IMPACT OF A QTL FOR PLASTICITY OF PRODUCTIVE TILLER NUMBER ON YIELD AND YIELD COMPETITIVE ABILITY OF SPRING WHEAT

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Plant Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2015

DEDICATION

To my parents, Mehdi and Najiah, *in memoriam*
To my martyred brothers, whose blood illuminated the path to freedom
Hamed, Abdel Reda, Mohammad Jawad and Mohammad Saleh
To my secret and ineffable reasons to live, my sisters; Alia, and Hana

ACKNOWLEDGMENTS

I would like to express my appreciation and deep gratitude to my major adviser, Dr. Luther Talbert, for the patient guidance he provided to me all along my journey, which he made fruitful and rewarding, as well as her much needed encouragements. My thanks go also to my committee members, Dr. John Martin, Dr. Jamie Sherman, and Dr. Michael Giroux, for the contribution each of them made to my knowledge growth during these years, with their valuable inputs and friendly support of my doctoral project. I would like to include as well my lab members, Nancy Blake, Dr. Haw-Young Heo, Dr. Jason Cook, and Andrea Varella for the warm collegiality each of them offered to me during those years. I will be forever grateful to the Establishment of Martyrs, which provided all the necessary resources and support for my studies in the US, the Scholarships department members; Amjad Al-Gharawi, Hader Al- Shareefi, and Sadeq Al-Gharrawi.

I deeply thanks the Ministry of Higher Education and Scientific Research, the Iraqi Cultural office in Washington Dc, I also extend my thanks to the Iraqi Foreign Ministry representations in the US, the General Consulate in Los Angeles, the General Consulate in Detroit, for their tireless help regarding formalities.

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ABSTRACT

Heat and drought stress are important limitations on wheat growth and reproduction. Therefore, there is a need to understand mechanisms that enable wheat plant adapted to heat and drought stress, and maintain plant growth, development, and productivity during stress periods. One of the most important plasticity traits in wheat is productive tiller number (PTN). This thesis reports two studies. The goal of the first study was to test the impact of a previously identified allele for high productive tiller number on yield and yield components, agronomics, and seed quality traits, in a set of near isogenic lines developed in three genetic backgrounds, including the crosses Vida/McNeal, Reeder/Choteau, and Reeder/Hank. Results from nine field locations showed that high productive tiller allele on *QTn.mst-6B* enhanced early tiller (ETN) formation regardless of the locations. Under favorable conditions, the large number of early tillers transferred into a capacity for high productive tiller number, which may enhance grain yield. Seed number per head and seed weight was affected negatively by the high tiller allele at *QTn.mst-6B* over all locations, and thus more tillers did not always equate to higher yield. Moreover the high productive tiller allele on *QTn.mst-6B* associated with high dry weight of roots based on a greenhouse study. The goal for second study was to assess the impact of *QTn.mst-6B* under different competition levels and levels of available water. Five near-isogenic line (NIL) pairs for two genetic backgrounds (Reader/Choteau, Vida/McNeal) were selected randomly from the three populations of our first study. Three competition levels were imposed on the NIL pairs in replicated experiments. Competition levels were 1) bordered rows representing high competition and limited water, 2) non-bordered rows representing less competition and more available water, and 3) space-planted rows representing no competition and abundant water. The experiment was planted over three locations on 2012 and 2013. The ETN more often developed into PTN in conditions with less competition levels, while did not develop into PTN in conditions of high competition and low water. The high plasticity of PTN was associated with high plasticity in grain yield, and low plasticity of seed weight.

CHAPTER ONE

INTRODUCTION

A hundred centuries ago, humans started domestication of plants and animals for their own benefit: this was the beginning of agriculture. Since then, humans strove constantly to improve agricultural practices, with the goal of increasing yield and yield quality. Even in the early stages of agriculture, farmers identified several developmental factors that would affect their yield. Early farmers understood the impact of temperature, light, water and insect. New and improved techniques, such as irrigation, crop rotation, use of fertilizers, and pesticides, were developed to help plant productivity in response to regional conditions. Today, the main concern of agriculture remains the same as in early times: identifying stress factors that can negatively affect crop yield and quality by distorting the plant from its normal useful growth and reproduction (Lonbani and Arzani, 2011), and controlling them to the maximum extent. Biotic stress factors include insects and diseases. There are abiotic stress factors too, which include drought, high and low temperature, wind, nutrient deficiency or overload, and soil condition (pH, structure and texture).

Abiotic stress factors are estimated to reduce the yield to less than half compared to its potential under normal growing conditions (Passioura, 2002). Drought and high temperature are thought to have the most negative impact in regard to crop growth and production (Anon et al., 2008), because they induce biological and biochemical changes at the plant cell level, affecting the whole plant and thus affecting yield and quality

(Akbar et al., 2001). At the whole plant level, water stress reduces cell size, while stomata closure, stomata density and xylem vessels of both roots and shoots are greater (Anon et al., 2008). Those signals are aimed at reducing water loss and increasing plant resistance to water loss. Drought and high temperature negatively affect germination, vegetative growth, productive tiller number, reproductive development, grain yield and grain quality (Akbar et al., 2001; Li et al., 2011). Anatomical structures are affected, not only at the tissue level, but also at the cellular level, resulting in poor plant growth and productivity (Wahid et al., 2007). As a consequence, in plants such as maize, pearl millet, and sugarcane, and sorghum, a significant decline in tillering, leaf area, relative growth rate, and root dry weight may occur (Ashraf and Hafeez, 2004). Furthermore, gametogenesis and fertilization are very sensitive to heat stress, with a short period of heat stress causing significant decrease in floral buds and floral abortions (Guilioni et al., 1997; Yang et al., 2006).

Since evolution is all about change and adaptation, plants have developed over time numerous strategies to counter drought and high temperature. One of them consists of escaping drought: the plant will complete one of its most sensitive stages of development, such as the reproductive stage, before the drought. Another strategy is drought avoidance: it involves decreasing water loss in the plant, by restraining transpiration and applying morphological changes (i.e., developing a deep root system), hence maintaining water circulation. During long-term dry periods, the plant will develop a low tissue water potential, in order to tolerate water deficiency (Fleury et al., 2010). Nowadays, with the development of genetics and molecular biology, it is known that drought tolerance is a quantitative trait with complex phenotype and genetic control. To evaluate new superior cultivars with high yield and acceptable quality especially in the case of spring wheat, either through conventional breeding programs or by using molecular markers technology, we need to understand the genetic basis for drought tolerance (Clarke et al., 2004). Drought has an impact on grain yield, which is another quantitative trait, encoded by numerous genes, This trait can be influenced by important environmental effects, as it is the final product of several contributing factors. Therefore, increasing grain yield requires combining measurements of agronomic traits and yield components.

Yield components include seed weight, seed number per plant, spike number per plant, and productive tiller number; whereas agronomic traits include heading date, days to physiological maturity, plant height, flag leaf area and chlorophyll content (Gebeyehou et al., 1982; Bhutta, 2006; Khan et al., 2010; Li et al., 2011). Together, yield components and agronomic traits determine what the yield may be, hence the interest of breeding improved varieties. When trying to improve varieties, an important trait in yield components is the number of productive tillers per plant (PTN). PTN determines spike number per plant, which in turn increases seed number per plant. Even though many tillers are started during plant development, only a subset of them will survive and produce spikes (Naruoka et al., 2011; Evers et al., 2006).   It may be important for a plant to start with a high number of tillers, and reduce this to an optimal number depending upon the environment. When it comes to wheat yield in particular, tillers are a vital component because of their potential of developing seed.

The tillering stage begins with the emergence of the tillers from the axils of true leaves, at the main stem of the plant. Primary tillers emerge from axils of the first three to four leaves of the main stem, while secondary tillers develop from the base of primary tillers. Of the large number of tillers initiated within the plant, most of them will undergo abortion, and only a few of them will survive and become productive. Tillers depend on the main stem for their nutrition during their development until they reach the three-four-leaf stage. Then they become independent by developing their own roots. Tiller efficiency determines the number of spikes per plant, which is a key component of grain yields. In addition, the architecture of the tiller system affects the plant's light harvesting potential, flowering, seed set, and the reproductive success of the plant (Young et al., 2004; Kuraparthy et al., 2007).

Breeding programs that aim to release successful cultivars typically grow several thousand genotypes in a target set of locations, in order to undertake phenotype selection for grain yield as well as other key traits. Genetic gain in yield is a function of the selection intensity, the extent of phenotype variability for yield and its heritability. Heritability is reduced if genotype × year (GY), genotype × location (GL) or genotype × location × year (GLY) interactions are significant, as they usually are in variable rainfed locations. While very important, grain yield is only one of many selected attributes in a breeding program. New varieties must also meet the requirements of consumers, processors, marketers and farmers. For example, bread wheat (*Triticum aestivum* L.) must have an acceptable color, a high milling yield, dough properties, specific water absorption rate and fair price to satisfy processors. Farmers will want high grain yield, resistance to a broad range of diseases and pests, and tolerance to abiotic stress.

Selection based on molecular markers first requires an association of marker and traits often through QTL mapping. Genotyping progeny that derive from a cross between distinct parents for the trait under study is the main principle of QTL mapping. The aim of a QTL map is to find a particular region showing statistically significant associations with trait variation by using phenotypic values for the interesting trait compared with molecular marker of the progeny (Slate, 2005; Sherman et al., 2010). QTL mapping has benefited from the progress made in molecular marker technology over the past few decades. Development of a large number of markers has enabled the generation of dense genetic maps and the performance of QTL mapping studies of complex traits (Borevitz and Nordborg, 2003). QTL analysis makes use of the natural variation present with species (Maloof, 2003) and has been successfully applied to various types of segregating populations.

Near isogenic lines (NILs) are important tools for genomic study. NILs can be developed through several generations of selfing a heterogeneous recombinant inbred line (RIL) population (Blake et al., 2010) or through backcrossing (Sherman et al., 2010; Blake et al., 2010; and Lanning et al., 2012). The RIL population is used to create a QTL map and identify genes that affect either quantitative or qualitative traits (Sherman et al., 2015). Meanwhile, the RILs are formed by crossing two inbred strains followed by repeated selfing to create new inbred lines whose genomes are a mosaic of the parental genomes (Blake et al., 2010; Sherman et al., 2015). Near isogenic lines may be developed by choosing F_4 RIL plants that are heterozygous for a locus of interest, and then selecting the homozygous types from the selfed progeny. The genome for those NIL will be equal mix from there two parents but each pair would share most of their genome except for the interesting gene. The power of a QTL at a specific locus basically depends on the difference in mean trait values between A and B genotypes for that particular locus, genetic interactions and genetic map quality. Because QTL power increases when variance for mean values decreases, QTL analysis can benefit greatly from multiple measurements.

In plants, NILs and RILs are the most common type of experimental populations used for analysis of quantitative traits. Each RIL contains several introgression fragments, and each genomic region is represented by an equal number of both parental genotypes in the population. In contract to RILs, NILs contain only one introgression per line, which increases the power to detect small-effect QTL. However, the presence of one introgression segment does not allow testing for genetic interactions, and thereby the detection of QTL expressed in specific genetic backgrounds. Moreover, most of the genetic background is identical for all lines, and NILs show more limited developmental and growth variation, increasing the homogeneity of growth stage within experiments (Xu et al., 2011).

The goal of this study was to use NILs in spring wheat for a productive tiller number QTL on chromosome 6B (*Qtn.mst-6B*), to assess the impact of the QTL across several locations in the spring wheat growing region of the Western United States, and to assess the value of *Qtn.mst-6B* under drought and heat stress typical of many spring wheat production locations.

