# QTL ANALYSES OF YIELD AND YIELD-RELATED TRAITS IN WHEAT USING A MAPPING POPULATION FROM A TAM 113/GALLAGHER CROSS

A Thesis

by

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# MASTER OF SCIENCE

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#### ABSTRACT

Understanding genetic architectures of yield and yield components of dryland and irrigated wheat (Triticum aestivum L.) is pivotal to developing modern high-yielding germplasm and cultivars, while maintaining end-use quality traits and tolerance to biotic and abiotic stresses. The aim of this study was to construct a genetic map and detect major quantitative trait loci (QTL) linked to yield and yield components using the biparental population developed from the cross 'TAM 113'/'Gallagher'. Field studies including 191 recombinant inbred lines (RILs) were conducted at McGregor, College Station, and Bushland in Texas during the 2018-2019, 2019-2020, and 2020-2021 growing seasons. A set of 8,261 single nucleotide polymorphisms (SNPs) markers was used to construct a high-density genetic map for all 21 chromosomes using JoinMap 4.0. Genomic regions associated with yield and yield components were detected through linkage analysis and QTL identification using IciMapping. A total of 160 QTL were detected for all traits collected in the study. Among them, 10 QTL were detected at individual environments and 12 cluster QTL regions were identified. One major QTL was located at 34 Mb on chromosome 2D, affecting multiple traits including two consistent QTL for heading date (Qhd.tamu.2D.34) and plant height (Qph.tamu.2D.34), overlapping with the major photoperiod gene Ppd-1. Another cluster QTL, detected on 2 D at 37 Mb, was very close to a previously identified cluster controlling multiple traits, including yield and kernel area. Other important QTL clusters were located between 52 Mb and 66 Mb on 7D including one consistent QTL for grain yield at 52 Mbp that increased yield up to 24.16 g m<sup>-2</sup>, increased harvest index up to 1 % and increased kernel diameter by 0.03 mm. This study dissects genetic mechanisms associated with yield and its components, thus providing valuable information for wheat improvement.

# DEDICATION

This thesis is dedicated to my parents and my sister.

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#### CONTRIBUTORS AND FUNDING SOURCES

### **Contributors**

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The mapping population was developed by the Wheat Genetics Program in Amarillo, TX. The population was genotyped using genotyping-by-sequencing by the Texas A&M AgriLife Research Genomics and Bioinformatics Service Center at College Station, TX. All field work and data collection were completed by the wheat genetic and breeding programs from Texas A&M AgriLife Research, and students from West Texas A&M University.

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#### NOMENCLATURE

- AbyE Additive-By-Environment Interaction
- ANOVA Analysis of Variance
  - BC Backcross
  - BLUE Best Linear Unbiased Estimators
  - BLUP Best Linear Unbiased Predictor
- BMYLD Biomass Grain Yield
  - CIM Composite Interval Mapping
  - CTAB Cetyltrimethylammonium Bromide
    - DH Double Haploid
  - DNA Deoxyribonucleic Acid
  - GBS Genotype-By-Sequencing
  - GEI Genotype-By-Environment Interaction
  - GS Genomic Selection
  - HD Heading Date
  - HI Harvest Index
  - ICIM Inclusive Composite Interval Mapping
    - KA Kernel Area
  - KASP Kompetitive Allele-Specific
    - KL Kernel Length
    - KPS Kernels spike<sup>-1</sup>

- KW Kernel Width
- LOD Logarithm of the Odds
- MAS Marker-Assisted Selection
- NIL Near-Isogenic Lines
- OAES Oklahoma Agricultural Experiment Station
  - PCR Polymerase Chain Reaction
    - PH Plant Height
  - QTL Quantitative Trait Loci
- REML Residual Maximum Likelihood
  - **RILs** Recombinant Inbred Lines
- SKCS Single Kernel Characterization System
- SKW Single Kernel Weight
- SPM Spikes meter<sup>-2</sup>
- SNP Single Nucleotide Polymorphism
- SRAP Sequence-Related Amplified Polymorphism
  - SSR Simple Sequence Repeats
- STM Sequence-Tagged Microsatellites
- TKW Thousand Kernel Weight

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#### **1. GENERAL INTRODUCTION**

Wheat (*Triticum aestivum* L.) is a widely grown crop, covering about 214 million hectares globally and producing about 734 million metric tons of grain (FAO, 2020). Wheat is an important source of energy for over 30% of the world's population. It also provides essential nutrients such as proteins, vitamins, minerals, phytochemicals, and dietary fiber (Shewry&Hey, 2015). Wheat is mainly utilized for bread, pizza, noodles, biscuit, vital gluten, and fermented beverages for human consumption. Wheat can also be used for animal grazing, cosmetics, and ethanol production (Shewry, 2009).

