested until the late spring. Earlier harvesting in winter wheat is a helpful trait, however, since many farmers follow winter wheat with soybeans.

Grain Yield

Grain yield may vary greatly depending upon genetics and environment. Environmental conditions which may affect yield include local conditions where the wheat was planted, due soil and water conditions (Major et al. 1988, Vaughan et al. 1990). Yield may be reduced due to pathogens, lodging, or even pests in the field, such as birds and deer.

Milling and Baking Quality Traits

Specific quality traits used to determine the quality of soft red winter wheat include softness equivalent, flour yield, flour protein, water retention capacity, lactic acid absorption, and sucrose solvent retention capacity (SRC).

Flour yield

Flour yield is the measurement of how much endosperm there is in the kernel which can be separated from the bran. It is measured as the percentage of flour per weight of grain milled. Larger flour yield is desired by the milling and baking industry and has been correlated with larger starch granules and more total starch (Gaines et al. 2000).

Flour protein

Flour protein relates to the rheological properties of dough (Uthayakumaran et al. 1999). Soft red winter wheat has low flour protein, allowing dough to absorb less water. This creates a softer dough more suitable for cookies or pastries. Hard wheat, on the other hand, has higher amounts of protein in the flour, which lends itself to bread making (Smith 1995). There are four different types of protein found in kernels of the Triticeae tribe. They are albumins, globulins, prolamins, and glutelins (Eliasson and Larsson 1993). Prolamins and glutelins form glutens. In wheat, gliadin is the prolamin, while the glutelin is glutenin. Together, gliadin and glutenin make up the gluten found in wheat flour.

Softness equivalent

Softness equivalent is determined by break-flour yield. Break-flour yield is the proportion of flour produced by the first break roll in the mill to the total amount of flour produced. It is an appropriate method for softness equivalent because it is an

indicator of the hardness of the wheat being milled. Softer wheat produces more break flour. This is because harder kernels have a stronger adhesion between starch and protein, causing resistance to fracture (Anjum and Walker 1991). Soft kernel texture is associated with larger starch granules, which form a more loosely compacted endosperm than in harder wheat, which has less surface area for bonding with other endosperm components (Gaines et al. 2000).

Solvent Retention Capacity

Solvent Retention Capacity is an influential trait with regards to the baking quality of flour. Higher solvent retention capacity causes flour to hold onto water more strongly, causing a longer baking time and a tougher end product (Guttieri et al. 2004). Low water-holding capacity is desirable in soft wheat flour (Faridi et al. 1994). Solvent retention capacity is measured in water retention capacity, lactic acid SRC, sucrose SRC, and sodium carbonate SRC (Bettge et al. 2002). Water retention capacity is a measure of the overall solvent retention capacity. Sodium carbonate SRC is determined by the amount of damaged starch created during the milling process. Good quality soft red winter wheat is low in damaged starch. Sucrose SRC is determined by the amount of gliadin and pentosan in the flour. Lactic acid absorption is a predictor of soft wheat flour gluten strength. Lactic acid absorption is important to know in order to determine the proper end use of the flour, as it is associated with glutenin characteristics (Slade and Levine 1994, Gaines 2000). Both cookies and crackers are made from soft wheat, but crackers require a strong gluten, while the best cookies are made from flour with weaker gluten.

Interclass hybridization

Many FHB resistance breeding programs rely on interclass hybridization. The new genetic combinations available may improve resistance to FHB, but the vastly different traits between two classes may have a negative effect on quality. In addition, Sumai 3 derived lines, which are commonly used, are exotic cultivars suited to a different environment. Agronomic as well as milling and baking quality traits may be affected by the introduction of FHB resistance. This could be due to the source of FHB resistance, linkage drag, or a combination of both. Linkage drag occurs during breeding when two genes are linked, but only one of them is desired. By selecting the desired gene in a cross, closely linked but undesired genes may also be selected (Brinkman and Frey 1977).

Campbell et al. (1999; 2001) studied milling and baking quality in a soft x hard wheat cross and found that only softness equivalence and damaged starch were affected by a single locus. Flour yield, flour protein, and water absorption were all quantitative traits, suggesting a more complex inheritance. Marza et al. (2006) evaluated agronomic traits in a cross between Ning7840 and Clark, a soft red winter wheat. They found QTL associated with grain yield on chromosomes 5A and 4B. They also discovered QTL associated with other traits which may affect grain yield, such as lodging, leaf rust reaction, and shattering on chromosomes 1B, 5A, and 7A.

Chapter 2: Scab Resistance QTL are Associated with Agronomic Traits of Soft Red Winter Wheat

Introduction

Fusarium head blight (FHB), or scab, is a widely documented and studied disease caused by species in the fungal genus *Fusarium*. FHB causes mycotoxin contamination, kernel damage, and yield loss. Methods of control include the use of fungicide, tillage, and host resistance. Sources of resistance to FHB have been reported from a number of wheat cultivars, including Sumai 3 (Gupta et al. 2000; Mardi et al. 2005). Lines derived from Sumai 3, such as Ning 7840, are widely used in breeding for resistance to FHB. Ning 7840 is a Chinese hard red spring wheat containing three FHB resistance QTL (Buerstmayr et al. 2009). These QTL are located on the 3BS, 2DL, and 5A chromosomes.