CHAPTER TWO

IMPACT OF A QTL FOR PLASTICITY OF PRODUCTIVE TILLER NUMBER ON YIELD AND YIELD COMPETITIVE ABILITY OF SPRING WHEAT

Literature Review

Drought Stress

Drought is one of the most important abiotic stresses that affect growth and development of wheat, therefore developing new cultivars which are drought tolerant is an important challenge to plant breeders. It's estimated that by the 2025 around 1.8 billion people will face absolute water shortage and 65% of the world population will live under drought (Nezhadahmadi et al., 2013). Many factors can affect plant response to drought, such as plant genotype, growth stage, severity and duration of stress, and physiological processes of growth. Drought stress can affect gene expression, which may influence protein content, osmotic adjustment, opening and closing of stomata, cuticle thickness, and inhibition of photosynthesis, chlorophyll concentration, root depth**,** and awn length**.** There have been several efforts to develop drought tolerant wheat cultivars through breeding (Jaleel et al., 2007).

Grain Yield

High yield potential under water stress is the target of crop breeding; those genotypes that show the highest harvest index and highest stability are drought tolerant **(**Blum, 2005). Taheri et al. (2011) reported reduction in grain per head and 100-grain weight caused low yield in wheat under drought conditions. Deswal et al. (1996) found in wheat that grain yield per spike showed a direct association with total biomass, grain per spike and individual seed weight. Drought stress during maturity is related to an approximate 10% decrease in yield, while moderate stress during early vegetative period has less effect on yield (Bauder, 2001; and Taheri et al., 2011). One of the most important yield components with a major effect on the grain yield in spring wheat is productive tiller number per unit area (Naruoka et al., 2011; Sherman et al., 2014; and Sherman et al., 2015).

Tiller Number

The tiller forms at the base in the axil of leaves of the main stem and coleoptile. Tillers in the axil of leaf 1 to 3 are usually strong enough to reach full canopy height and to set grain. These tillers produce fewer leaves than the main stem, which has the effect of synchronizing spike emergence, pollen release, grain growth and maturity. Tillers in the axil of leaf 4 and above are secondary tillers, which form in the axil of the leaves and tillers themselves. The late tillers may die as the plant matures. Grasses and cereals such as wheat have high plasticity in the number of tillers. The number of productive tillers per plant helps determine seed number per plant in spring wheat and is a key component of grain yield (Young et al., 2004; and Li et al., 2011). To varying degrees most of the yield comes from primary and secondary tillers. Even for the plant that has a large number of tillers, 95-100% of the grain yield comes from the main stem, primary tiller and secondary tiller (Goos and Johnson, 2001). Meanwhile, McMaster et al., (1994) reported main stem, primary tiller and secondary tiller contribute 83 to 92% of the grain yield depending on irrigation time. The development of tillers is affected by various environmental factors including fertilization, planting density, and climate condition, such as light, temperature and water supply. Wiersma et al. (2005) found that early planting, with cold weather from emergence to reproductive stage, favors tillering and development of large spikes, therefore early seeding rate is important in maximizing tiller production and grain yield. Black and Siddoway, (1977) found that delaying of seeding caused reduced tiller formation due to the high temperature during reproductive stage.

Nitrogen represents one of the most important expensive factors in wheat production. The response of spring wheat to nitrogen fertilizer varies with nitrogen level and timing of application relative to plant growth stage. Low tillering cultivars may respond differently to varying N fertilizer and seeding rates, compared to cultivars that typically produce high tiller number (Oscarson et al., 1995).

In wheat, growth is affected by water stress, which reduces the final number of tillers per plant by increasing tiller mortality and decreasing tiller production (Fisher, 1973). Nisar et al. (2007) found that the number of seeds per head was reduced by water stress during the 15 days before anthesis, while water stress during seed filling caused reduced seed weight. The yield decreased when the water stress occurred at filling stage, but less than if it had happened before anthesis (Farooq et al., 2014). Drought is an important limitation to cereal crops production. Therefore, there is a need to understand better the mechanism that enables the plant to adapt to water deficits and maintain growth, development and productivity during a stress period, which might help in breeding for drought resistance (Budak et al., 2013).

Quantitative Trait Loci

A promising method for identifying useful genes for breeding is the use of QTL analysis. Since 1980, molecular markers have been used extensively to map quantitative trait loci (QTL). A number of QTL controlling tillering were discovered in barley (Buck-Sorlin, 2002; Babb and Muehlbauer, 2003; Franckowiak et al., 2005), rice (Li et al., 2003; Liu et al., 2006; Zhao et al., 2008, Liu et al., 2009), and rye (Malyashev et al., 2001; Lukaszewski et al., 2004; Yamada et al., 2004). Only a few studies have been carried out in wheat. Law (1967) discovered that the factor responsible for tiller number on chromosome 7B in wheat could be either the marker e1, acting pleiotropically on this trait, or a factor tightly linked to the marker. Shah et al. (1999) mapped a significant QTL for tillering on chromosome arm 3AL in wheat. Li et al. (2002) reported that QTLs with significant effect on tiller number per plant were located on 1D, 2D and 6A in winter/spring wheat. A tiller inhibition (tin3) gene was identified on chromosome 3A (Kuraparthy et al., 2007). Plants with tin3 produced one main stem compared to the wild type with many tillers in an F_2 wheat population. Naruoka et al. (2011) identified the QTL on chromosome 6B, *QTn.mst-6B,*that influenced productive tiller in a set of spring wheat crosses.

Many population structures have been used for QTL detection and mapping in plants. Recombinant inbred lines, F_2, half sib and full sib families have all demonstrated utility in QTL identification and confirmation (Knapp, 1998; Edward et al., 1992). Usually it is difficult to precisely determine the effects of specific plant traits on grain yield, because these effects are usually limited and often influenced by location in which the plant is grown. These traits can be determined accurately using near isogenic lines. Near isogenic lines are those lines that are not used to identified QTLs but to confirm and further study their effects, and essentially genetically identical except that they vary for a single known gene or locus (Watanabe, 1994; Sherman et al., 2015).

In molecular breeding it is important to work with specific populations, in order to identify genes associated with this trait of interest (Semagn et al., 2010). Near isogenic lines (NIL) vary only in alleles that are responsible for the trait of interest. Near isogenic lines are typically developed through crossing a genotype containing an allele of interest (donor parent) to a genotype containing the desired background alleles (recurrent parent) (Kuraparthy et al., 2007). Making crosses by using different genetic backgrounds in order to create many NILs to assess the informativeness of markers for the QTL and the effectiveness of the QTL in different genetic backgrounds. The resulting QTL-NILs may be directly useable in a breeding program, as opposed to other QTL validation methods that may produce new parental material for the plant breeding program.

QTn.mst-6B Locus

Naruoka et al. (2011) identified *QTn.mst-6B* that influenced productive tiller number based on experiments over two years in Bozeman MT. Based on a nursery in Bozeman, Naruoka et al. (2011) found that the high tiller allele had a positive impact on grain yield under favorable and unfavorable locations, and a negative impact on seed number per head and seed weight. In order to verify the effect of the *QTn.mst-6B*, Naruoka et al. (2011) created a NIL population by selecting a heterozygote for *QTn.mst-6B* markers from a RIL Reeder/Conan population. The objective of experiments reported in this paper was to evaluate the impact of *QTn.mst-6B* at multiple environments and genetic backgrounds utilizing the NILs, and to assess the value of *QTn.mst-6B* under heat and water stress conditions typical of many spring wheat production environments.

Materials and Methods

Plant Materials

Thirteen NILs with contrasting alleles at *QTn.mst-6B* were developed from three crosses, including Reeder/Choteau, Reeder/Hank, and Vida/McNeal. Reeder and Vida contained high productive tiller allele (designated allele 1) and McNeal, Choteau, and Hank had the low productive tiller allele (designated allele 2) (Table 1). To create the NILs in this study, 100 F_4 plants developed by single seed descent were screened with microsatellite markers linked to Two markers *(gwm88 and gwm193)* were used to identify heterozygous lines containing both high productive tiller allele and low productive tiller allele. The marker *xgwm88* was used because it is the most closely linked marker with *QTn.mst-6B* (Naruoka et al., 2011). Heterozygous F_4 plants were self-pollinated, and progeny homozygous for the low and high PTN alleles were selected. Homozygous plants were self-pollinated to generate NILs for field-testing. The F_4 plants are 94% genetically identical, and NILs developed from a single F_4 plant are expected to share 97% genetic identity. The NIL populations allowed testing the effects of the QTL in different genetic backgrounds.

Experimental Design

Thirteen NIL pairs from three crosses with their five parents were evaluated in replicated trials using a Randomized Complete Block Design at two locations in Montana (Bozeman, and Huntley) and two locations in in Washington (Pullman, and Lind) in 2012 and 2013 (Table 1). The locations differed in precipitation, temperatures, and soil nutrients (Tables 2, and 3). All trials included three replications, where each replication included 31 plots. Each plot had four rows of approximately 3 m in length. A total of two NIL pairs from Vida/McNeal, seven pairs from Reeder/Choteau, and four pairs from Reeder/Hank were used in this study.

Phenotypic Data Collection

Phenotypic data collected at all locations included productive tiller number (PTN), days to heading, plant height, grain yield, test weight, and grain protein. In addition, early tiller number, seeds per head, flag leaf length and width, seed weight and harvest index were determined at a subset of locations (Table 2). Early tiller number was counted at 3-1 stage for Zadoks code when the first node was detectable (Zadoks et al., 1974), while PTN (number of tillers that produced spikes) was determined near maturity on a 0.3 m section of row. Heading date was defined as the number of days after Jan 1 when 50% of the main spikes were fully emerged. Flag leaf length (cm) was measured from the flag leaf on the main culm while flag leaf width (cm) was measured at the widest portion of the blade on the leaf. Five leaves were measured per plot. Flag leaf chlorophyll content was measured by a SPAD meter, SPAD is an acronym for special products analysis division of Minolta. Days to senescence from Jan. 1 were defined as the day that 50% of the flag leaves within the plot had lost green color. Plant height was measured from the base of the plant at ground level to the top of the spike excluding awns. The degree of stem solidness was obtained using five stems per plot pulled randomly near crop maturity. A cross section was cut through the center of each internode. Five internode measurements were obtained per stem using a 1 to 5 scale, in which 1 designates a hollow stem and 5 designates a solid stem. Internode scores were summed for each stem to give a number between 5 (hollow) and 25 (completely solid). Single stem scores were averaged for one final reading per plot. Biomass was measured by cutting a row of each plot at ground level and weighing the bundle before threshing. The weight of threshed grain was obtained. Harvest index was calculated as bundle grain weight divided by biomass. Grain yield was determined from the raw grain weight of each plot. Test weight was measured from a sample of cleaned grain on Seedburo (Chicago, IL) test weight scale. A subsample of seed from each plot was analyzed using the single kernel characterization system 4100 (Perten, Hudding, Sweden) to determine seed weight. Protein concentration was obtained on whole grain samples using a Foss Infracted 1241-Grain analyzer (Tecator, Höganas, Sweden)**.** The number of seed per spike was calculated as an average over five spikes randomly sampled from each plot.

Statistical Data Analysis

Data were analyzed using PROC MIXED in SAS (SAS Institute, 2004) over locations and years. All analyses were done using the mean of lines representing each high productive tiller allele and low productive tiller allele. Sources of variation included main effects of location, allele, crosses, families (NIL pair), and interactions allele*cross, allele*location, allele*family. All factors except replications were considered fixed effects (Table 4). The effect of alleles at *QTLn.mst-6B* was compared using a P value from ESTIMATE statements with significance levels set at $p < 0.05$.