The current world population is over 7 billion and is estimated to reach 9 billion in the next 30 years (UN, 2019). This population increase creates a gap in food supplies. Expanding the area of production may not be possible due to limited arable land to fill the gap. Therefore, vertical yield increase per area remains the only viable option. The U.S. wheat grain production has increased steadily over the years, while the planted area remained unchanged (USDA, 2019). Increasing wheat production can be achieved using high-yielding varieties and applying best management practices (Bailey-Serres, Parker, Ainsworth, Oldroyd, Schroeder, 2019).

Humans have a long history of selecting desired plant types at basic levels after domestication. After Gregor Mendel discovered the basic principles of heredity, plant breeding became a scientific concept (Smýkal et al., 2016). Plant breeding became more sophisticated with the adoption of new technologies and approaches, such as doubled haploidy, marker-assisted selection (MAS), genomic selection (GS), recombinant DNA, and genome editing (Yan et al., 2017). In general, the use of these technologies in applied plant breeding contributes to time and effort saving in the process, ultimately reducing costs associated with breeding (Ahmar et al., 2020).

Quantitative Trait Loci (QTL) mapping provides the opportunity to associate complex phenotypic traits (quantitative traits) to specific regions in the chromosomes, which can be useful in the application of MAS shemes (Xu, Li, Yang, Xu, 2017). Many studies have been carried out to identify QTL associated with yield and yield-related traits using different DNA markers (Yang et al., 2020). The objectives of this study were twofold:

1) To determine the major yield components contributing to grain yield in hard red winter wheat RILs derived from a cross between 'TAM 113'/'Gallagher' grown in different Texas environments and to understand the effects of environmental fluctuations on the dynamics of grain yield determination in this population. 2) To identify major QTLs associated with grain yield, yield components, and other agronomic traits in RILs grown under different environmental conditions through the single environment and across environment analyses.

#### 2. LITERATURE REVIEW

#### **2.1. Molecular Markers**

Molecular markers are handy tools to understand complex traits and have been steppingstones for plant breeding (Jaganathan, Bohra, Thudi, Varshney, 2020). Molecular markers enable identifying variations for specific DNA regions that provide genetic information about individuals (Al-Samarai & Al-Kazaz, 2015). DNA-based markers can be categorized into two groups, Polymerase chain reaction (PCR)-based markers including randomly amplified polymorphic DNA (RAPD), Simple sequence repeats (SSR), amplified fragment length polymorphism (AFLP), single nucleotide polymorphism (SNP), and non-PCR-based marker such as restriction fragment length polymorphism (RFLP) (Agrawal & Shrivastava, 2014).

Single nucleotide polymorphisms have become popular recently, which created a high potential for high throughput genotyping at low costs. Furthermore, abundance in the genome and genetic stability are influential factors in making SNP preferable for plant breeding and genetic studies. Genomic selection, QTL mapping, seed identity testing, and pedigree analysis are brief applications for SNP markers in plant breeding (Smýkal et al., 2016).

# 2.2. QTL Mapping Studies

Improving grain yield is the primary objective of most wheat breeding programs. Grain yield is a complex trait controlled by many genes or QTL that can be dissected into components such as thousand kernel weight (TKW), single kernel weight (KW), and plant height (PH) (Ren et al., 2018), among other traits. In the last decades, immense progress has been made in the detection of genes and major stable QTLs associated with yield-related traits in different crops (Li et al., 2010). Additive, dominant, and epistatic gene actions are also essential to understanding the genetic structure, and QTL mapping analysis is an excellent way to decipher genetic information caused by allelic effects (Yang et al., 2018).

QTL mapping studies can be carried out using different mapping populations, such as recombinant inbred lines (RILs), doubled haploids (DH), F2 backcross (BC), and nearisogenic lines (NIL). An F2 segregating population has one cycle of selfing with the lowest cost, but this population is not replicable, and lack of recombination constitutes a significant weakness for mapping (Endelman & Jansky, 2016). RIL populations are considered as the most effective population, but this population requires 5-6 generations to attain an adequate level of homozygosity, and dominance deviation cannot be estimated because most alleles are homozygous (Seymour et al., 2012). Additionally, meiosis occurs at each cycle, increasing the chance of recombination among loci closely linked to each other (Silva, Cruz, Moreira, Barros, 2007). Wheat DH lines are developed from F1 lines using anther culture, microspore culture, or maize pollination, and provide completely homogenous line in a shorter time (Kiviharju, Moisander, & Tanhuanpaa, 2017; Mochida & Tsujimoto, 2001).