Because it carries these three QTL, Ning 7840 is often used in crosses with other wheat classes, such as soft red winter wheat. Soft red winter wheat is grown in the Eastern United States. It is characterized by its soft endosperm, red bran, and may require a vernalization period for onset of reproduction growth. Ning 7840 is a Chinese hard red spring wheat, not locally adapted to the Eastern United States, has a hard endosperm, and does not require vernalization. Agronomic traits also differ between Ning 7840 and soft red winter wheat cultivars. Ning 7840 has increased lodging, height, susceptibility to powdery mildew, lower test weight, and grain yield compared to soft red winter wheat cultivars.

Ohe et al. (2010) studied whether agronomic and quality traits were associated with the 3BS or 5A QTL in crosses of Ning 7840 with two European winter wheat cultivars. While they found both QTL to have positive effects on FHB resistance, there were only very small negative associations with yield, and no association was found between the FHB QTL with heading date or with plant height.

McCartney et al. (2007) generated three backcross populations from different FHB resistant parents in order to assess FHB QTL in Canadian spring wheat. One of the backcross populations was used to look at the three QTL derived from Sumai 3. While all three QTL affected FHB resistance, none of them were associated with plant height or anthesis date.

Both of these studies that found similar results evaluated FHB resistance and agronomic traits. However, Ohe et al. (2010) assessed hard winter wheat adapted to Europe, while McCartney et al. (2007) looked at hard spring wheat from Canada. Since the backgrounds of these cultivars differ from soft red winter wheat, FHB resistance and agronomic traits may also be different.

The purpose of this study was to assess differences in agronomic traits between recombinant inbred lines (RILs) with and without resistance QTL to determine whether the 3FHB resistance QTL from Ning 7840 had negative trait associations in soft red winter wheat. Traits tested were test weight, moisture content, height, heading, yield, powdery mildew, and lodging. Traits relating to FHB resistance were also measured, including scab incidence, scab severity, percentage of FDK, scab index, DON content, and one thousand kernel weight. The presence of the

FHB QTL was detected using simple sequence repeat (SSR) markers on either side of each QTL (Song et al. 2005).

Materials and Methods

Plant Materials

A population of 86 wheat recombinant inbred lines was derived from a cross between 'Ning 7840' and 'Pioneer 2643'. Ning 7840 is a Chinese hard red spring wheat cultivar derived from an Aurora/Anhui 11//Sumai 3 cross. Pioneer 2643 (Experimental Pioneer line XW522) is a soft red winter wheat cultivar. Recombinant inbred lines were created by selfing each of the 86 F2 lines resulting from the cross by single seed descent until the F7 generation.

The 86 recombinant inbred lines and the parental cultivars, Ning 7840 and Pioneer 2643, were planted at the University of Maryland's Lower Eastern Shore Research and Education Center (LESREC) in Salisbury, MD in the fall of 2007, 2008, and 2009 in 1.2 m long rows in a block design with two replications. The nursery was inoculated with corn infested with FHB in the early spring of each year and misted (Paulitz et al, 1996). In the Spring of 2008 in Salisbury, frost damage occurred, so the study was not used in this evaluation. In both 2009 and 2010 in Salisbury, height, incidence, severity, percentage of Fusarium damaged kernels (FDK), DON content and 1000 kernel weight (1000 W) were measured. In 2010 powdery mildew was observed in the field, and was also scored using a 0-9 scale. Scab incidence was visually estimated by percentage as the amount of plants infected with scab. Scab severity was estimated visually by percentage by how scabby the heads of the infected plants were. Plant height was measured, from the soil to the top

of the spike excluding awns, at plant maturity. Approximately ten random heads were selected from each row and threshed. From each sample, 200 seeds were randomly selected by hand, and the percent of Fusarium damaged kernels (FDK) was determined. The 200 seeds were then weighed and the weight was multiplied by 5 to convert to 1000 kernel weight. All of the threshed seeds were then sent to Yanhong Dong at the University of Minnesota where the DON content was determined in parts per million (ppm).

The Ning 7840 by Pioneer 2643 population was also planted at the Wye Research and Education Center (WREC) in Queenstown, MD in the fall of 2007, 2008, and 2009 in 4 m long, 7 row plots with 0.15 m spacing between rows. In 2008 in Queenstown, moisture content, test weight, height, grain yield, lodging and powdery mildew were measured. Lodging and powdery mildew did not occur in 2009 or 2010 so was not recorded in those years. In 2009, moisture content, test weight, height, and heading days in Julian (days from January 1) were recorded. Natural FHB occurred in 2009, so a sample of each RIL was harvested and tested for DON content, percentage of FDK, and 1000 kernel weight (as described above). In 2010, moisture content, test weight, and grain yield were recorded.

Marker Analysis with SSR markers

Simple sequence repeat markers were obtained from the population, and the two parental lines. Seeds were germinated in the lab in trays, and 2.5cm long cuttings were taken from the first leaf of each plant. The leaves were then desiccated to be evaluated for SSR markers. The SSR marker evaluation was done by Gina Brown

Guedira at the Raleigh (NC) USDA Genotyping Lab. A total of six SSR markers (two markers corresponding to each QTL) were scored on the RIL population. The markers used for the QTL on the 3BS chromosome were umn10 (Liu et al, 2008) and gwm533; for the QTL on the 2DL chromosome, cfd233 and gwm 539 were used; and the markers used to detect the QTL on the 5A chromosome were gwm304 and wmc705 (Somers et al. 2004). The distance between the markers cfd233 and gwm539 is 12cM, while the distance between gwm304 and wmc705 is 4cM (Somers et al. 2004). The allele size of the SSR marker relating to each parent is shown in Table 1.