Greenhouse Experiment

An experiment with three replications was conducted using the 13 NIL pairs plus parents (Table 1), where three plants were grown per pot in a Randomized Complete Block Design to study the effect of alleles at *QTn.mst-6B* under favorable conditions (nutrition, water, light, and temperature). Sand was used instead of soil as a potting medium to facilitate root washing after harvest. Several fertilizer applications were used to maintain fertility. First, 2.00 g/pot of Osmocote plus 15-9-12 slow release fertilizer was added with the sand before planting. Second, Peter's Professional 20- 20- 20 Everris Company, Doblin / Ohio (Soluble Trace Element Mix) was applied every five to seven days. Third, 2.00 g/pot of Ironite was added every 5-10 days the concentration of Peter's used was 200 ppm. Plants were watered depending on the moisture of the sand. Early tiller number was counted at 3.1 Zadoks score, while the productive tiller number was counted after senescence. The roots were washed before maturity, dried in a plant dryer (temperature was 48.9 ºC) for one week. Dry root weight and above ground dry matter were determined. Data were analyzed using PROC MIXED in SAS (SAS Institute, 2004). Source of variance was including the main effects of allele, cross, families (NILs) and the interaction, allelex*cross, allelex*family. All factors except replication were considered as fixed effects, allele effects were compared by using a P value from ESTIMATE statements with significance levels set at $p < 0.05$.

Results

Naruoka et al. (2011) identified a QTL, termed *QTn.mst-6B*, controlling productive tiller number (PTN) in an RIL population of spring wheat grown over two years in Bozeman MT. In order to evaluate the impact of the allele in different genetic background at multiple locations, near-isogenic lines with alternative alleles at the locus were developed based on selection using the linked microsatellite marker *gwm88* (Table 1). Parents used to donate the high tiller were Reeder and Vida. Vida is a progeny line of Reeder.

To estimate the frequency of the high tiller allele, SNP genotyping data from the Triticeae CAP spring wheat AM panel (available in the T3 database give the T3 website URL) was examined. Based on tetraploid wheat consensus map (Maccaferri et al., 2014 composed of SNP and SSR markers, three SNP markers co-segregating with *gwm88*, and mapped on the spring wheat AM panel were identified. The Vida haplotype for these three markers was shared by 31% of the AM panel lines.

Thirteen pairs of near-isogenic lines with alternative alleles for *QTn.mst-6B* were evaluated in replicated trails in nine locations in Montana and Washington in 2012 and 2013). Table 2 shows temperature range and water condition, while table 3 shows the available soil nutrients for the nine locations. The irrigated nursery in Bozeman 2013 and the 2012 Pullman nursery received greater than 45 cm of annual water. Growing season temperature varied from 12.6 to16.6 °C (Figure 1; Table 2) over the locations. Productive tiller number was measured at all locations while early tiller at Zadoks 3.1 was collected at five locations. Yield component traits were collected over eight locations (Table 2), while physiological and seed-quality traits were collected at a subset of locations (Table 2). Results from the experiments allow determination of direct and indirect effects of *QTn.mst-6B.*

The high tiller allele at *QTn.mst-6B* caused significantly higher early tiller number averaged over all five locations. The number of productive tillers was significantly higher based on the mean over all nine locations. However, the difference between alleles for PTN was significant at only two locations. Based on means over all locations measured, the allele for high tillers also resulted in fewer seeds per head and smaller seed size. The net effect of the high tiller allele on grain yield was not significant based on means over all locations. However, a positive effect of the high tiller allele on grain yield was observed in Bozeman 2012, while the effect of the high tiller allele was negative at Pullman 2013. No significant effect of alleles at *QTn.mst-6B* on grain yield was observed for seven locations (table 5).

Table 6 shows the impact of the high tiller allele on several physiological and agronomic traits. Alleles at *QTn.mst-6B* were neutral for heading date, plant height, harvest index, senescence date, and chlorophyll content. Lines with the high tiller allele had significantly shorter flag leaves in two locations and based on means over all locations. Lines with the high tiller alleles also had significantly less solid stems.

Table 7 shows the effects of alternative alleles at *QTn.mst-6B* on several seed quality traits. No effect was observed for grain protein or grain hardness. However, lines with the high tiller allele had seed with significantly smaller diameter and a higher test weight than lines with the low tiller allele.

The NIL used in these experiments derived from three separate genetic crosses (Table 1). The donors of the high tiller allele at *QTn.mst-6B,* Reeder and Vida, are closely related. However, the cultivars McNeal, Choteau, and Hank have no obvious relationship based on pedigree (unpub. data). Partitioning the results by cross showed that *QTn.mst-6B* significantly impacted productive tiller number in all crosses and early tiller number in two crosses.

Table 8 shows that the NILs showed the expected phenotypes, as NIL with alleles from Vida or Reeder had high tiller number, while NIL with alleles from the other parents had lower tiller number. Thus, the NIL derivation process was successful in developing lines with contrasting alleles. The high tiller allele tended to decrease seed weight and seed per head in all three crosses, though this effect was only significant when combined over all three crosses (Tables 1 and 8).

An experiment was conducted in the greenhouse to assess the impact of *QTn.mst-6B* on roots growth. The high productive tiller allele on *QTn.mst-6B* was associated with large dry roots weight across our three populations tested in the greenhouse, and had a positive effect on dry weight (Table 9).

Discussions

Genetic mapping studies in wheat have identified several quantitative trait loci QTL for yield and its components (Quarrie et al., 2006; Maccaferri et al., 2008). A common observation is that the QTL effects identified in a particular population are not consistent across genetic backgrounds. Additionally, genes and traits that provide an advantage in a particular environment may not function similarly in different locations. Recently, Naruoka et al. (2011) identified a QTL designated *QTn.mst-6B* for increased yield in wheat that was associated with differences in productive tiller number.

The goal of this study was to develop near isogenic lines (NIL) for QTn.mst-6B in several genetic backgrounds, to assess the impact of the QTL across several environments in the spring wheat growing region of the Western United States, and to assess the value of *QTn.mst-6B* under drought and heat stress typical of many spring wheat production environments. The current study focused on the impact of *QTn.mst-6B* on yield, yield components, agronomic traits and seed quality under different locations.

Impact of *QTn.mst-6B* on Yield and Yield Components

Fisher (1985) and reviewed by Naruoka et al. (2011) reported that heat and water stress inhibited the initiation, growth, survival, and reproduction of tillers in wheat. The sensitivity of young tillers to heat and drought stress causes tiller mortality and a reduction of potential fertile tillers (Ahmed et al., 2010; McDowell et al., 2008). These results are consistent with our results on early tiller and productive tiller number. Lines with the favorable allele at *QTn.mst-6B* showed a larger number of early tillers in all five locations tested (Table 4). However, high early tiller number did not typically lead to a high number of productive tillers. Although the mean productive tiller number was higher for the favorable allele over all nine locations, PTN was significantly higher for the high tiller allele in only two individual locations. These locations received the highest amount of rainfall or irrigation during the growing season of the nine tested locations (Table 2). This suggests that ample moisture resulted in low rates of abortion of the early tillers.

The impact of *QTn.mst-6B* on seed number per head and individual seed weight were measured in several locations. In general, the allele for high tiller number at *QTn.mst-6B* resulted in fewer seed per head and smaller seed (Table 4). Previous studies have shown a negative relationship between seed number per head and seed weight (Burstin et al., 2007; Naruoka et al., 2011). The allele for high tillers caused a decline in both of these yield components over-all, significantly in Huntley, Lind, Pullman 2012, and Huntley 2013. Thus, seed number per head and individual seed weight were negatively impacted by the high tiller allele even in cases where high productive tiller number did not occur. Naruoka et al. (2011) also found that there was a negative correlation between productive tiller number and seed number per head. Seed number per head is determined during morphogenesis stage, while seed weight is determined during grain filling phase. Heat and water stress during morphogenesis stage may negatively affect pollen viability and fertilization thereby reducing seed number per head, while heat and water stress after flowering or during seed filling stage decreases seed growth period resulting smaller seed (Ceccarelli, 1987). The allele for increased tiller number appears to negatively impact both of these parameters.

Grain yield is a complex trait determined by genotype, other traits and environmental conditions. Several studies reported a negative correlation between productive tiller number per plant and grain yield per plant at genetic and phenotypic levels (Khan et al., 2010; Iftikhar et al., 2012). Conversely Ali et al. (2009) found that there was a strong and positive association between productive tillers per plant and grain yield. Elhani et al. (2007) reported that genotypes with high productive tiller number showed grain yield similar to genotypes with low productive tiller number under heat and water stress. This is consistent with our results, in that we found lines with high productive tiller allele at Q*Tn.mst-6B* had similar grain yield as lines with the low productive tiller allele in most locations and based on mean over-all locations. Two reasons are apparent. First, although the favorable allele caused increased early tiller number, this did not translate into higher PTN except in the highest moisture locations. Second, the high tiller allele was associated with reduced seed per head and reduced seed size. Thus, the direct effect of the positive allele for tiller number at *QTn.mst-6B* was negated by indirect effects of few seed per head and small seed.

Impact of *QTn.mst-6B* on Agronomic Traits

Other studies reported that heat and water stress reduced plant height (Irfaq et al., 2005; and Nezhadahmadi et al., 2013). Semi-dwarf lines with *Rht-B1b* or *Rht-D1b* also show high productive tiller number, more seed per head, later heading, smaller seed, lower test weight and lower protein (Irfaq et al., 2005). Naruoka et al. (2011) reported that plant height was not associated with *QTn.mst-6B.* This is consistent with our results. Flag leaf length and flag leaf width are also important agronomic traits that may influence final grain yield.

Our results showed that lines with high tiller allele had shorter flag leaves in two of three locations than lines with low tiller allele. The loss of photosynthetic capacity due to smaller flag leaves may contribute to smaller seed in lines with the high tiller allele at

QTn.mst-6B. Solid stems are an important trait for resistance to the wheat stem sawfly *Cephus cinctus* Norton (Sherman et al., 2010; and Sherman et al., 2014).

An important trait in areas of the northern Great Plains is resistance to the wheat stem sawfly (*Cephus cinctus* Norton). Damaged caused by the insect is due to larval feeding inside the stem. The primary means of control is pith-filled or solid stems, to inhibit the larvae inside the stem (Cook et al., 2004). Our results showed that lines with high tiller allele had significantly less solid stems than lines with the low tiller allele, suggesting a potentially negative impact of the high tiller allele at *QTn.mst-6B* on wheat stem sawfly resistance.

Impact of *QTn.mst-6B* on Seed Quality

The goal of wheat breeders is to improve both yield and quality. Therefore our study involved quality traits protein, hardness, diameter, and test weight. Lines with high tiller allele had fewer seed per head and smaller seed size. However, our results showed that *QTn.mst-6B* allele for high tillers did not affect protein content or hardness. Although lines with high tiller allele were significantly smaller, they showed higher test weight over all locations.

Impact of *QTn.mst-6B* Over Crosses

Most traits that plant breeders are interesting in quantitative and complex traits, which are determined by genetic structures, environmental factors and the interactions between genetics and environments. Thus, a gene may have different effects depending on genetic background. We studied the impact of *QTn.mst-6B* on several traits using NIL developed from three populations, Vida/McNeal, Reeder/Choteau, and Reeder/Hank. Vida and Reeder contain the high tiller allele, and Vida is a progeny from the cross Reeder/Scholar (Lanning et al., 2012). The high productive tiller allele significantly affected early tiller number at all five locations that we measured this trait in and over our three crosses Vida/McNeal, Reeder/ Choteau, and Reeder/Hank. Productive tiller number was affected significantly in only one cross (Reeder/Choteau) (Table 8). Thus, the impact of *QTn.mst-6B* was consistent for early tiller, but inconsistent for productive tiller number. However, the high tiller allele reduced seed number per head and seed weight over all three crosses, and seed weight in one cross. Grain yield was not impacted by *QTn.mst-6B* in any of the three crosses. Thus, the impact of *QTn.mst-6B* was consistent for early tiller number and seed per head, but inconsistent for productive tiller number and other agronomic traits. This is reflected in the fact that yield was not typically impacted by *QTn.mst-6B.*

Greenhouse Experiment

Several studies have suggested that lines with high productive tiller are more beneficial for yield productivity under semiarid environments, as high tiller number is associated with larger root size which improves water and nutrient absorption **(**Narayanan and Prasad 2014).Other studies reported that lines with low productive tiller number would be more beneficial for yield productivity under semiarid conditions (Naruoka et al., 2011). In a greenhouse experiment, lines with the high tiller number allele produced a greater root weight than lines with low tiller number allele (An et al., 2006). This suggests that the high tiller number allele may be beneficial in arid conditions due to greater root growth.