Many statistical methods have been developed to detect QTL and intra-locus genetic effect estimates. One of the most preferred methods is composite interval mapping (CIM), but inclusive composite interval mapping (ICIM) with a two-step mapping strategy is considered a more efficient statistical method because the algorithm of CIM is not sufficient to complete background control (Meng, Li, Zhang, & Wang, 2015).

Many QTL have been found using linkage maps built by SNP markers for plant height (PH), heading date (HD), total biomass, TKW, and KW in previous studies (Gao et al., 2015; Li et al., 2019; Xin et al., 2020; Dhakal et al., 2021; Yang et al., 2020). It is important to note that the expression of QTL is affected by the environment (Li, Dong, Niu, 2006; Sari et al., 2018; Wang, Vanden Langenberg, Wen, Wehner, & Weng, 2018). The consistency of the QTL is partially attributed to the heritability of the trait involved, and it is generally difficult to detect consistent QTL for low heritable traits (Gahlaut et al., 2017).

### 2.3. Yield and Yield Components

#### 2.3.1. Grain Yield

Improving grain yield is one of the main goals of modern wheat breeding programs targeting sustainability and food security. Grain yield is quantitatively inherited and strongly affected by the environmental conditions, but it can be dissected into multiple yield components. Therefore, dissecting yield components is essential to develop higher-yielding wheat varieties (Zheng et al., 2010; Liu et al., 2020). During the second half of the twentieth century, the genetic gain has shown a significant increase; however, it has slowed over time. Therefore, to boost genetic gain for grain yield, molecular markers have become indispensable (Ahrends, Eugster, Gaiser, Rueda-Ayala, & Hüging, 2018).

Grain yield in wheat can be defined by three main components, spike m<sup>-2</sup> (SPM), and kernels spike<sup>-1</sup> (KPS), thousand-kernel weight (TKW). Grain yield is considered the

combination of grain number per unit area and grain weight, while grain weight is one of the marketing standards of wheat (Kuchel, Williams, Langridge, Eagles & Jefferies, 2007).

Due to its commercial importance, wheat has been extensively studied to detect genomic regions associated with grain yield. Azadi et al. (2015) mapped twenty-four QTL across ten chromosomes in a RIL population (186 RILs), the majority of these QTL had a minor effect, and the phenotypic variation explained by each QTL was less than 10%. In another study involving 107 DH lines derived from a cross between 'Fukuho-kumogi', Japanese wheat cultivar, and 'Gigas', an Israeli wheat line, and with the use of different markers (AFLP, RFLP SSR, RAPD on two morphological traits, a QTL associated with grain yield was detected on chromosome 6A, 6B, and 6D (Heidari, Sayed-Tabatabaei, Saeidi, Kearsey, & Suenaga, 2011).

The expression of QTL for grain yield and its components can be influenced by environmental conditions, including seasonal precipitation, temperature, and soil fertility (Zheng et al., 2010). Several QTL studies showed inconsistent yield QTL detection due to the occurrence of genotype-by-environment interactions (Tura et al., 2020).

#### 2.3.2. Kernel Per Spike

Kernel per spike in wheat is a key trait controlling yield (Shi, Hao, Zhang, Cheng, & Zhang, 2017). According to previous studies, kernel per spike has a significant negative correlation with TKW. Therefore yield increase can be realized either through increase in grain number or TKW (Wurschum, Leiser, Langer, Tucker, & Longin, 2018).

Bindraban et al. (1998) divided wheat development stages into three phases. The second stage, after the passage of anthesis and floret maturation, is critical for the determination of kernel per spike and is often affected by environmental factors like solar radiation and temperature fluctuations. Heat and drought stresses are also considered significant factors affecting kernel per spike by reducing kernel number and kernel size (Sehgal, Sita, Siddique, Kumar, Bhogireddy, 2018). Rustgi, Shafqat, Kumar, Baenziger, & Ali (2013) reported eleven QTL associated with kernel per spike with 3A specific recombinant inbred chromosome lines (3A-RICLs) population using RFLP, SSR, sequence-tagged microsatellites (STM), and diversity array technology (DArT) markers.