Statistical Analyses

For each QTL, the RILs were scored according to which SSR markers were present. If both markers were derived from Ning 7840, the QTL was scored as A (QTL present). If both markers coincided with Pioneer 2643, the QTL was scored as B (QTL absent). If the two markers were not derived from the same parent the QTL was scored as either C or D (QTL presence unknown), depending on which marker was derived from each parent. Means for each trait were then analyzed by pairwise comparison between the presence or lack of the QTL. The means of the RILs with an unknown QTL were disregarded for the purpose of comparison. The number of RILs included for the pairwise comparisons of each QTL are shown in Table 1. Because it was expected that the presence of the FHB QTLs derived from Ning 7840 would have a negative impact on the RILs, a one-tailed probability was used. Pairwise comparisons were obtained using the LSMeans and pdiff statements in Proc GLM in SAS version 9.1 (SAS Institute Inc., Cary, NC).

| | 3BS | | | 5A | | | 2 | - | |
|------------------|-------|--------|----|--------|--------|----|--------|--------|----|
| Origin of QTL | umn10 | gwm533 | n | gwm304 | wmc705 | n | cfd233 | gwm539 | n |
| Ning 7840 (A) | 239 | 145 | 33 | 217 | 168 | 45 | 276 | 126 | 35 |
| Pioneer 2643 (B) | 236 | 129 | 38 | 199 | 162 | 35 | 273 | 137 | 35 |
| Unknown (C) | 239 | 129 | 0 | 217 | 162 | 0 | 276 | 137 | 8 |
| Unknown (D) | 236 | 145 | 9 | 199 | 168 | 0 | 273 | 126 | 3 |

 Table 1. Size (in base pairs) of SSR marker fragments derived from Ning 7840 and Pioneer 2643.

 The number (n) of recombinant inbred lines of each genotype is also shown.

| Table 2. Mean values of agronomic traits for each FHD QTL | Τa | able | 2. | Mean | values | of | agronomic | traits | for | each | FHB | QTL |
|---|----|------|----|------|--------|----|-----------|--------|-----|------|-----|------------|
|---|----|------|----|------|--------|----|-----------|--------|-----|------|-----|------------|

Scab incidence and scab severity were measured in Salisbury in 2009 and 2010. FDK, DON, and 1000 kernel weight were measured in Salisbury in 2009 and 2010, as well as in Queenstown in 2009. Height was measured in Salisbury in 2009 and 2010 and in Queenstown in 2008 and 2009. Moisture content and test weight were measured in Queenstown in 2008, 2009, and 2010. Grain yield was measured in Queenstown in 2008 and 2010. Powdery mildew was measured in Salisbury in 2010 and Queenstown in 2008. Lodging was recorded in Queenstown in 2008.

| QTL | Inc ¹ | Sev ¹ | FDK ¹ | Index ¹ | DON | 1000 W ¹ | Height | MC ¹ | TW^1 | Yield ¹ | Heading | $\mathbf{P}\mathbf{M}^1$ | Lodging |
|-----------------|------------------|------------------|------------------|--------------------|-------|----------------------------|--------|-----------------|---------|--------------------|----------|--------------------------|---------|
| (+/-) | (%) | (%) | (%) | | (ppm) | (g) | (cm) | (%) | (kg/hL) | (g) | (Julian) | (0-9) | (0-9) |
| 3BS + | 14.2 | 24.4* | 3.2* | 12.6* | 1.26* | 30.8 | 82.0 | 12.6 | 72.4 | 1973 | 122 | 3.6 | 4.2 |
| 3BS- | 16.2 | 31.0* | 4.7* | 15.9* | 2.16* | 30.7 | 86.4 | 12.6 | 72.0 | 1934 | 122 | 3.2 | 4.9 |
| 2DL + | 13.7 | 24.1 | 3.1 | 12.4 | 1.36* | 29.2* | 88.7 | 12.6 | 72.7 | 1836* | 124 | 3.4 | 4.6 |
| 2DL - | 16.7 | 26.6 | 3.9 | 14.4 | 2.05* | 32.1* | 88.1 | 12.7 | 72.3 | 2090* | 124 | 2.9 | 5.1 |
| 5A + | 13.7 | 26.5 | 3.6 | 13.11 | 1.69 | 30.0* | 86.9 | 12.6 | 72.2 | 1833* | 123 | 3.4 | 5.6* |
| 5A - | 15.6 | 28.2 | 4.1 | 14.6 | 1.89 | 31.9* | 86.1 | 12.6 | 72.6 | 1982* | 122 | 3.9 | 4.2* |
| Ning 7840 | 7.4* | 19.2* | 1.1* | 8.4* | 0.27* | 27.4* | 81.8* | 12.6 | 73.6 | 1576* | 119 | 5.1* | 8.0 |
| Pioneer 2643 | 26.5* | 32.7* | 5.8* | 20.0* | 2.32* | 34.9* | 73.6* | 13.1 | 74.1 | 2635* | 122 | 2.7* | 3.0 |

*Mean values significantly different at p=0.05

1. Inc= percentage of scab incidence, Sev= percentage of scab severity, FDK= percentage of fusarium damaged kernels, 1000W = weight of one thousand kernels, MC= moisture content, TW= test weight, Yield= grain yield per plot, PM = powdery mildew

Results

3BS QTL

The presence of the 3BS QTL was associated positively with most of the FHB resistance traits (Table 2). Scab severity, percentage of FDK, index, and DON content were significantly lower in the RILs containing the 3BS QTL compared to the RILs without the 3BS QTL. None of the other traits were associated with the 3BS QTL.