Conclusion

In conclusion, our results show that *QTn.mst-6B* has significant effects on early tiller number, regardless of the location or genetic background. Interestingly we found that productive tiller number was significantly impacted by *QTn.mst-6B* at only at two locations. Overall, our results suggest that *QTn.mst-6B* leads to high early tiller initiation. This translates into higher productive tiller number in locations with ample moisture at tiller initiation. However, higher tiller number due to *QTn.mst-6B* led to increased yield in only one of nine locations tested. This is likely due to a decrease in seed number per head and seed size also associated with the high tiller allele. Our results showed that lines with high tiller allele on *QTn.mst-6B* had similar production as lines with alternative allele under heat and water stress. Thus, the high tiller allele at *QTn.mst-6B* provides the plant with the ability to produce extra tillers when conditions are favorable, which is sensed by the plant after tiller initiation. If conditions are not favorable, our results suggest that the early tillers are aborted with no yield penalty. Thus, the high tiller allele provides plasticity to the plant to allow increased tiller production in favorable years. However, in the environments tested, increased tiller number did not lead to increased yield potential in most cases.

Table 1. Crosses and number of near-isogenic pairs per cross-used to study the effect of alternative alleles for tiller number at *QTn.mst-6B*

Cross	**Pedigree**	**No. NIL Pairs**
1	Vida/McNeal	2
2	Reeder/Choteau	7
3	Reeder/Hank	4

Allele 1 = High tiller allele represented by Reeder and Vida parent
Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank.

Table 2. Temperature (°C) and precipitation (cm) for nine locations used to compare 13 sets of near-isogenic lines varying for alleles at *QTn.mst-6B.*

Location	**Year**	**Water Applied (cm)**		**Temperature (°C)**	**Measured Traits†**		
		Sep-Aug	**Apr-Jul**	**Apr-Jul**	**Yield Components**	**Plant Traits**	**Seed Related**
Bozeman-dry	2012	22.9	14.1	14.1	ETN, PTN, SPH, SW, GY	HD, PH, SD, Ch, SS,HI, FLW, FLL	TW, GP, Di, Hr
Bozeman-dry	2013	27.8	17.9	12.6	ETN, PTN, SPH, SW, GY	HD, PH, SD, Ch, SS, HI , FLW, FLL	TW, GP, Di, Hr
Bozeman-irrigated	2013	58.3	48.4	12.6	ETN, PTN, , SPH, SW, GY	HD, PH, SD, Ch, SS, HI, FLW, FLL	TW, GP, Di, Hr
Huntley-dry	2012	21.3	8.8	16.6	ETN, PTN, SPH, SW, GY	HD, PH, Ch, SS, HI	TW, GP, Di, Hr
Huntley-dry	2013	31.1	21.8	14.3	ETN, PTN, SPH, SW, GY	HD, PH, SS, HI	TW, GP, Di, Hr
Lind-dry	2012	23	11.9	15.4	PTN, SPH, SW, GY	HD, PH, SD	TW, GP, Di, Hr
Lind-dry	2013	22.2	5.2	16.1	PTN, SPH, SW, GY		
Pullman-dry	2012	45.1	11.2	13.3	PTN, SPH, SW, GY	HD, PH, SD	TW, GP, Di, Hr
Pullman-dry	2013	37.4	12.5	13.5	PTN, SPH, SW, GY	HD, PH, SD	TW, GP, Di, Hr

†ETN= Early tiller number, PTN = Productive tiller number, SPS= Seed per head, SW = Seed Weight, GY = Grain yield, TW= test weight, GP= Grain protein, Di= Seed diameter, Hr= Seed hardness, HD = Heading date (days from Jan 1), PH = plant height, HI = Harvest index, SS = Stem solidness, FLS = Flag leaf senes°ence(days from Jan 1), FLW= Flag leaf width, FLL= Flag leaf length

Table 3. Soil test for Nitrogen, phosphate, and potassium over all the nine locations where we planted our NILs trail

Location	**Nitrogen ppm**	**Phosphate ppm**	**Potassium ppm**	**PH**	**Organic matter %**
Bozeman-dry 12	50	14	243	8.0	2.5
Bozeman-dry 13	50	18	283	7.4	2.1
Bozeman-irrigated13	50	20	413	8.2	2.6
Huntley-dry12	16	15	336	8.3	3.2
Huntley-dry13	13	10	359	8	1.3
Lind-dry12	45.5	18	393	5.9	0.97
Lind-dry13	7	5.1	465	6.2	1.15
Pullman-dry12	5.5	25	149	5.8	2.1
Pullman-dry13	9.75	21	165	5.1	1.88

Table 4. Sources of variance used on SAS code to analyze data for 13 NIL pairs grown over nine locations.

Source of variance	**Method**
LOC	Fixed
Rep	Fixed
REP (LOC)	Random
Cross	Fixed
LOC*Cross	Fixed
Family	Random
Family (Cross)	Random
LOC*Family (Cross)	Random
ALLELE	Fixed
LOC*ALLELE	Fixed
Cross*ALLELE	Fixed
LOC*Cross*ALLELE	Fixed
Family*ALLELE (Cross)	Random
LOC*Family*ALLE (Cross)	Random

Table 5. Impact of alternative alleles at *QTn.mst-6B* in set of spring wheat near-isogenic lines on tiller number and yield components traits based on trials over nine locations.

Location	**Early tiller number (m^{-1})**		**Productive tiller number (m^{-1})**		**Seed number per head**		**Seed weight (mg)**		**Yield (kg/ha)**	
	Allele 1	**Allele2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele2**	**Allele 1**	**Allele 2**
Boz DRY12	81.74**	68.98	50.00*	47.96	31.30	31.90	33.92	35.26	3688* *	3449
BozIRRI 13	111.46***	86.66	61.09***	54.00	39.11	38.67	35.89	35.82	3832	3738
BozDRY 13	78.21***	64.52	49.72	47.23	39.52	39.94	30.91	30.42	2355	2469
Hun12	88.84**	77.99	48.52	47.58	38.84*	41.12	27.38	28.05	2458	2522
Hun13	70.99**	59.11	51.17**	45.15	35.83	36.348	32.76	34.08	3292	3346
Lind 12	-	-	16.04	14.95	32.70	34.43	37.32*	39.26	1745	1727
Lind13	-	-	16.93	15.51	30.49	32.09	30.49	32.09	1520	1401
Pul12	-	-	27.40	26.61	41.22	42.04	32.64*	35.02	4564	4593
Pull13	-	-	30.40	28.85	38.17	38.90	38.39	39.63	3824*	4043
Mean	86.23***	71.45	39.03***	36.43	36.46**	37.23	33.31***	34.40	3031	3032

*, **, ***. Significant at P < 0.05, 0.01, and 0.001.

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Ha

Table 6 a. The impact of alleles at *QTn.mst-6B* on several agronomic and physiological traits for a set of spring near-isogenic lines grown in nine locations.

Location	**Head Date (days from 1 Jun)**		**Plant Height (cm)**		**Harvest Index (%)**		**Senescence Date (days from 1 Jan)**	
	Allele1	**Allele2**	**Allele 1**	**Allele2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele2**
Boz12	184.34	184.97	76.23	76.71	43.11	42.91	218.2	218.54
BozIRR13	184.2	184.9	89.54	88.68	40.64	41.8	219.66	219.01
BozDRY13	184.51	184.13	79.45	79.7	43.34	45.01	211.96	211.66
Hun12	162.32	161.64	84.14	84.12	39.53	40.06	-	-
Hun13	170.45	169.94	87.29	86.7	39.35	39.51	-	-
Lind 12	156.37	155.91	66.12	67.2	-	-	191.17	191.32
Lind13	155.75	155.1	57.9	58.79	-	-		
Pull12	178.45	177.96	80.93	81.25	-	-	206.9	206.77
Pull13	166.71	166.29	91.14	92.67	-	-		
Mean	171.46	171.09	79.19	79.54	41.19	41.87	209.58	209.46

*, **, *** Significant at $P < 0.05$, 0.01, and 0.001.

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

† Solid stem is on a scale of 5-25, where 5 is hollow and 25 is completely solid.

Table 6 b. The impact of alleles at *QTn.mst-6B* on several agronomic and physiological traits for a set of spring near-isogenic lines grown in nine locations.

Location	**Chlorophyll (%)**		**Flag Leaf Width (cm)**		**Flag Leaf Length (cm)**		**Solid Stem†**	
	Allele 1	**Allele2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**
Boz12	51.9	51.75	1.75	1.63	19.19*	19.9	13.6	14.97
BozIRR13	53.0799	52.63	1.61	1.67	22.245	22.89	8.94	10.13
BozDRY13	39.5274	39.94	1.57	1.63	20.16**	21.31	9.52	9.93
Hun12	47.95	47.42	-	-	-	-	10.06	10.69
Hun13	-	-	-	-	-	-	13.04	14.34
Lind 12	36.47*	39.17	-	-	-	-	-	-
Lind13	-	-	-	-	-	-	-	-
Pull12	48.61	48.16	-	-	-	-	-	-
Pull13	-	-	-	-	-	-	-	-
Mean	46.26	46.51	1.65	1.64	21.01***	21.43	11.24***	12.2

*, **, *** Significant at $P < 0.05$, 0.01, and 0.001.

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

† Solid stem is on a scale of 5-25, where 5 is hollow and 25 is completely solid.

Table 7. Impact of alternative alleles at *QTn.mst-6B* in set of spring wheat near-isogenic lines on seed traits over nine locations on seed traits.

Location	**Protein%**		**Diameter (mg)**		**SKCS Hardness**		**Test weight (kg m^{-3})**	
	Allele 1	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**
Boz12	14.97	14.93	2.89	2.94	76.7	76.234	782.88	779.53
BozIRR13	15.03	15.5	3.1	3	72.91	73.91	786.8***	777.91
BozDRY13	15.84	15.78	2.77	2.77	76.9***	80.81	754.81	752.41
Hun12	13.14	13.15	2.64	2.66	88.22	87.53	778.35*	756.19
Hun13	10.16	10.04	2.81	2.86	83.55	82.49	791.81	788.2
Lind 12	16.62	16.63	3.01***	3.1	72.54	71.58	760.18	763.58
Lind13	-	-	-	-	-	-	-	-
Pull12	11.35	11.48	2.79***	2.88	85.4	82.96	796.88	794.08
Pull13			-	-	-	-	784.64	780.31
Mean	13.79	13.57	2.85***	2.89	79.46	79.36	773.39***	769.92

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001.

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 8. Impact of alternative alleles at *QTn.mst-6B* in a set of spring wheat near-isogenic lines on yield component traits for near-isogenic lines derived from three crosses averaged over environments.

Cross	**Early tiller number (m-^{1})**		**Productive tiller number (m-^{1})**		**Seed number per head**		**Seed weight (mg)**		**Yield (kg/ha)**	
	Allele 1	**Allele2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**	**Allele 1**	**Allele 2**
Vida/McNeal	102.12**	79.93	42.16	40.444	35.531	36.6177	33.69	34.84	3327	3410
Reeder/Choteau	88.44**	74.93	40.66***	36.984	36.36	37.3459	31.09*	32.37	2820	2851
Reeder/Hank	68.13*	59.49	34.27*	31.862	37.158	37.8412	35.16	36.00	2947	2836
Mean	86.23***	71.45	39.03***	36.43	36.46**	37.23	33.31***	34.4	3031	3032

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001.