#### 2.3.3. Spikes Per Square Meter

Spikes per square meter is a yield component that significantly contributes to grain yield in wheat (Mian, Begum, & Saha, 2020). It is known that there is an association between planting date and the number of spikes per unit area. Early sowing increases tiller number. However, the spikes may not be fertile due to the elongated vegetation period. There is also strong evidence that increases in seeding rate positively contribute to increases in number of spikes per unit area (Shah, Harrison, Boquet, Colyer, & Moore, 1994; Zhu, Chu, Dai, & He, 2019).

Under drought conditions, the number of spikes per square meter negatively impacts kernel number per spike and single kernel weight (Moral, Rharrabti, Villegas, & Royo, 2003). Mengistu, Baenziger, Eskridge, Dweikat, and Wegulo (2012), using SSR and sequence-tagged microsatellites (STM) markers on a DH population, identified one stable QTL, QSsm.neb-3A, associated with spike number on chromosome 3A. In another instance, Tang et al. (2011), using 184 SSR markers and 34 sequence-related amplified polymorphism markers (SRAP) in a RIL population derived from 'Chuanmai', a synthetic hexaploid wheat (SHW), and 'Chuannong', a Chinese spring wheat variety, identified nine QTL associated with spikes per square meter across six chromosomes, PVE value ranged from 5.5 to 21%.

#### **2.3.4. Kernel Traits**

Kernel traits, including TKW, kernel length (KLEN), kernel width (KWID), kernel area (KE), and perimeter, are key components affecting grain yield in wheat (Liu et al., 2020). TKW is one of the vital yield components that has been progressively improved over time (Wang, Ge, Hao, Dong, & Zhang, 2012). Thousand kernel weight is a highly heritable trait with estimates ranging from 0.59 to 0.8 (Wang, Ge, Hao, Dong, & Zhang, 2012). Thousand kernel weight contributes up to 20% of yield improvement and is considered the main factor for developing superior high-yielding wheat cultivars (Ma et al., 2012). In general, a negative association between TKW and grain number is observed, as increases in kernel number lead to a decrease in kernel weight and size (Tura et al., 2020). Hou, Liu, Hao, Li, and Liu (2020) reported six QTL associated with TKW on chromosomes 2A, 2B, 4A, and 7A in 300 wheat accessions in 2017 and 2018. Kernel width and kernel length are two sub-components of kernel weight, which are positively correlated with kernel weight (Kumar, Mantovani, Seetan, Soltani, & Echeverry-Solarte, 2016).

Kernel morphology can influence market value. Therefore, understanding the genetic basis of kernel weight plays a significant role in developing desired commercial

varieties (Prashant, Kadoo, Desale, Kore, & Dhaliwal, 2012). A large kernel is desired in wheat breeding due to its positive correlation with TKW. Besides, KLEN has shown a positive impact on seedling vigor (Cheng, Kong, Zhang, Xie, & Jia, 2017; Cui, Ding, Li, Zhao, & Li, 2011).

Groos, Robert, Bervas, and Charmet (2003) mapped nine QTL associated with TKW on chromosomes 1D, 2B, 2D, 5B, 6A, 6D, 7A, and 7D in a RIL population derived from a cross between 'Renan' and 'Récital'. Three of these QTL showed significance in all of the environments where these materials were evaluated. The QTL for TKW on chromosome 5B and 7B also control grain protein content and grain yield. In another study, Hai, Guo, Wagner, Xiao, and Friedt. (2008) identified two genomic regions associated with TKW on chromosomes 2B and 7B using 168 SSR markers in a 108-line DH population. The detected QTL explained around 14 % of the phenotypic variation, and one of these QTL was co-localized with kernel per spike.

# **2.4. Agronomic Traits**

#### 2.4.1. Heading Date

Although environmental factors play a significant role in plant growth and development, wheat growth strongly depends on photoperiod, vernalization, their interaction, and earliness *per se* (González, Slafer, & Miralles, 2002). From a breeding perspective, heading date is a selection criterion based on a specific growing area since very early or delayed heading can lead to grain yield losses (Ochagavía, Prieto, Zikhali, Griffiths, & Slafer, 2019). For instance, the grain filling stage is susceptible to temperature. High temperature limits grain filling, which can lead to a drop in grain yield

(Ye et al., 2019). Heading date in small grains is influenced by photoperiod and vernalization genes (Grogan, Brown-Guedira, Haley, McMaster, & Reid, 2016). Vernalization response genes (VRN-1, VRN-2, VRN-3, etc.) regulate the period of exposure to low temperature (Loukoianov, Yan, Blechl, Sanchez, & Dubcovsky, 2005; Whittal, Kaviani, Graf, Humphreys, & Navabi, 2018). Previous studies have shown that several major genes control vernalization and photoperiod response (Guedira et al., 2016; Huang et al., 2018). Photoperiod response genes (Ppd) are another group of genes that control heading date by regulating plant physiology for daylight perception, which is vital for the accumulation of dry matter (Royo, Ammar, Alfaro, Dreisigacker, & del Moral, 2018).