2DL QTL

The presence of the 2DL QTL was not positively associated with scab incidence, scab severity, FDK, or index, but it was associated with a decrease in DON content. The 2DL QTL was negatively associated with one thousand kernel weight and grain yield. No associations were observed for height, moisture content, test weight, heading, powdery mildew, or lodging for the 2DL QTL.

5A QTL

The 5A QTL was not positively associated with any of the FHB resistance traits in this study. However, it was negatively associated with thousand kernel weight, grain yield, and lodging.

Discussion

Ning 7840 was lower than Pioneer 2643 for scab incidence, scab severity percentage of fusarium damaged kernels, index, and DON content. Ning 7840 also had lower one thousand kernel weight and grain yield, and higher height and powdery mildew score. There was no significant difference between Ning 7840 and Pioneer

2643 for moisture content, test weight, and heading date. However, Ning 7840 had higher lodging than Pioneer 2643.

Of the FHB resistance traits which Ning 7840 was expected to positively influence, scab severity, fusarium damaged kernels, index and DON content, decreased by the presence of the 3BS QTL, while only DON content was lowered by the presence of the 2DL QTL. None of the FHB resistance traits were significantly different between the lines with or without the 5A FHB QTL.

The 3BS FHB QTL was not associated with any negative agronomic traits. Both the 2DL FHB QTL and the 5A FHB QTL were associated with significantly lower one thousand kernel weight, as well as lowered grain yield, while the 5A FHB QTL was also associated with an increase in lodging.

These results indicate that the 3BS FHB QTL, while being the most effective for FHB resistance, was not negatively associated with any of the traits evaluated. The 2DL QTL showed some effectiveness in scab resistance, but was also associated with kernel weight and grain yield. The 5A FHB QTL showed no effect on FHB resistance in this study and was negatively associated with three agronomic traits.

Ohe et al. (2010) studied the influence of Ning 7840 in two European winter wheat germplasm. They found neither heading date nor height were associated with the 3BS or 5A FHB QTL, which is consistent with the findings in this study.

McCartney et al. (2007) previously reported the 3BS, 2DL, and 5A FHB QTL each had an effect on the percentage of fusarium damaged kernels and DON content, while both the 3BS and 2DL FHB QTL lowered index in three backcross spring wheat populations derived from Sumai 3. Their findings on the 3BS FHB QTL is

similar to this study, however I did not find the 2DL or 5A FHB QTL to be associated with the percentage of FDK, or the 2DL FHB QTL to be associated with scab index. This may be due to a difference in background in the parental populations or perhaps an environmental difference. McCartney et al. (2007) also found no effect on height by any of the FHB QTL, which corresponded to my study.

Conclusions

The 3BS FHB QTL was successful at providing FHB resistance without negatively affecting agronomic traits. The 2DL FHB QTL provided some FHB resistance, but also influenced some agronomic traits. The 5A FHB QTL was the least successful; it did not provide any improved scab resistance but negatively affected agronomic traits.

Chapter 3: Scab Resistance QTL are Associated with Quality Traits of Soft Red Winter Wheat

Introduction

Fusarium head blight (FHB), or scab, is a widely documented and studied disease caused by species in the genus *Fusarium*. FHB causes mycotoxin contamination, kernel damage, and yield loss. Methods of control include the use of fungicide, tillage, and host resistance. Sources of resistance to FHB have been reported from a number of wheat cultivars, including Sumai 3 (Gupta et al. 2000; Mardi et al. 2005). Lines derived from Sumai 3, such as Ning 7840, are widely used in breeding for resistance to FHB. Ning 7840 is a Chinese hard red spring wheat containing three FHB resistance QTL (Buerstmayr et al. 2009). These QTL are located on the 3BS, 2DL, and 5A chromosomes.

Because it carries these three QTL, Ning 7840 is often used in crosses with other wheat classes, such as soft red winter wheat. Soft red winter wheat is characterized by its soft endosperm, red bran, and requirements of a vernalization period to initiate reproductive growth. While Ning 7840 also has red bran, it has a hard endosperm, and does not require vernalization. Endosperm hardness is an important quality trait determining end use in wheat. Wheat with hard endosperm is typically used in bread making, while wheat with soft endosperm is used in the production of cookies, cakes, and pastries (Smith 1995). The milling and baking qualities desired in soft red winter wheat differ greatly from those for hard red spring wheat. Among the quality characteristics desired for soft red winter wheat are higher flour yield, lower flour protein, and lower solvent retention capacity than hard wheat.

The objective of this study was to determine whether these quality traits are associated with the three FHB resistance QTL in Ning 7840. In order to accomplish this, simple sequence repeat (SSR) markers were used. SSRs are a type of genetic marker capable of detecting short, repeating DNA sequences. By determining how large the repeat sequence is, it was possible to determine from which parent a progeny has inherited its DNA. Similarly, using SSRs on either side of each QTL of interest demonstrated whether the FHB resistance QTL was present in the progeny.

Similar studies have been performed on other wheat types. Ohe et al. (2010) evaluated the association of agronomic and quality traits with the 3BS or 5A QTL in two European hard winter wheat cultivars. They found no association with protein content, and a positive association between the 3BS QTL and test weight. This relationship may or may not carry over to soft red winter wheat because of the inherent difference between hard and soft wheat for test weight.