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 9. Results from a greenhouse trial using near-isogenic lines to determine the effects of (*QTn.mst-6B)* on early tiller number, productive tiller number, root weight and shoot dry weight.

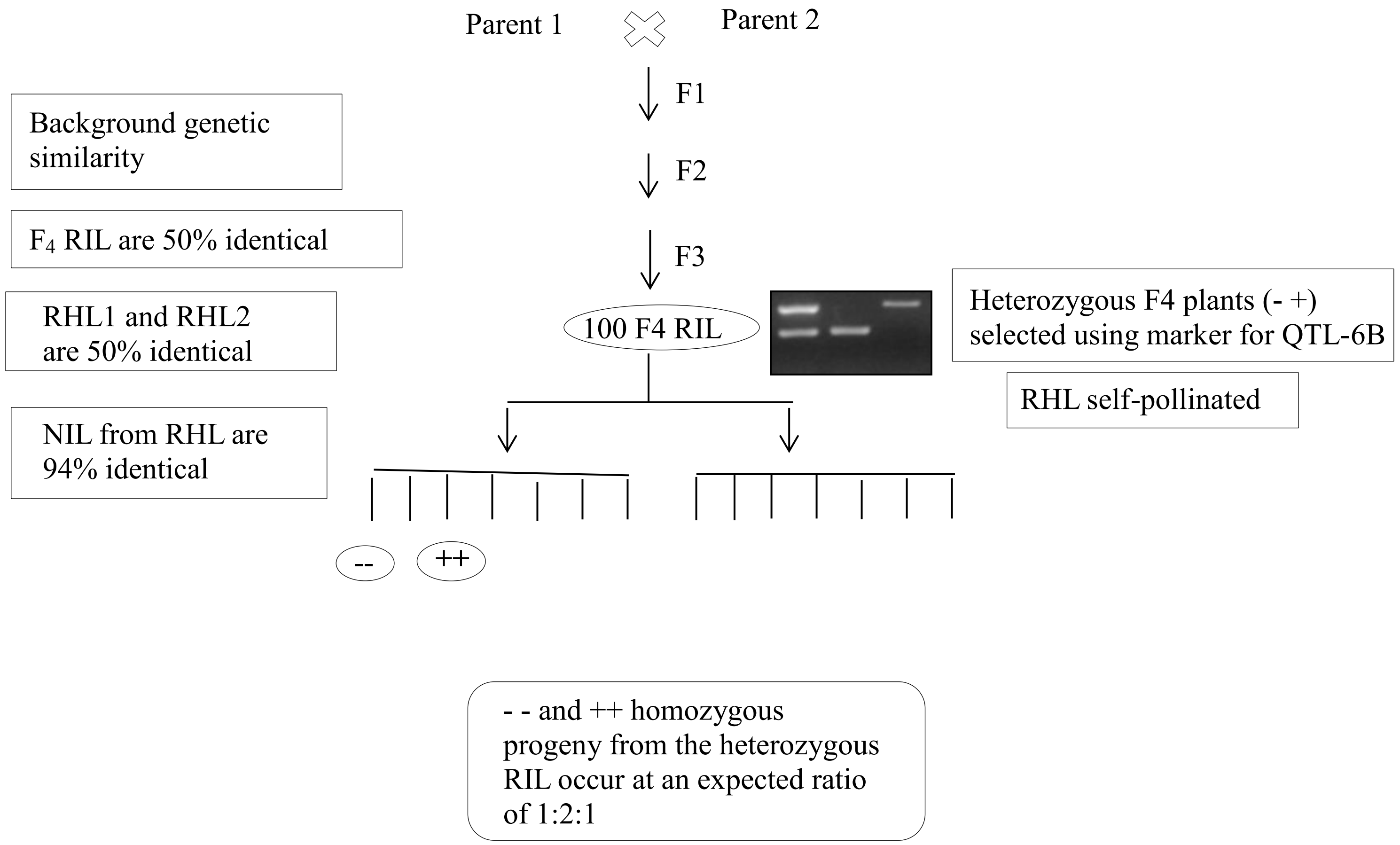
Early tiller number (pot)		Productive tiller number (pot)		Root weight (mg)		Dry weight (mg)	
Allele 1	Allele2	Allele 1	Allele2	Allele 1	Allele2	Allele 1	Allele2
23.04***	17.5	16.04***	10.99	12.19***	10.76	44.77	42.46

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Figure 1. Method for derivation of near isogenic lines investigated determines the effects of alleles at *QTn.mst-6B* on agronomic traits in spring wheat. RIL= Recombinant inbred Line, RHL = Residual Heterozygous Line, NIL= Near Isogenic Line. Parent 1 is Vida or Reeder, while parent 2 is McNeal, Choteau, or Hank.



CHAPTER 3

A TILLER GENE AFFECTS THE PHENOTYPIC PLASTICITY ON SPRING WHEAT

Literature Review

Competition

Competition is a negative interaction among organisms whenever two or more organisms require the same limited resource. Plants require soil nutrients, light, and water for growth, reproduction, and survival, while animals require food and water. However organisms cannot acquire a resource when other organisms consume the same resource, therefore competitors reduce each other's growth, reproduction, and survival. There are two basic types of competition, including competition within species called intraspecific competition, and competition among species called interspecific competition. Intraspecific competition occurs between individuals within species that require the same limited resources, and some individuals may not acquire enough resources. This may result in death or lack of reproduction, leading to slow population growth. Interspecific competition occurs between individuals in different species when plants require the same limited resources. In this case, interspecific competition could change the population size of many species populations at the same time (Sharifi et al., 2009).

Competition Components

Competitive interactions involve two different processes; including the effect of plant or species on others, and the ability of one plant, or species to inhibit the growth of another plant, or species. Competitive response is the ability of a plant to resist competition with its neighbors (Goldberg and Werner, 1983; Goldberg and Fleetwood, 1987; Goldberg, 1990; Goldberg and Landa, 1991; and Goldberg, 1996). Plants or species differ in their ability to compete for water, soil nutrients and light resources (Goldberg, 1996; and Keddy et al., 2002). When resources are limited, a plant's competitive ability may influence its ability to survive, grow, and reproduce (Fageria et al., 2008; and Wilson and Keddy, 1986). There are three types of interaction between competitive effect and competitive response. These include: 1- small effect on and response to other plants, or species in the community which are not limited by the same resources and will not be affected by changes in the abundance of the other plants, or species in the community; 2- asymmetric competitive ability means large competitive effect on but little competitive response to other species or individuals due to using a common resources; and 3- large competitive effects and response to one another. The first two types could occur among species, while the third one could be either between plants within species, or between two different species (Aarssen, 1983; Miller and Werner, 1987).

Organisms such as plants that cannot move when the environmental conditions are unfavorable may evolve four main strategies in response to environmental variation; 1- phenotypic plasticity; whereby the plant could alternate phenotypes produced in response to the change in environmental conditions; 2- generalization, involving a single general purpose phenotype; 3- specialization involving a single well-adapted phenotype; and 4- bet hedging, including either several phenotypes or single phenotypes generated probabilistically (Dewitt and Langerhans, 2004; Keunen and Fischer, 2004; and Sadras and Rebetzke, 2013). The work reported in this thesis involves phenotypic plasticity in spring wheat plants.

Phenotypic Plasticity

Phenotypic plasticity can be defined as the ability of individuals to alter physiology, morphology and/or behavior in response to a change in the environmental conditions. Principles of plasticity include 1- the plasticity of a trait is an independent property of that trait and it's under own specific genetic control; 2- plasticity is specific for a trait related to particular environmental influence; and 3- there is a hierarchy of plasticity (usually, stable traits associated with plastic traits). The amount by which the expressions of individual traits of a genotype are changed by different environments is a measure of the plasticity. Plasticity can have two manifestations, morphological and physiological. All changes impact physiology. In cases where physiological changes have predominantly morphological end effects, the change could occur during the course of development. These are likely to be permanent for the organ involved. In contrast, physiological change could be occur at any time, even in mature organs, and may be reversible and not permanent. In an individual genotype some traits may remain the same in different environmental conditions. These traits are called non-plastic. Non-plastic traits in wheat include leaf shape, leaf margin serration, shape of inflorescence, and floral characters. Traits that are changed in different environments are called plastic traits. Plastic traits in wheat involve size of vegetative parts, number of tillers, number of leaves, and elongation of stem (Bonaparte and Brawn, 1975; Nicotra et al., 2010).

The number of tillers is one of the most important plastic traits in wheat. Tiller number can be greatly modified by environmental conditions including management through soil nutrients, plant density, temperature, and water. Tiller number is under genetic control (Innes et al., 1981). Several genes determine tiller number in spring wheat. An allele at *QTn.mst-6B* was identified recently by Naruoka et al. (2011), which caused increased tiller formation. The locus *QTn.mst-6B* determines productive tiller number (PTN) in spring wheat based on an RIL population of spring wheat grown over two years in Bozeman MT (Naruaoka et al., 2011). Other genes influence free tiller number. These include *tin* and *3tin* on chromosomes 1A and 3A respectively (Mitchell et al., 2012; Sadras et al. 2013). The goal of this study was to assess the impact of alleles at *QTn.mst-6B* under different intraspecific competition levels and different levels of available water.

Materials and Methods

Plant Material and Experimental Design

Five pairs of near-isogenic lines (NILs) were chosen randomly from thirteen NILs with contrasting alleles at *QTn.mst-6B* described in the previous chapter. These pairs derived from two genetic backgrounds, two pairs from Vida/McNeal, and three pairs from Reeder/Choteau. Three treatments were imposed which differed in their competition levels. ‘Border’ (the highest competition level) was comprised of three rows with the space between row was 0.3m. The center row was one of the NILs, while the two border row was planted with the semi dwarf variety Reeder. ‘No Border’ (intermediate competition level) had a NIL planted in the center row, while the two border rows were empty. Thus, there was 0.6m between the NIL rows and the adjacent row. In the first two treatments, Border and no Border, the number of plants in the NIL row was approximately 100. For the ‘Spaced’ treatment (lowest competition level), the Space between two rows was 0. 6m. each row contained approximately five plants in 2012, and ten plants on 2013 from one of the NILs planted in the center row. Competition experiments were planted at three environments: Bozeman dry in 2012 and Bozeman dry and irrigated in 2013. All trials included three replications of 30 plots, including 10 experimental lines (5 pairs of NILs) and three treatments (Border, No Border, and Spaced). Each plot consisted of three rows of approximately 3m in length.

Phenotypic Data Collection

Early tiller number (ETN) per m-1 was not counted in this study as early tiller number for the same populations and environments has already been determined as described in the previous chapter. Secondly, since the counting of early tillers is destructive, there were not sufficient plants for the Space treatment. Productive tiller number (PTN) was measured at maturity; Productive tiller number was given for five plants in the Spaced treatment and divided by five to count PTN per plant. Yield was measured by using kg/ha for Border and No Border treatments and g/plant for Space treatment. All other traits, yield components (seed number per head and seed weight), agronomic traits (heading date, chlorophyll content, plant height, and flag leaf length and width), and quality traits (protein content, seed hardness, test weight, and seed diameter) were measured as described in the previous chapter.

Statistical Data Analysis

A randomized complete block design was used in 2012, while a split plot design was used in both dryland and irrigated nurseries in 2013 to evaluate the impact of treatments. Treatments were considered main plots, and the NILs were subplots. Data for all traits except productive tiller number and yield for Space treatment were analyzed using PROC MIXED in SAS (SAS Institute, 2004) separately for 2012 and combined over environments in 2013. Productive tiller number and yield for Space treatment were analyzed separately in that units of measurement were different sources of variation considered as fixed factors where treatment, allele, crosses, while replication and families (NIL pairs) were considered as random factors for 2012 (Table 10). In 2013, a split plot design was employed. Sources of variation included environment, treatment, cross, and allele. Treatments and allele were considered as fixed factors, whereas replication and cross were considered as random factors (Table 9). The effect of alleles at *QTLn.mst-6B* was compared from the ESTIMATE statements with significance levels set at $p < 0.05$.