Chen, Sun, Li, Wang, and Shi (2020) reported three additive QTL associated with heading date on chromosomes 1A, 1B, and 2D in introgression line (IL) populations derived from 'Lumai 14'/ 'Shaanhan 8675' evaluated at eight environments for five years.

In another study conducted by Chen, Cheng, Chai, Wang, and Du (2020), five stable QTL were detected on chromosomes 2A, 5B, 6B, 7A, and 7D in a RIL population derived from 'Yi5029' and 'Nongda4332' varieties. Three QTL regions for HD co-localized with spikelet numbers on chromosomes 2A, 7A, and 7D.

### 2.4.2. Plant Height

Plant height is a valuable agronomic trait associated with grain yield, biomass, lodging resistance, and disease resistance (Lu et al., 2019). Plant height has a positive relation with spike length and the number of grains per spike. An increase in wheat yield has been attributed to the introduction of reduced height (Rht) genes during the Green

Revolution period (Wurschum, Langer, Longin, Tucker, & Leiser, 2017). Furthermore, semi-dwarf plants are relatively resistant to some diseases and insects, which contributes to yield under high plant density (Liu, Zhang, Feng, & Tian, 2020).

Several dwarfing genes were detected on different chromosomes including Rht-A1 on 4A, Rht-B1 and Rht-11 on 4B, Rht-D1 on 4D Rht8 on 2D, Rht-9 and Rht-3 on 7B, Rht12 on 5A, Rht23 on 5D, and Rht24 on 6A (Chai, Yao, Zhang, Xiao, & Fan, 2021; Daba, Tyagi, Brown-Guedira, & Mohammadi, 2020; Kang, Lin, Song, Yuan, and Zhong, 2012). After integrating reduced height genes into wheat breeding programs, a significant increase in harvest index (HI) has been observed. Harvest index is defined as the ratio between the grain yield and above biomass yield (Dai, Bean, Brown, Bruening, & Edwards, 2016). Gao et al. (2015) identified seven QTL associated with plant height on chromosomes 2BL, 4AL, 4BS, 4DS, 5AS, and 7AL using 246 F8 RILs derived from 'Zhou 8425B'/'Chinese Spring'. This study hypothesized that discovering grain yield and yield-related QTL via phenotyping biparental (RILs) populations under different environmental conditions could help to understand and dissect the genetic control of highyielding modern cultivars.

#### 3. MATERIAL AND METHODS

#### **3.1. Plant Material**

A set of 191 Recombinant inbred lines (RIL) derived from a cross between winter wheat varieties 'TAM 113' and 'Gallagher' was developed by single-seed descent method. Gallagher was released by the Oklahoma Agricultural Experiment Station (OAES) in 2012, and the pedigree of Gallagher is OK99711/OK93P656-RMH3299. It is an early maturing variety with good resistance to leaf rust (*Puccinia triticina*), stripe rust (*Puccinia striiformis*), Hessian fly (*Mayetiola destructor*), and soil-borne mosaic virus (Marburger, Silva, Hunger, Edwards, Van der Laan, 2021). TAM 113 was released by Texas A&M AgriLife Research in 2010 and has excellent yield potential and drought tolerance (Rudd et al., 2013). The pedigree of TAM 113 (Rudd, Devkota, Baker, Ibrahim, Worrall, 2013) is TX90V6313/TX94V3724. In the 2018-2019 season, 137 lines were planted, and 191 lines were planted with parents both in 2019-2020 and 2020-2021 growing seasons.

#### **3.2. Field Experimental Design**

Field studies were conducted in 2019, 2020, and 2021 at the Texas A&M AgriLife Research stations in College Station ( $30^{\circ}32'34.8"N 96^{\circ}25'47.3"W$ ), Bushland ( $35^{\circ}09'35.3"N 102^{\circ}05'02.9"W$ ), and McGregor ( $31^{\circ}22'24.8"N 97^{\circ}27'05.9"W$ ) (Table 4) At each site the experiment consisted of alpha-lattice experimental design with two replications. The plot size was  $4.57 \times 1.52$  m ( $15 \times 5ft$ ) and seeded at 50g per plot with standard agronomic practices. Irrigated environment consisted of 2019BSP while other environments dry environment 19CS, 19MCG, 20CS, 20MCG, 20EMN, and 21BD.