McCartney et al. (2007) generated three backcross populations from different FHB resistant parents to assess FHB QTL in Canadian spring wheat. These populations included one population derived from Sumai 3 which contained the three FHB QTL. The quality traits evaluated in their study included test weight, protein content, and flour yield. They found an increase in both test weight and flour protein was associated to the presence of the 2DL QTL, while flour yield was not significant. McCartney et al. (2007) focused on hard spring wheat, so the relationship they observed with test weight may or may not translate into soft red winter wheat.

The purpose of this research was to determine whether the 3 FHB resistance QTL introduced into a soft red winter wheat cultivar from Ning 7840 were negatively

associated with quality traits. The ultimate aim is to be able to develop FHB resistant soft red winter wheat without reducing milling and baking quality.

Materials and Methods

Plant Materials

A population of 86 wheat recombinant inbred lines was created from a cross between 'Ning 7840' and 'Pioneer 2643'. Ning 7840 is a Chinese hard red spring wheat cultivar derived from an Aurora/Anhui 11//Sumai 3 cross. Pioneer 2643 (Experimental Pioneer line XW522) is a soft red winter wheat cultivar. Recombinant inbred lines were created by selfing each F2 genotype resulting from the initial cross by single seed descent until the F7 generation.

The 86 RILs, Ning 7840, Pioneer 2643, and two checks, Sisson and Renwood 3260, were planted at the Wye Research and Education Center (WREC) in Queenstown, MD in the fall of 2007 and 2008 in 4 m long, 7 row plots with 0.15 m spacing between rows. In 2008 one replication was harvested for quality analysis, while in 2009 both replications were harvested. Samples of grain for each RIL were sent to Dr. Edward Souza at the USDA Soft Wheat Quality Lab, Wooster, OH for milling and baking quality analysis. Milling score, baking score, softness equivalence score, test weight, adjusted flour yield, flour protein percent, lactic acid SRC, sucrose SRC, sodium carbonate SRC, and water RC were measured on each sample.

Marker Analysis with SSR markers

Simple sequence repeat markers were obtained from the population, and the two parental lines. Seeds were germinated in a soil-less mix at room temperature, and

cuttings were taken from the first leaf of each plant. The leaves were then desiccated to be evaluated for DNA extraction SSR markers. The SSR marker evaluation was done by Dr. Gina Brown Guedira at the Raleigh (NC) USDA Genotyping Lab. A total of six SSR markers (two markers corresponding to each QTL) were scored on the RIL population. The markers used for the QTL on the 3BS chromosome were umn10 (Liu et al, 2008) and gwm533; for the QTL on the 2DL chromosome, cfd233 and gwm 539 were used; and the markers used to detect the QTL on the 5A chromosome were gwm304 and wmc705 (Somers et al. 2004). The distance between the markers cfd233 and gwm539 is 12cM, while the distance between gwm304 and wmc705 is 4cM (Somers et al. 2004). The size of the SSR marker relating to each parent is shown in Table 1.

Statistical Analyses

For each QTL, the RILs were scored according to which SSR markers were present. If both markers were derived from Ning 7840 the QTL was scored as A (QTL present), if both markers coincided with Pioneer 2643 the QTL was scored as B (QTL absent). If the two markers were not derived from the same parent the QTL was scored as either C or D (QTL presence unknown), depending on which marker was derived from each parent. Means for each trait were then analyzed by pairwise comparison between the presence or lack of the QTL. The means of the RILs with an unknown QTL were disregarded for the purpose of comparison. The number of RILs included for the pairwise comparisons of each QTL are shown in Table 1. Because it was expected that the presence of the FHB QTLs derived from Ning 7840 would have

a negative impact on the RILs, one-tailed probability was used. Pairwise comparisons were obtained using the LSMeans and pdiff statements in Proc GLM in SAS version 9.1 (SAS Institute Inc., Cary, NC).

| QTL | Milling Score | Baking Score | Soft. Eq. Score | TW^1 | Flour Yield | Flour Protein | Lactic Acid SRC | Sucrose SRC | Water RC | Sodium Carb SRC |
|--------------|------------------|-----------------|--------------------|---------|----------------|------------------|--------------------|----------------|-------------|--------------------|
| (+/-) | (%) | (%) | (%) | (kg/hL) | (%) | (%) | (%) | (%) | (%) | (%) |
| 3BS + | 53.3 | 33.6 | 55.4 | 74.6 | 67.1 | 9.5 | 87.1 | 86.7 | 55.2 | 67.9 |
| 3BS - | 51.9 | 30.9 | 54.3 | 74.8 | 66.8 | 9.6 | 87.5 | 87.4 | 55.3 | 68.2 |
| 2DL + | 49.0* | 30.1* | 49.6* | 75.4 | 66.2* | 9.9* | 84.1 | 85.9 | 55.4 | 67.3 |
| 2DL - | 56.9* | 34.5* | 55.9* | 75.2 | 67.8* | 9.4* | 86.3 | 86.7 | 55.2 | 67.8 |
| 5A + | 49.3* | 29.1* | 49.0* | 74.3* | 66.3* | 9.8* | 83.4* | 86.5 | 56.0* | 68.6* |
| 5A - | 55.2* | 33.5* | 59.3* | 74.5* | 67.5* | 9.4* | 91.1* | 87.9 | 54.8* | 67.6* |
| Ning 7840 | 58.8 | 13.0* | 22.7* | 74.0 | 68.2 | 11.0* | 70.1* | 84.5 | 61.9* | 74.3* |
| Pioneer 2643 | 65.8 | 55.3* | 65.6* | 75.6 | 69.6 | 7.8* | 101.0* | 83.5 | 54.7* | 66.3* |

Table 3. Means of milling and baking quality traits measured on wheat harvested.