Competition effects were determined by differences between treatments or differences between high and low productive tiller alleles at *QTn.mst-6B* within and among treatments. Response to competition (RC) was calculated by using this equation:

Phenotypic plasticity = RC = 100*(Tɪɕ -Tɦɕ)/ Tɦɕ

Where Tɪɕ was trait mean in No Border treatment, and Tɦɕ was trait mean in Border treatment.

Greenhouse Experiments

A randomized complete block competition experiment with five replications was conducted to study the effects alleles at *QTn.mst-6B* under different levels of competition. Two NIL pairs were tested under three competition levels: 2 plants per pots, 6 plants per pot, and 12 plants per pot (Table 11). Pot size was 1500 ml. Pots were filled with standard greenhouse soil mixture several fertilizer applications were used based on treatment to maintain fertility. First, Peter's Professional 20- 20- 20 Everris Company, Doblin / Ohio (Soluble Trace Element Mix) was applied every fifteen days in to the low competition treatment (2 plants per pot), and every ten days for the intermediate competition level (6 plants per pot), and every five days for the high competition treatment (12 plants per pot) the concentration that used for peter was 200 ppm. Secondly, 2.00 g/pot of Ironite were added every five days to all treatment levels. Plants were watered depending on the moisture of soil (0- 2 times per day).

This experiment was repeated using sand instead of soil as a potting medium to facilitate root washing after harvest. Several fertilizer applications were used to maintain fertility. First and 2.00 g/pot of Osmocote Plus 15-9-12 slow release fertilizer was added with the sand before planting. Second, Peter's Professional 20-20-20 Everris Company, Doblin / Ohio (Soluble Trace Element Mix) was applied every seven days in low competition treatment (2 plants per pot), every five days for the intermediate competition level (6 plants per pot), and every three days for the highest competition treatment (12 plants per pot) the concentration that used for peter was 200 ppm. Third, 2.00 g/pot of Ironite were added every 5-10 days to all treatments according to the appearance of the individual plants. Plants were watered depending on the moisture of the sand (1-3 times per day).

Early tiller number (ETN) was counted at 3.1 Zadoks score (Zadoks et al., 1974), while the productive tillers number (PTN) was counted at maturity. The roots were washed at plant harvest, placed in a plant dryer for one week at 48.9 ºC, after which dry root weight. Data were analyzed using PROC MIXED in SAS (SAS Institute, 2004). Sources of variation included treatment, allele, cross, family (NILs) and their interaction; all factors except family and replication were considered as fixed factors, allele effects were compared by using ESTIMATE statements with significance levels set at $p < 0.05$.

Results

One of the most important plastic yield components in wheat is productive tiller number (PTN). Like most yield components PTN is a quantitative trait. Naruoka et al. (2011) identified *QTn.mst-6B* as one of the QTL that determined productive tiller number. Using five pairs of near-isogenic lines (NILs) differing for high and low tiller number, in two genetic backgrounds to test the effect of allelic variation at *QTn.mst-6B* under different competition levels and levels of available water. The goal of this study was to assess the value of *QTn.mst-6B* under drought and heat stress typical of many spring wheat production environments, and to assess the impact of *QTn.mst-6B* under different intraspecific competition levels. This study imposed three levels of competition on NILs that varied for alleles at a locus for tiller production, *QTn.mst-6B*.

The high tiller allele at *QTn.mst-6B* had a significant effect on initiation of early tiller number over five environments (Chapter 2), including the three environments for the current study (Table 4). Table 11 shows that the high tiller allele at *QTn.mst-6B* affected the productive tiller number significantly only in the lowest competition Space treatment in 2012. In 2013, *QTn.mst-6B* had a significant effect on Productive tiller number in both No Border, and Space treatments in the dryland nursery and in all three treatments in the irrigated nursery with the greatest effect seen in the Space treatment (Table 14). The high PTN allele in the Space treatment in 2012 was associated with high seed number per head, while high PTN allele at *QTn.mst-6B* affected seed number per head only in No Border, treatment in the irrigated nursery. Seed weight was affected significantly by alternative allele at *QTn.mst-6B* and over all treatments in 2012. In 2013 there was a significant effect for the alternative allele at *QTn.mst-6B* only at the two treatments with low competition levels for both dry and irrigated nurseries. There was no significant effect for the high tiller allele *QTn.mst-6B* on yield under any competition levels in 2012. The effect of *QTn.mst-6B* on yield was only significant in the No Border, treatment in the irrigated nursery (Tables 11 and14).

Tables 12 and 15, show the effects alternate allele at *QTn.mst-6B* on several physiological and agronomic traits under different levels of competition for 2012 and 2013, respectively. Alternative alleles at *QTn.mst-6B* affected plant height in Border, and Space treatments at the dry nursery 2013, and harvest index in No Border, treatment. Alternative alleles at *QTn.mst-6B* affected flag leaf width for the No Border, treatment at irrigated nursery in 2013. The high tiller allele at *QTn.mst-6B* affected senescence date in Space treatment for both dry and irrigated nurseries in 2013.

Tables 13 and 16 show the effects of high productive tiller number at *QTn.mst-6B* on several seed traits. The alternative allele affected test weight only in the border treatment in 2012. This trait was not measured in 2013, also alternative alleles at *QTn.mst-6B* affected seed diameter over all competition levels in the dry nursery in 2012. Diameter was only affected by *QTn.mst-6B* for the two treatments with lowest competition levels, No Border, and Space, in the irrigated nursery in 2013. Alleles at *QTn.mst-6B* affected grain hardness only in the Border, treatment and protein in Space treatment in 2012 (Table 12). There were no effects for *QTn.mst-6B* on hardness or protein in either dry or irrigated nurseries 2013 (Table 16).

Response to competition for the low and high tiller alleles was calculated for only the highest competition levels (Border, No Border) treatments. The Space treatment was not included as yield and PTN data was recorded on a per plant basis rather than a row basis as for the Border, No Border, plots (Table 17). None of the differences between alleles were significant ($P < 0.05$) but several trends were observed. Figure 2 shows that the high tiller allele at *QTn.mst-6B* resulted in a greater response to competition than the alternative allele for dry land nurseries in both 2012 and 2013. The low tiller allele showed greater response to competition levels than high tiller allele in the irrigated nursery in 2013. Figure 3 shows the impact of alleles at *QTn.mst-6B* under Border, (high competition level) and No Border, (lower competition level) treatments on seed number per head. The low tiller allele showed higher response in the dryland nursery in 2012 and the irrigated nursery in 2013. The high tiller allele showed a higher response to competition in the dryland nursery in 2013. Both alleles at *QTn.mst-6B* showed a high response to competition for seed weight over all environments (Figure 4). Figure 5 shows that the low tiller resulted in higher response to the competition for yield in the dry nursery 2012. The high tiller allele showed a high response at the irrigated nursery in 2013, while in the dryland nursery in 2013 both alleles had the same response to competition.

Greenhouse Competition Experiments

Two experiments were conducted in the greenhouse to test the impact of *QTn.mst-6B* on root weight under different competition levels, and to test the relationships between productive tiller number and root weight under three competition treatments. Two growth media, including sand and soil mix, were used. The NIL pairs used in these experiments are shown in Table 1. Vida and Reeder provided the high tiller allele *QTn.mst-6B* for our NIL pairs while McNeal and Choteau provided the alternative allele. Table 17 shows that the *QTn.mst-6B* affected early tiller number significantly for the two treatments with lower competition levels (2 plants per pot, 6 plants per pot) for the sand experiment. For the soil experiment, *QTn.mst-6B* had an impact only at the lowest competition level (2 plants per pot). Alleles at *QTn.mst-6B* affected the productive tiller number significantly at the two lower competition levels (2 plants per pot, 6 plants per pot) for both sand and soil nurseries (Table 18). Alleles at *QTn.mst-6B* affected root weight significantly at the two treatments that had the lowest competition levels (Table 17). This was measured only in the sand treatment.

Discussion

Interspecific competition has significant effects on yield, yield components, physiological, agronomic and seed traits. If competition is too high the competition for available resources (water, nutrients, and lights) will affect growth and reproduction. If plant density is lower than optimum, then the production per hectare will be lower (Jacquard, 1968; Sharifi et al., 2009) Competition effects can be defined as the ability of a plant to reduce the performance of other plants, and competition response may be defined as the ability of a plant to perform relatively well in the presence of competition (Sharifi et al., 2009). Several studies have concentrated on competition effects, others concentrated on competition response, but only a few studies concentrated on both competition effects and response. We studied competition effects and response to test the impact of *QTn.mst-6B* on yield and yield components under different competition levels. Naruoka et al. (2011) reported that *QTn.mst-6B* impacted productive tiller number in spring wheat under favorable and unfavorable environments.

Impact of *QTn.mst-6B* on Yield and Yield Components Under Three Competition Levels

Productive tiller number is an important yield component and a trait that shows plasticity. For the experiments reported here, the allele at *QTn.mst-6B* for high productive tiller number influenced PTN in the No Border treatment in the 2012 and the dry land nursery in 2013. This QTL influenced tiller number at all competition levels in the irrigated nursery in 2013. Aisawi and Foulkes (2012) found that lines lacking the *tin* allele for reduced tillers produced more productive tillers than lines with the *tin* allele under low competition level. These results are supported by Wilkinson, 1963; Duggun et al., 2005. Other researchers (Kirby and Faris 1972; Goldberg et al., 1987; Hussain et al., 2001; Donaldson et al., 2009; and Nasire et al., 2012) found that high-density increases tiller number per unit area due to decreased space between plants. While high plant density increases productive tiller number per unit area, low plant density increased productive tiller number per plant, but those increases did not compensate from decreased productive tiller number per unit area.

Our results show that the high tiller allele at *QTn.mst-6B* caused reduced seed number per head in the Space treatment (the low competition level) on dryland 2012, and on No Border treatment (the intermediate competition level) at irrigated nursery 2013. Duggan et al. (2005) reported that NIL lines with *tin* allele for reduced tiller number in general produced greater seed number per head particularly at lower competition level. Seed number per head for lines with *tin* allele was reduced by terminal drought. Hussain et al (2003) reported that the high number of seed number per head was seen at the highest row spacing due to more resources (nutrients, water, lights) that could be utilized by the plants. However, Sadras et al. (2011) and Nasire et al. (2012) found that there was a significant effect on seed number per head at high competition level. Seed number results from floret survival, therefore increasing floret survival is important to increase yield.

Our results show that the alternative allele at *QTn.mst-6B* affected seed weight at all competition levels in 2012 and at the two lower competition levels in 2013 in both dry land and irrigated nurseries. Duggan et al. (2005) reported that individual seed weight increased for lines with *tin* allele under terminal drought as a result from reducing seed number per head. Sheikh et al. (1995), Ayaz et al. (1999), and Hussain et al. (2003) found that seed weight increased with increase row spacing, whereas Aisawi and Foulkes (2012) found that lines without the *tin* allele produced heavier seed than their pair with *tin* allele either at high or low competition level. Khohar et al. (1985), Hussain et al. (2001), Sadras (2007), and Sadras et al. (2011) reported a negative relationship between productive tiller number and seed weight. Naseri et al. (2012) found that high density reduced seed size by reducing the dry matter accumulation in seeds.