Location	Year of Harvest	Plot Number	<b>Environment Code</b>
Bushland	2019	274	19BSP
Bushland	2020	400	20EMN
Bushland	2021	400	21BD
College station	2019	274	19CS
College station	2020	400	20CS
McGregor	2019	274	19MCG
McGregor	2020	200	20MCG

Table 1. General information of the trials established in Texas for the evaluation of grain yield and yield component traits using a population derived from a cross between TAM 113 and Gallagher.

BSP= Bushland South Pivot, EMN= Emeny land, MCG= McGregor, CS= College Station, BD= Bushland Dryland

#### 3.3. Phenotypic Data Collection

Days to heading were recorded on a plot mean basis as the number of days from planting to 50% of spikes protrution from the flag leaf. Plant height was recorded on a plot mean basis and consistent on a measurement from the base of soil to the top of the plant, excluding awns. This trait was collected in all experiments except BSP19. At maturity, whole plots were harvested with a combine harvester for grain yield of each plot from all the trials except the ones at McGregor in 2019. Kernel moistures during harvesting measured by combine harvester ranged from 8.3% (20CS) to (22% 21BD). Yield data were recorded as bushels per acre (Bus/Ac) and converted to gram per square meter (g/m<sup>2</sup>). Kernel Characteristics such as kernel hardness index (HARD), kernel diameter (DIAM), moisture content, and single kernel weight (SKW) were collected with a Perten Model Single Kernel Characterization System (SKCS) 4100 (Perten Instruments North America Inc.) based on 300 randomly selected kernels per plot from the study at McGregor in 2020. Samples from half-meter long inner rows were cut from the ground in each plot at the physical maturity stage, which uniformly represents the whole plot for biomass grain yield (BMYLD), total biomass (BM), TKW, and SPM in three experiments 19BSP, 20EMN, and 21BD (Table 2). All samples were dried in a drying room at 60 °C for three days to reduce moisture before weighing biomass and grain. The harvest index (HI) and KPS were collected according to Yang et al. (2020). Approximately 10 grams of seeds were scanned for each line using an HP 11956A scanner, and Grain Scan software (Whan et al., 2014) was used to determine seed area, perimeter, kernel length, kernel width, and grain number. Thousand kernel weight was calculated by dividing the scanned seed weight by seed number and multiplying by 1000. Lastly, single stem head weight, single head dry weight, and single head grain weight were calculated following the procedure described by Yang et al. (2020).

Trait	19BSP	19MCG	20EMN	20MCG	20CS	21BD
YLD	~	×	~	~	~	~
PH	~	~	~	~	~	~
HD	~	~	~	×	~	~
HeadWt	~	×	~	×	×	~
TKW	~	×	~	×	×	~
SPM	~	×	~	×	×	~
KPS	~	×	~	×	×	~
KA	~	×	~	×	×	~
PERI	~	×	~	×	×	~
KLEN	~	×	~	×	×	~
KWID	~	×	~	×	×	~
BM	~	×	~	×	×	~
BMYLD	~	×	~	×	×	~
HI	~	×	~	×	×	~
SSHW	~	×	~	×	×	~
SHDR	~	×	~	×	×	~
SHGW	~	×	~	×	×	~

 Table 2. Summary of the phenotypic data collected by environment for three growing seasons.

YLD: Grain Yield, PH: Plant Height, HD: Heading Date, TKW: Thousand Kernel Weight, SPM: Spikes m<sup>-2</sup>, HeadWt: Total Head Weight g m<sup>-2</sup>, KPS: Kernels Spike<sup>-1</sup>, KA: Kernel Area, PERI: Perimeter, KLEN: Kernel Length, KWID: Kernel Width

Only yield was measured from 19CS.