*Mean values significantly different at p=0.05 1. TW= test weight

Results

3BS

There were no negative effect on milling or baking quality traits associated with the presence of the 3BS FHB QTL from Ning 7840 (Table 3).

2DL

Significant differences were observed for milling score, baking quality score, softness equivalent score, flour yield, and flour protein for the lines carrying the 2DL QTL. The milling, baking, and softness equivalent scores, as well as the flour yield were lowered in the RILs containing the 2DL FHB QTL, while flour protein was increased in the RILs with the 2DL QTL (Table 3).

5A

The milling and baking quality traits were all negatively associated with the presence of the 5A QTL from Ning 7840, except for sucrose SRC, which did not differ significantly between the two groups of RILs. The means for milling score, baking score, softness equivalent score, test weight, flour yield, and lactic acid SRC were all lower in the RILs carrying the 5A QTL, while means of flour protein, water retention capacity, and sodium carbonate SRC were higher in the RILs containing the 5A FHB QTL than the RILs without the 5A FHB QTL (Table 3).

Discussion

Ning 7840 had a lower baking score and softness equivalence score than Pioneer 2643. Ning 7840 also had lower lactic acid solvent retention capacity, and higher flour protein, water retention capacity, and sodium carbonate solvent retention capacity. Ning 7840 did not differ from Pioneer 2643 for milling score, test weight, flour yield, or sucrose solvent retention capacity.

Milling score, baking score, and softness equivalence score were each decreased by the presence of both the 2DL FHB QTL and the 5A FHB QTL. The 2DL FHB QTL was also associated with a decrease in flour yield and an increase in flour protein, while the 5A QTL was negatively associated with every quality trait tested, with the exception of sucrose SRC.

Ohe et al. (2010) studied the effect of the 3BS and 5A QTL on test weight and protein content. They found an increase in test weight associated with the 3BS QTL. In this evaluation the 3BS QTL did not increase test weight In the study by Ohe et al. (2010) there was no change in protein content associated with either the 3BS or 5A FHB QTL. While the 3BS QTL was not associated with an increase in flour protein in this study, the 5A QTL was. This may have been because the cultivars Ohe et al. (2010)used had higher protein content than those used in this study. The parental soft red winter wheat Pioneer 2643 had much lower protein content than Ning 7840.

McCartney et al. (2007) evaluated the influence of the 3BS, 2DL, and 5A FHB QTL on test weight, protein content, and flour yield in hard spring wheat. They found no significant differences in flour yield associated with any of the three QTL. Because flour yield is generally higher in soft wheat than hard wheat, it was expected that there would be overall decrease in flour yield associated with the FHB QTL that was not observed by McCartney et al. (2007).I did not observe a decrease in flour yield in the 2DL and 5A FHB lines containing Ning 7840 alleles. McCartney et al. (2007) also found an increase in test weight associated with the 2DL FHB QTL,

while this study I found no decrease in test weight between the RILs with and without the 2DL QTL. McCartney et al. (2007) also reported an increase in flour protein associated with the 2DL FHB QTL similar to the results of this study.

Conclusion

The presence of the 3BS QTL from Ning 7840 was not negatively associated with end-use quality traits in soft red winter wheat. Both the 2DL QTL and the 5A QTL, however, were associated with negative trends on quality traits. Overall, the 5A QTL was more consistently negatively associated with quality traits than the 2DL QTL. This may be due to how each QTL functions, or it may be caused by linkage drag (Brinkman and Frey 1977). Reducing the size of the QTL may reduce linkage drag. Further research could be done to test this by measuring the sizes of the QTL on each chromosome. If QTL size is an important factor, alternate breeding methods may be used to decrease linkage drag. For instance, backcrossing may lead to less of the genome from the resistant parent being passed on. Researching the effects of other sources of FHB resistance to combine them with the 3BS QTL may also be a successful strategy to avoid negative consequences of breeding for FHB resistance.