The aim for any wheat breeder is to create new cultivars with high yield and good quality. Yield is a result of the interaction between many traits and the environment. Our results show that there was no significant effect of the high tiller allele at *QTn.mst-6B* on yield at any treatments. Aisawi and Foulkes (2012) reported that lines without the *tin* allele produced higher yield than lines with the *tin* allele but only under low competition level. This increase was caused by large number of seed or high seed weight. At high competition level, lines with *tin* allele produced the same yield as their pair from lines without the *tin* allele. However lines without the *tin* allele produced more PTN per meter than lines with *tin* allele. There was reduction in yield for lines without the *tin* allele at high competition level. Duggan et al. (2005) reported that there was no significant effect on yield between lines with *tin* allele and without the *tin* allele. However there was a positive association between productive tiller number and yield, and a negative association with seed weight; yield wasn't affected significantly by the high tiller allele at *QTn.mst-6B*. These results are inconsistent with Nazir et al. (1987) Hussain et al. (2001)

and Naseri et al. (2012) who reported that there was a significant effect on yield among cultivars and competition level. Snayedon (1984) found that there were negative effects between competition level and yield due to stem lodging. Lodging breaks the resource flow and photosynthetic transformation, which result in small seeds, and may decrease floret survival. High density (high competition level) decreased yield due to increasing competition between neighbor plants especially due to interspecific competition, which require the same resources. Conley et al. (2005) found that grain yield in sorghum would increase on row space in favorable environmental conditions with little risk of reduced yield in unfavorable environmental conditions.

Impact of *QTn.mst-6B* on Agronomic Traits Under Three Competition Levels

Tables 12 and 15 show the impacts of *QTn.mst-6B* on agronomic traits in 2012 and 2013. Our results show that plant height was affected by competition level (competition levels) only on dryland 2013 in high and lowest competition levels. Richards (1988) found that *tin* allele reduced plant height. Husssain et al. (2001) and Naseri et al. (2012) reported that the high competition level increased plant height. Our results show that there was a significant effect of *QTn.mst-6B* only in No Border treatment in 2012. These results are consistent with Duggan et al. (2005), who found that harvest index was not affected by *tin* allele at low competition level, but decreased in high competition level for lines with and without the *tin* allele. Richards (1988) found that the *tin* allele increased harvest index, while Nasire et al. (2012) also found that there was a significant effect of cultivars and competition level on harvest index. The negative interaction between harvest index and competition level reduced photosynthetic matter transformation and resource distribution. Harvest index could be reduced by 90% due to increasing the competition between neighbor plants. Our results show that there were significant effects of *QTn.mst-6B* for the Border treatment in the irrigated nursery 2013 on leaf width. Hussain et al. (2001) and Naseri et al. (2012) found that there was a significant effect of competition level on leaf area, leaves on plants at high competition increase faster and decrease faster at the end of the season. Our results show that there was a significant effect of *QTn.mst-6B* on senescence date for the Border treatment in 2012 and the Space treatment in both dry land and irrigated nurseries in 2013. Richards (1988) and Willenborg et al. (2009) reported that high competition caused early senescence date.

Impact of *QTn.mst-6B* on Seed Quality Traits Under Three Competition Levels

Tables 12 and 15 show the results for seed quality traits for 2012 and 2013. Test weight and grain hardness were significantly affected by *QTn.mst-6B* in the Border treatment in 2012. There were significant effects of alleles at *QTn.mst-6B* for the lowest competition level. Similarly, Mazurek (1984) Khalig et al. (1999), Hussain et al. (2001) and Naseri et al. (2012) found that seed quality was not affected by varieties and competition level and their interaction.

Plasticity of *QTn.mst-6B* on Yield and Yield Components Under Three Competition Levels

Bradshaw (1965) determined that seed weight was more stable (less plastic) than productive tiller number and seed number per head. Reynolds et al. (1994) found that seed number per head was more responsive to competition than productive tiller number per plant, and that seed number per head responded to density more than seed weight. Sadras and Rebetzke (2013) reported that the low tiller *tin* allele reduced the plasticity of productive tiller number and yield in some genotypic backgrounds. The reduced of plasticity associated with the *tin* allele (the low tiller allele) had two components: small reduction in productive tiller number under low yielding environments, and large reduction in the high yielding conditions. Motzo et al. (2004), Duggan et al. (2005) and Sadras and Rebetzke (2013) reported a negative association between plasticity of productive tiller number and seed number per head and seed weight. High plasticity of productive tiller number was negatively associated with yield under unfavorable environment. Peltonen-Sainio et al. (2011) found an association between yield under unfavorable environments and yield plasticity. These results are inconsistent with our results, which show that there was no significant effects of plasticity on yield and yield components (productive tiller number, seed number per head, and seed weight).

Greenhouse Experiments

Table 17 shows the results for two competition experiments conducted in the greenhouse. There were significant effects of alleles at *QTn.mst-6B* on early tiller number at the low competition levels (2 plants and 6 plants) per pot in sand media, and only at lowest competition level (2 plants) per pot in soil media. Hussain et al. (2001) and Naseri et al. (2012) also found that low competition level increased productive tiller number per plant, but decreased productive tiller number per unit area. Donaldson et al. (2009) and Dewey and Albrechtsen (1985) found that 50 to 70% of early tillers failed to produce productive tillers with heads and seeds. Results shows that the allele for high PTN at *QTn.mst-6B* was associated with high root dry weight, which is consistent with results of Romero and Benitez-Vega, 2010 results (Table 18).

Conclusion

In conclusion, our results show that *QTn.mst-6B* causes high early tiller number. The amount of competition determines whether early tillers will continue to develop and produce productive tillers. Alleles at *QTn.mst-6B* had a significant effect In PTN in the no Border treatments in dry land nurseries for 2012 and 2013. The QTL had a significant effect at all competition levels (Border, No Border, and Space) in the irrigated nursery 2013. There was a negative association between productive tiller numbers and seed weight. Alleles at *QTn.mst-6B* affected seed weight at all competition levels (high, intermediate, and low) in 2012 and the two lower competition levels, in 2013 for dry land and irrigated nurseries. The high tiller allele at *QTn.mst-6B* led to increased yield only at intermediate competition level (No Border) in the irrigated nursery 2013. Many agronomic traits were also affected by *QTn.mst-6B.* Plant height was affected significantly on high and low competition levels on dry land 2013, while harvest index was affected in the No Border treatment only on dry land 2012. There was a significant effect on flag leaf width only at high competition level (Border) in irrigated nursery 2013. Seed diameter was influenced by *QTn.mst-6B* at all levels of competition. Thus, the high PTN allele provides plasticity, and may provide a yield advantage if conditions are favorable. Decrease in seed number per spike, and seed weight may negate high PTN such that yields not impacted in many environments.

Table 10, Sources of variance used on SAS code to analyze data for 5 NIL pairs grown over three environments.

Random Complete Block Design – 2012		**Split Plot Design – 2013**	
Source of variance	**Model**	**Source of Variance**	**Model**
Rep	Random	Loc	Fixed
Treat	Fixed	Treat	Fixed
Family	Random	Loc*Treat	Random
Allele	Fixed	Family	Random
Treat*Family	Random	Loc*Family	Random
Treat*Allele	Fixed	Treat*Family	Random
Family*Allele	Random	Loc*Treat*Family	Random
Treat*Family*Allele	Random	Allele	Fixed
		Loc*Allele	Fixed
		Treat*Allele	Fixed
		Loc*Treat*Allele	Fixed
		Family*Allele	Random
		Loc*Family*Allele	Random
		Treat*Family*Allele	Random
		Loc*Treat*Allele	Random
		Rep(Loc)	Random
		Rep*Treat(Loc)	Random

Table 11. Impact of alternative alleles at *QTn.mst-6B* in five pairs of near isogenic lines on yield and yield components based on competition trails 2012 .

Treatment	**Allele**	**Productive tiller number (m^{-1})**	**Seed number per head**	**Seed weight (mg)**	**Yield (kg/ha)**
Border	1	187.37	43.32	29.04**	2615.03
	2	165.03	42.37	31.05	2280.42
No Border	1	306.95*	43.83	29.24***	5797.15
	2	250.33	45.59	31.65	5274.86
Space	1	‘25.43	56.13*	30.66**	‘21.81
	2	22.66	52.97	32.42	21.76

*, **, ***. Significant at P < 0.05, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

‘PTN counted per plant on Space treatment on both environments

'Yield also counted as gm per plant on Space treatment

Table 12. The impact of alleles at *QTn.mst-6B* on several agronomic and physiological traits for five pairs of near-isogenic lines based on competition trials 2012.

Treat	**Allele**	**Head Date (days from 1 Jun)**	**Plant Height (cm)**	**Length (cm)**	**Width (cm)**	**Senescence Date (days from 1 Jan)**	**Harvest Index (%)**
Border	1	189.46	63.53	15.75	1.32	219.33*	47.47
	2	189.4	62.76	15.16	1.32	217.8	49.54
No Border	1	190.4	65.23	16.78	1.37	222.4	45.16*
	2	189.73	61.90	16.22	1.41	221.8	47.36
Space	1	191.2	62.56	15.23	1.326	224	52.07
	2	192.06	61.79	15.43	1.34	223.8	53.09

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 13. Impact of alternative alleles at *QTn.mst-6B* in five pairs of near-isogenic lines on seed traits based on competition trails in what year.

Treatment	**Allele**	**Test weight (kg m^{-3})**	**Diameter (mm)**	**SKCS Hardness**	**Protein (%)**
Border	1	707.26**	2.68***	74.78**	15.42
	2	**524.17**	2.78	71.2	15.36
No Border	1	713.92	2.68***	77.6	15.46
	2	669.88	2.8	76.45	15.31
Space	1	0	2.73***	74.6	-
	2	0	2.82	75.2	-

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 14. Impact of alternative alleles at *QTn.mst-6B* in five pairs of NIL on yield and yield components based on competition trials in 2013.

Treatment	**Allele**	**Environment**	**Productive tiller number (m^{-1})**	**Yield (kg/ha)**	**Seed weight (mg)**	**Seed number per head**
Border	1	Dry	161.98	2869.91	27.41	38.7
	2	Dry	155.38	2838.11	28.16	39.82
No Border	1	Dry	263.80**	5838.81	31.19***	44.1
	2	Dry	220.13	5801.63	33.49	44.13
Space	1	Dry	22.25	8.3849	33.69*	54.16
	2	Dry	21.42	8.1707	35.08	54.42
Border	1	Irrigated	239.42**	5733.19	32.27	38.62
	2	Irrigated	198.04	5470.61	33.2	38.94
No Border	1	Irrigated	345.29**	8963.10*	33.06*	53.86**
	2	Irrigated	307.46	8229.85	34.35	58.28
Space	1	Irrigated	31.86**	'10.86	33.57*	39.4
	2	Irrigated	24.98	10.24	35.35	39.74

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

'PTN counted per plant on Space treatment at both environments

'Yield also counted as gm per plant on Space treatment at both environments

Table 15, Impact of alleles at *QTn.mst-6B* on several agronomic and physiological traits for five pairs of near-isogenic lines over two environments, based on competition trails 2013.

Treatment	**Allele**	**Environments**	**Head Date (days from 1 Jun)**	**Plant Height (cm)**	**Flag Leaf Width (cm)**	**Flag Leaf Length (cm)**	**Senescence Date (days from 1 Jan)**	**Harvest Index (%)**
Border	1	Dry	186.87	68.93*	1.49	21.11	209.87	41.52
	2	Dry	186.2	71.40	1.52	21.19	209.13	41.72
No Border	1	Dry	187.73	72.00	1.54	21.28	219.4	43.62
	2	Dry	187.2	72.20	1.51	21.08	219.53	44.57
Space	1	Dry	187.2	62.13*	1.564	20.52	226.73*	38.33
	2	Dry	187.13	59.93	1.58	20.18	224.93	36.87
Border	1	Irrigated	186.73	84.80	1.54*	22.64	219.33	46.78
	2	Irrigated	186.6	85.66	1.60	22.86	218.93	43.97
No Border	1	Irrigated	187.47	82.06	1.65	23.53	223.33	45.24
	2	Irrigated	186.87	81.06	1.65	23.10	222.07	46.09
Space	1	Irrigated	187.6	65.46	1.63	20.45	230.93*	42.607
	2	Irrigated	187.4	65.93	1.66	20.61	229.93	44.48

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 16. Impact of alternative alleles at *QTn.mst-6B* in five pairs of near-isogenic lines on seed traits over two environments based on competition trails.