#### **3.4. Statistical Analysis**

The following linear statistical model was used for the statistical analysis at each environment:

$$Y_{ijk} = \mu + R_i + B_{j(Ri)} + G_k + \varepsilon_{ijk}$$

Where  $Y_{ijk}$  = the observation of the  $k^{th}$  genotype within the  $k^{th}$  block of the  $i^{th}$  replicate,  $\mu$  = overall mean,  $R_i$  = the effect of the  $i^{th}$  replicate,  $B_{j(Ri)}$  = the effect of the  $j^{th}$  incomplete block within the  $i^{th}$  replicate,  $G_k$  = the effect of the  $k^{th}$  genotype, and  $\mathcal{E}_{ijk}$  = residual error. For the analysis of the combined data across environments, the following liner statistical model was used:

$$Y_{ijkl} = \mu + E_i + R_{j_{(Ei)}} + B_{k(EiRj)} + G_l + G_k E_{il} + \varepsilon_{ijkl}$$

Where  $Y_{ijk}$  = the observation of the  $l^{th}$  genotype within the  $k^{th}$  block of the  $j^{th}$  replicate in the  $i^{th}$  environment,  $\mu$  = the overall mean,  $E_i$  = the effect of the  $i^{th}$  environment,  $R_{j}_{(Ei)}$  = the effect of the  $j^{th}$  replicate within the  $i^{th}$  environment,  $B_{k(EiRj)}$  = the effect of the  $j^{th}$  replicate in the  $i^{th}$  environment,  $G_{1}$  = the genotype effect of the  $l^{th}$  genotype,  $GxE_{il}$  = the interaction effect of the  $l^{th}$  genotype and the  $i^{th}$  environment, and  $\mathcal{E}_{ijk}$  was the pooled residual error.

Best linear unbiased predictor (BLUP) values for each individual genotype were estimated using the restricted maximum likelihood (REML) method, assuming a random model in META-R software (Alvarado et al., 2020). BLUP values were used to calculate Pearson's correlation coefficients among the variables included in the study and used for QTL mapping. Besides, broad sense heritability, based on an entry-mean basis within individual environments and combined across environments, was estimated using the following statistical formulas:

$$H^{2} = \frac{\sigma_{g}^{2}}{\sigma_{g}^{2} + \frac{\sigma_{\varepsilon}^{2}}{n \, Re \, p}}$$

Where  $H^2$  = broad-sense heritability in individual environment,  $\sigma_g^2$  = the genotypic variance,  $\sigma_c^2 =$  the error variance, and nRep = the number of replications (Alvarado et al., 2020).

$$H^{2} = \frac{\sigma_{g}^{2}}{\sigma_{g}^{2} + \frac{\sigma_{g\varepsilon}^{2}}{n \, Re \, p} + \frac{\sigma_{\varepsilon}^{2}}{(n Envs \, x \, n \, Re \, p)}}$$

Where  $H^2$  = broad sense heritability across environments,  $\sigma_g^2$  = the genotypic variance, , $\sigma_g^2 \epsilon$  = the genotype-by-environment interaction variance, nEnvs = the number of environments and nRep = the number of replications, and  $\sigma_e^2 \epsilon$  = the error variance.

# 3.5. Genotypic, Linkage Mapping and QTL Analysis

Genomic DNA was extracted from leaf samples of all RILs using the Cetyltrimethyl Ammonium Bromide (CTAB) method (Doyle, 1991). Following that, DNA concentrations were quantified by comparing the intensity with the known size standards on agarose gel, and DNA was diluted to the correct concentration. Genotyping was performed by the Genomic and Bioinformatics Center at Texas A&M University using the ddRADseq genotyping protocol in Illumina Hiseq400 sequencing system (Peterson, Weber, Kay, Fisher, & Hoekstra, 2012). The SNP's calling was conducted based on the Chinese Spring reference genome from the International Wheat Genome Sequencing Consortium (IWGSC, 2014) using a web alignment tool at Genomics and Bioinformatics Service of Texas A&M AgriLife Research (Dhakal et al., 2021; Yang, Basnet, Ibrahim, Rudd, & Chen, 2019). After removing redundant SNPs through the BINNING function of Icimapping software and removing more than 20% missing data on Excel spreadsheet, 8,075 out of 99,288 SNP markers were used for constructing linkage map.

Joinmap software 4.0 (Van Ooijen, 2006) and QTL analysis using ICIMapping software version 4.1 (Meng, Li, Zhang, & Wang, 2015) were used for the construction of the linkage map. Detailed procedures for linkage and QTL analyses described in Dhakal et al. (2021) and Yan et al. (2020) were followed. Detected QTL were named as *Qtrait.tamu.chrom.Mbp*, where *Q* was the acronym of QTL, *trait* was the corresponding trait abbreviation, *tamu* was the abbreviation of Texas A&M University, *chrom* indicated chromosome numbers, and *Mbp* was the peak physical location of QTL.