References

- Andersen, A. L. 1948. The Development of *Gibberella zeae* headblight of wheat. Phytopathology 38:595-611.
- Anderson, J.A., R.W. Stack, S. Liu, B.L. Waldron, A.D. Fjeld, C. Coyne, B. Moreno-Sevilla, J.M. Fetch, Q.J. Song, P.B. Cregan, and R.C. Frohberg. 2001. DNA markers for Fusarium head blight resistance QTLs in two wheat populations. Theoretical and Applied Genetics 102:1164-1168.
- Anjum, F.M., and C.E. Walker. 1991. Review on the significance of starch and protein to wheat kernel hardness. Journal of the Science of Food and Agriculture 56:1-13.
- Bai, G., and G. Shaner. 1994. Scab of wheat: Prospects for control. Plant Disease 78:760-766.
- Bai, G.H., G. Shaner, and H. Ohm. 2000. Inheritance of resistance to *Fusarium* graminearum in wheat. Theoretical and Applied Genetics 100:1-8.
- Brinkman, M.A., and K.J. Frey. 1977. Yield component analysis of oat & lines that produce different grain yields. Crop Science 17:165-168.
- Buerstmayr, H., B. Steiner, M. Lemmens, and P. Ruckenbauer. 2000. Resistance to Fusarium Head Blight in Winter Wheat: Heritability and Trait Associations. Crop Science 40: 1012-1018.
- Buerstmayr, H., Ban, T. and Anderson, J. A. 2009. QTL mapping and marker-assisted selection for Fusarium head blight resistance in wheat: a review. Plant Breeding 128: 1–26.
- Bushnell W.R., B.E. Hazen, and C. Pritsch. 2003. Histology and physiology of Fusarium head blight. In: Leonard K, Bushnell, WR, eds. Fusarium head blight of wheat and barley. St. Paul, Minnesota: APS Press. 44 p.
- Campbell, K.G., and P.E. Lipps. 1998. Allocation of Resources: Sources of Variation in Fusarium Head Blight Screening Nurseries. Phytopathology 88:1078-1086.
- Campbell, K.G., C.J. Bergman, D.G. Gualberto, J.A. Anderson, M.J. Giroux, G. Hareland, R.G Fulcher, M. E. Sorrells, and P.L. Finney. 1999. Quantitative Trait Loci Associated with Kernel Traits in a Soft × Hard Wheat Cross. Crop Science 39: 1184-1195.
- Desjardins, A.E., and R.H. Proctor. 2007. Molecular biology of Fusarium mycotoxins. International Journal of Food Microbiology 119:47-50.
- Dill-Macky, R., and R.K. Jones. 2000. The Effect of Previous Crop Residues and Tillage on Fusarium Head Blight of Wheat. Plant Disease 84:71-76.
- Easterbrook, G. 1997. Forgotten benefactor of humanity. The Atlantic Monthly 279: 75–82.
- Faridi, H., C. Gaines, and P. Finney. 1994. Soft wheat quality in production of cookies and crackers. Pages 154-168 in: Wheat Production Properties and Quality. W. Bushuk and V. F. Rasper, eds. Blackie Academic and Professional: Glasgow.

- Fernandez, M.R., and J.M.C. Fernandes. 1990. Survival of wheat pathogens in wheat and soybean residues under conservation tillage systems in southern and central Brazil. Canadian Journal of Plant Pathology 12: 289–294.
- Forsyth, D. M., T. Yoshizawa, N. Morooka, and J. Tuite. 1977. Emetic and refusal activity of deoxynivalenol to swine. Applied and Environmental Microbiology 34:547-552.
- Gaines, C. S., M.O. Raeker, M. Tilley, P.L. Finney, J.D. Wilson, D.B. Bechtel, R.J. Martin, P.A. Seib, G.L. Lookhart, and T. Donelson. 2000. Associations of starch gel hardness, granule size, waxy allelic expression, thermal pasting, milling quality, and kernel texture of 12 soft wheat cultivars. Cereal Chemistry 77:163-168.
- Gupta, R. B., I.L. Batey, and F. MacRitchie. 1992. Relationships between protein composition and functional properties of wheat flours. Cereal Chemistry 69:125-131.
- Gupta, A., P.E. Lipps, and K.G. Campbell. 2000. Finding quantitative trait locus associated with Fusarium head blight of wheat using simple sequence repeat markers, p. 28-32. 2000 National Fusarium Head Blight Forum Proceedings, Erlanger, KY.
- Guttieri, M.J., C. Becker, and E.J. Souza. 2004. Application of wheat meal solvent retention capacity tests within soft wheat breeding programs. Cereal Chemistry 81: 261-266
- Khonga, E. B., and J.C. Sutton. 1988. Inoculum production and survival of *Gibberella zeae* in maize and wheat residues. Canadian Journal of Plant Pathology 10:232-239.
- Kolb, F.L., G.H. Bai, G.J. Muehlbauer, J.A. Anderson, K.P. Smith, and G. Fedak. 2001. Host plant resistance genes for fusarium head blight: Mapping and manipulation with molecular markers. Crop Science 41:611-619.
- Leonard K.J., W.R. Bushnell, eds. 2003. *Fusarium Head Blight of Wheat and Barley*. St Paul, MN: APS Press. 512 pp.
- Lewis S., M.E. Faricelli, M.L. Appendino, M. Valarik, and J. Dubcovsky. 2008. The chromosome region including the earliness *per se* locus *Eps-Am1* affects the duration of early developmental phases and spikelet number in diploid wheat. Journal of Experimental Botany 59: 3595-3607.
- Liu, Z.Z., 1984. Recent advances in research on wheat scab in China. p. 174–181. *In:* Wheats for more tropical environments. CIMMYT, Mexico, D.F., Mexico.
- Liu, S., M.O. Pumphrey, B.S. Gill, H.N. Trick, J.X. Zhang, J. Dolezel, B. Chalhoub, and J.A. Anderson. 2008. Toward positional cloning of Fhb1, a major QTL for Fusarium head blight resistance in wheat. Cereal Research Communications 36:195-201.
- Major, D.J., B.L. Blad, A. Bauer, J.L. Hatfield, K.G. Hubbard, E.T. Kanemasu, R.J. Reginato. 1988. Winter wheat grain yield response to water and nitroen on the North American Great Plains. Agricultural and Forest Meteorology 44: 141-149.
- Mardi, M., H. Buerstmayr, B. Ghareyazie, M. Lemmens, S.A. Mohammadi, R. Nolz,

and P. Ruckenbauer. 2005. QTL analysis of resistance to Fusarium head blight in wheat using a 'Wangshuibai'-derived population. Plant Breeding 124:329-333.