Treat	**Allele**	**Environment**	**Diameter (mm)**	**SKCS Hardness**	**Protein (%)**
Border	1	Dry	2.56*	76.87	16.06
	2	Dry	2.62	77.58	16.05
No Border	1	Dry	2.76***	79.74	15.51
	2	Dry	2.87	78.52	15.08
Space	1	Dry	2.86*	77.04	16.02
	2	Dry	2.93	77.37	16.14
Border	1	Irrigated	2.81	76.13	15.14
	2	Irrigated	2.85	77.46	15.09
No Border	1	Irrigated	2.87**	78.2	15.19
	2	Irrigated	2.95	77.26	15.22
Space	1	Irrigated	2.88*	79.29	15.43

*, **, ***. Significant at P < 0.05, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 17, Response to competition levels on yield and yield components (Border vs No Border,) treatments 2012 and 2013. Response to competition was calculated as phenotypic plasticity

Environment	**Response to competition**	**Allele**	**Productive tiller number (m-1)**	**Yield (kg/ha)**	**Seed weight (mg)**	**Seed number per head**
Dry 2012	Border VS No Border	1	85.34	137.06	0.63	32.37
		2	60.42	143.43	5.22	22.99
Dry 2013	Border VS No Border	1	66.52	108.76	16.39	39.26
		2	38.03	107.4	20.76	55.47
Irrigated 2013	Border VS No Border	1	50.28	59.78	3.33	9.26
		2	55.10	48.66	6.11	1.50

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank

Table 18. Results from a greenhouse trial using two pairs of near-isogenic lines to determine the effects of *QTn.mst-6B* on early tiller number, productive tiller number, root weight under different competition levels, and type of soil.

Treat	Media	Allele	Early tiller number (pot)	Productive tiller number (pot)	Dry root weight (mg)
2 plant per pot	sand	1	36.86*	24.09*	10.92*
	sand	2	27.75	19.79	9.67
6 plant per pot	sand	1	38.59*	23.53*	10.94*
	sand	2	28.76	19.23	9.93
12 plant per pot	sand	1	31.62	24.51	10.91
	sand	2	29.64	21.84	10.04
2 plant per pot	soil	1	41.24**	19.36*	
	soil	2	27.63	15.09	
6 plant per pot	soil	1	27.84	22.58**	
	soil	2	21.73	16.36	
12 plant per pot	soil	1	26.68	17.28	
	soil	2	22.82	14.88	

*, **, ***. Significant at $P < 0.05$, 0.01, and 0.001

Allele 1 = High tiller allele represented by Reeder and Vida parent

Allele 2= Low tiller allele represented by McNeal, Choteau, and Hank.

Figure 2.Response to competition for alleles at *QTn.mst-6B* for productive tiller number in three experiments.

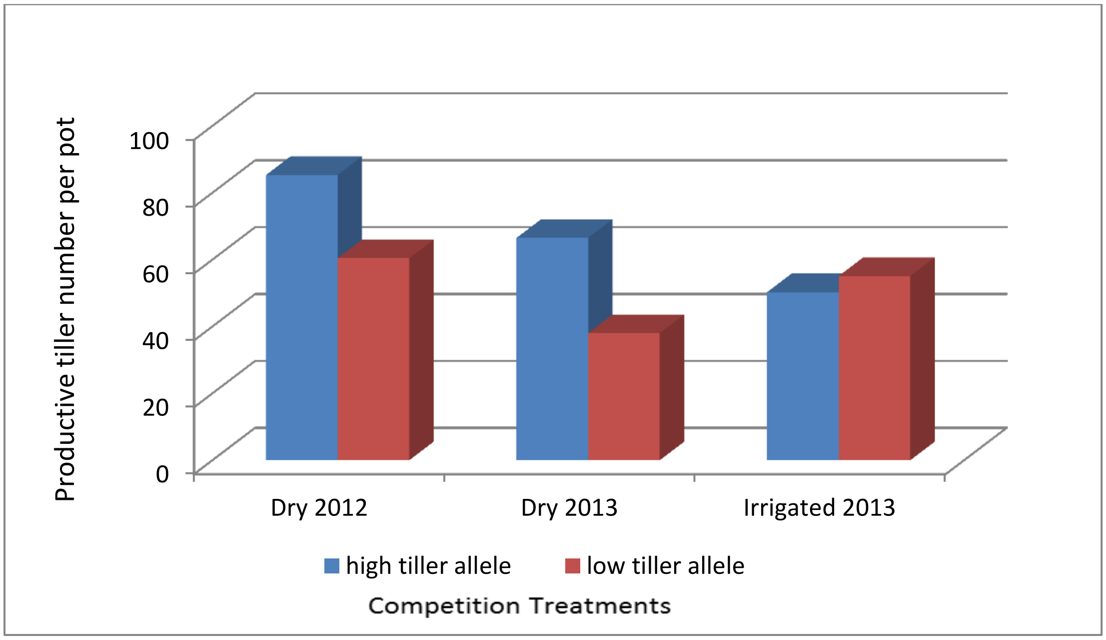


Figure 3. Response to competition for alleles at *QTn.mst-6B* for seed number per head.

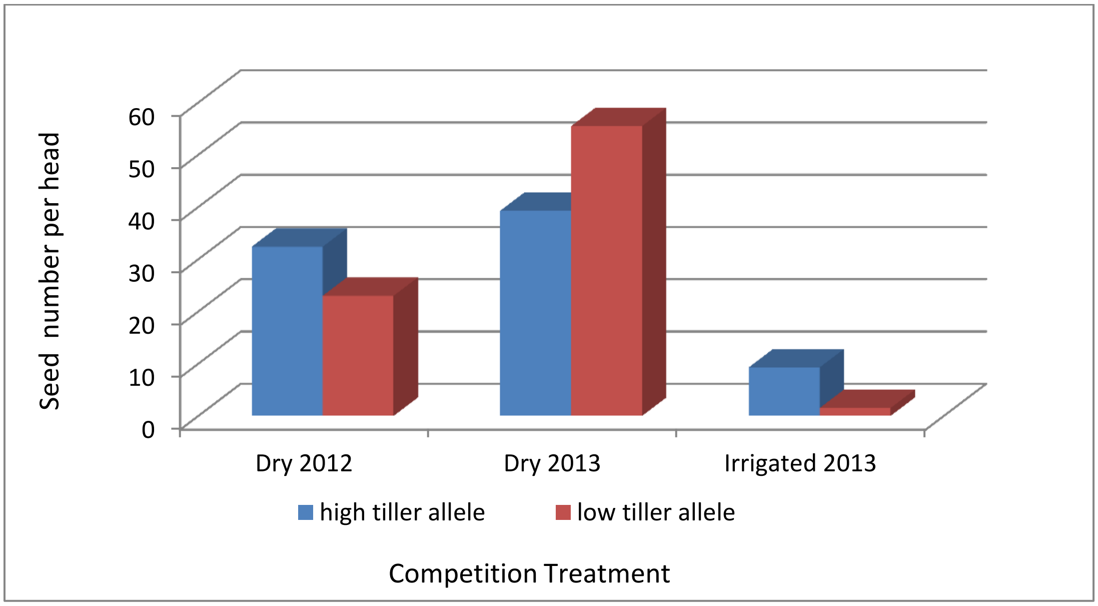


Figure 4. Response to competition for alleles at *QTn.mst-6B* for seed weight traits.

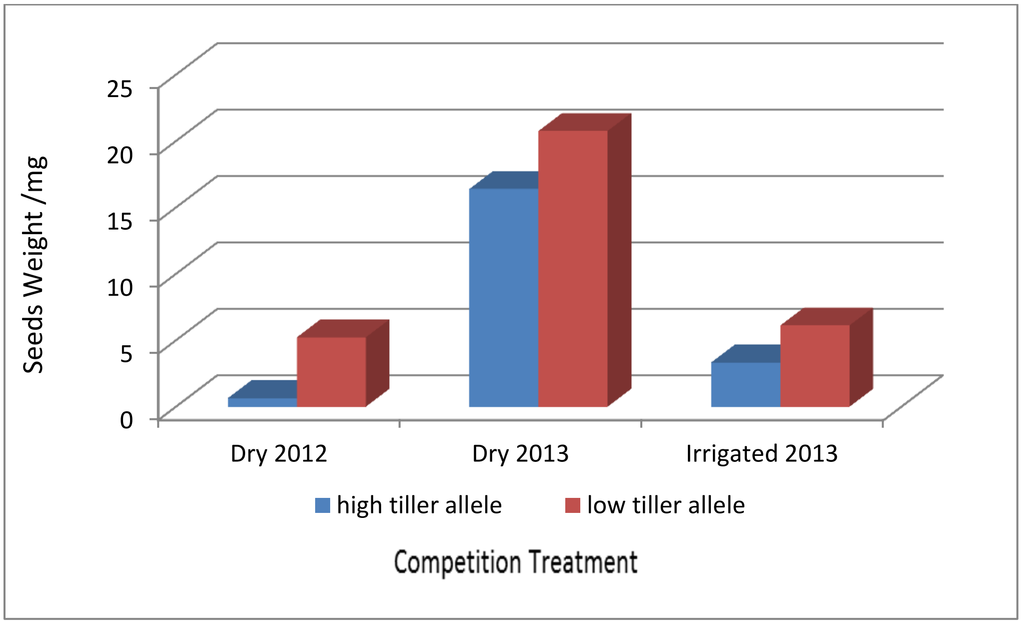
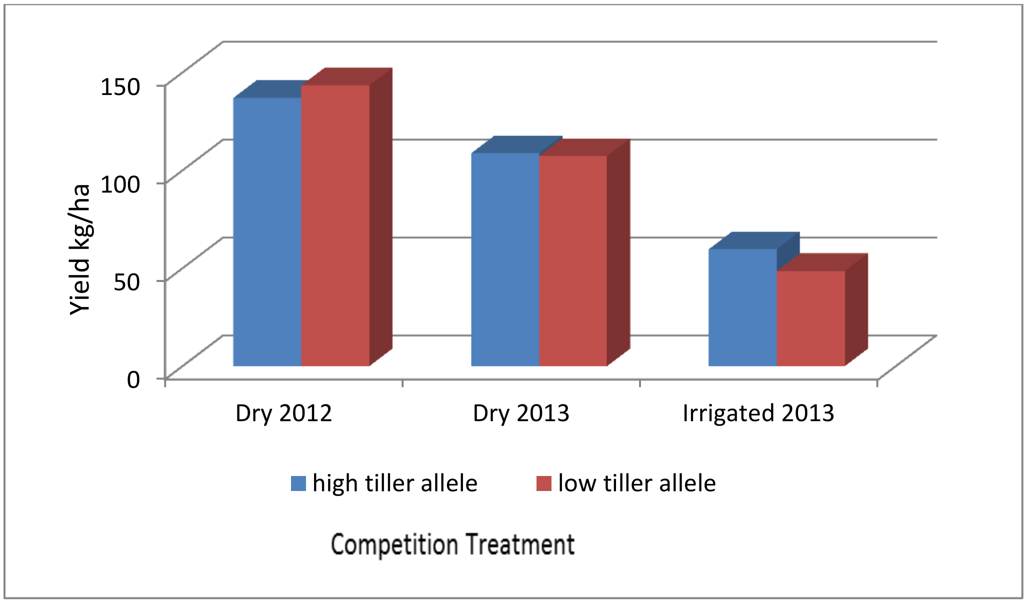


Figure 5. Response to competition for alleles at *QTn.mst-6B* for grain yield.



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