- Marza, F.G., H. Bai, B.F. Carver, and W.C. Zhou. 2006 Quantitative trait loci for yield and related traits in the wheat population Ning 7840 x Clark. Theoretical and Applied Genetics 112:688-698
- McCartney, C.A., D.J. Somers, G. Fedak, R.M. DePauw, J. Thomas, S.L. Fox, D.G. Humphreys, O. Lukow, M.E. Savard, B.D. McCallum, J. Gilbert, and W. Cao. 2007. The evaluation of FHB resistance QTLs introgressed into elite Canadian spring wheat germplasm. Molecular Breeding 20:209-221.
- McMullen, M., R. Jones, and D. Gallenberg. 1997. Scab of wheat and barley: A reemerging disease of devastating impact. Plant Disease 81:1340-1348.
- McMullen, M., S. Halley, B. Schatz, S. Meyer, J. Jordahl, and J. Ransom. 2008. Integrated strategies for Fusarium head blight management in the United States.

Cereal Research Communications 36:563-568.

- Neish, G.A., and H. Cohen. 1981. Vomitoxin and zearalenone production by Fusarium graminearum from winter wheat and barley in Ontario. Canadian Journal of Plant Science 61: 811-815.
- Ohe, C., E. Ebmeyer, V. Korzun, and T. Miedaner. 2010. Agronomic and quality performance of winter wheat backcross populations carrying non-adapted Fusarium head blight resistance QTL. Crop Science 50:2283-2290.
- Parry, D.W., P. Jenkinson, and L. McLeod. 1995. Fusarium ear blight (scab) in small grain cereals-a review. Plant Pathology (Oxford) 44:207-238.
- Paulitz, T.C. 1996. Diurnal release of ascospores by *Giberella zeae* in inoculated wheat plots. Plant Disease. 80: 674-678.
- Pritsch, C., G.J. Muehlbauer, W.R. Bushnell, D.A. Somers, and C.P. Vance. 2000. Fungal development and induction of defense response genes during early infection of wheat spikes by Fusarium graminearum. Molecular Plant-Microbe Interactions 13:159-169.
- Pugh, G.W., H. Johann, and J.G. Dickson. 1933. Factors affecting infection of wheat heads by *Gibberella saubinetti*. Journal of Agricultural Research 46: 771-797.
- Rudd, J.C., R.D. Horsley, A.L. McKendry, and E.M. Elias. 2001. Host plant resistance genes for Fusarium head blight. Crop Science 41: 620-627.
- Schuler, S. F., R. Bacon, P.L. Finney, and E. Gbur. 1995. Relationship of test weight and kernel properties to milling and baking quality in soft red winter wheat. Crop Science 35:949-953.
- Slade, L., and H. Levine. 1994. Structure-function relationships of cookie and cracker ingredients. Pages 23-141 in: The Science of Cookie and Cracker Production. H. Faridi, ed. Chapman and Hall: New York.
- Somers, D.J., P. Isaac, and K. Edwards. 2004. A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theoretical and Applied Genetics. 109:1105-1114.
- Song, Q.J., J.R. Shi, S. Singh, E.W. Fickus, J.M. Costa, J. Lewis, B.S. Gill, R. Ward, and P.B. Cregan. 2005. Development and mapping of microsatellite (SSR) markers in wheat. Theoretical and Applied Genetics 110:550-560.

- Sutton, J.C. 1982. Epidemiology of wheat head blight and maize ear rot cause by *Fusarium graminearum*. Canadian Journal of Plant Pathology 4: 195-209.
- Tshanz, A.T., R.K. Horst, and P.A. Nelson. 1976. The effect of environment on sexual reproduction of *Giberella zeae*. Mycologia 68: 327-340.
- Uthayakumaran, S., P.W. Gras, F.L. Stoddard, and F. Bekes. 1999. Effect of varying protein content and glutenin-to-gliadin ratio on the functional properties of wheat dough. Cereal Chemistry 76: 389-394.
- Van Ginkel, M., W. Van Der Schaar, and Z. Yang. 1996. Inheritance of resistance to scab in two wheat cultivars from Brazil and China. Plant Disease 80:863-867.
- Vaughan, B., D.G. Westfall, and K.A. Barbarick. 1990. Nitrogen and timing effects on winter wheat grain yield, grain protein, and economics. Journal of Production Agriculture 3: 324-328.
- Vesonder, R.F., and C.W. Hesseltine. 1981. Vomitoxin: natural occurrence on cereal grains and significance as a refusal and emetic factor to swine. Process Biochemistry 81:12-15.
- Wanyoike, M.W., K. Zhensheng, and H. Buchenauer. 2002. Importance of cell wall degrading enzymes produced by *Fusarium graminearum* during the infection of wheat heads. European Journal of Plant Pathology 108: 803-810.
- Wheat Foods Council. updated 2010. Grains of truth about wheat production and consumption. http://www.wheatfoods.org/_FileLibrary/Product/43/Wheat%20Prod.%20&%

http://www.wheatfoods.org/_FileLibrary/Product/43/Wheat%20Prod.%20&% 20Consumption.pdf

- Wilcoxson, R.D. 1993. Historical overview of scab research, p. 1–5. In Proc. (1st) Regional Scab Forum, Moorhead, MN. Publ. Minn. Wheat Res. & PromCouncil, Red Lake Falls, MN.
- Zhou, W.C., F.L. Kolb, G.H. Bai, L.L. Domier, L.K. Boze, and N.J. Smith. 2003. Validation of a major QTL for scab resistance with SSR markers and use of marker-assisted selection in wheat. Plant Breeding 122: 40-46.