#### 4. RESULTS

#### 4.1. Analysis of Variance and Heritability

Significant variation among environments, genotypes, and genotype-byenvironment interactions for most of the phenotypic traits was observed (Table 3). All traits were highly significant for genotypic effects except BM, HeadWt, and BMYLD. Similarly, GbyE interaction variance is significant for all traits except BM, HI, SPM and HeadWt. For environmental variance, the difference between BM, HD, PH, SPM, HeadWt, TKW, YLD, KPS, SHDW, SSHW, and SHGW were statistically significant but not for HI and seed-related traits (Table 3). Variance components (i.e., genotypic variance, GbyE variance, and Environmental variance) for yield and agronomic traits (i.e., PH and HD) were large due to highly significant effects (P < 0.001). Broad-sense heritability ( $H^2$ ) was classified into three groups: low heritable trait ( $\leq 0.3$ ), moderate heritable trait (0.4-0.6), and high heritable trait (>0.6). HD, PH, KA, PERI, KLEN, KWID, TKW, YLD, and SHDW showed higher broad sense heritability ranging from 0.64 - 0.91. Heritability of BM, HeadWt, and BMYLD was low at 0.02, 0.30, and 0.29, respectively. Heritability for SPM, HI, KPS, SSHW, and SHGW were moderate and ranged from 0.49 to 0.56 (Table 3).

Traits <sup>a</sup>	Units	σ <sup>2</sup> Gen <sup>b</sup>	$\sigma^2 G \; X \; E^{\; c}$	σ <sup>2</sup> Env <sup>d</sup>	σ <sup>2</sup> Res <sup>e</sup>	$\mathrm{H}^{2\mathrm{f}}$	Mean ± SD <sup>g</sup>	LSD <sup>h</sup>	CV <sup>i</sup>	Gallagher	TAM113
YLD	g m <sup>2</sup>	1040.7***	1668.2***	5220.8***	683.60	0.70	$231.6\pm38.80$	50.9	11.3	290.7	230.6
TKW	g	8***	1.4***	0.5*	3.20	0.80	$27.1\pm3.10$	3.6	6.6	28.1	29.5
SPM	spikes m <sup>-2</sup>	3884.2***	926.7ns	20004.1*	13832.40	0.50	$772 \pm 107.00$	132.2	15.2	715.6	840.4
KPS	kernels spike-1	2.7***	1.6*	84.9**	7.60	0.50	$23.2\pm2.70$	3.5	11.9	25.5	22.7
HI	%	0.0005**	0.0002 ns	0.002	0.00	0.50	$0.3\pm0.03$	0.0	13.7	0.3	0.3
HD	days	20.6***	5.6***	685***	1.80	0.90	$105\pm4.90$	4.8	1.3	102.7	106.6
PH	cm	12***	6.2***	276.6***	10.70	0.80	$70.4\pm3.92$	4.3	4.7	70.4	72.7
BMYLD	g m <sup>-2</sup>	1096.4 ns	2094.8**	10868.4**	6114.00	0.30	$467.4\pm71.50$	80.3	16.7	511.7	532.6
BM	g m <sup>-2</sup>	196.01 ns	5024.17 ns	492527.5**	35872.40	0.02	$1728.5 \pm 129.15$	38.6	11.0	1,736.1	1,831.9
HeadWt	g m <sup>-2</sup>	1606.3 ns	1792.5 ns	17219.2**	11263.50	0.30	$691.2\pm86.74$	97.3	15.4	737.3	746.7
KA	mm <sup>2</sup>	0.4***	0.05**	0.03 ns	0.17	0.90	$11 \pm 0.70$	0.8	3.7	11.3	11.7
KLEN	mm	0.04***	0.004**	0.0014 ns	0.02	0.90	$5.8\pm0.20$	0.2	2.1	5.8	5.9
KWID	mm	0.01***	0.001**	0.0025 ns	0.00	0.80	$2.4\pm0.10$	0.1	2.2	2.5	2.5
PERI	mm	0.3***	0.02*	0 ns	0.12	0.90	$17.1\pm0.60$	0.6	2.0	17.3	17.5
SHDW	mg <sup>-1</sup>	0.01***	0.002 *	0.1**	0.00	0.60	$0.9\pm0.10$	0.2	10.6	1.0	0.9
SSHW	mg <sup>-1</sup>	0.02***	0.01*	0.1***	0.10	0.50	$2.4\pm0.21$	0.3	10.0	2.5	2.4
SHGW	mg <sup>-1</sup>	0.004***	0.003***	0.1***	0.00	0.60	$0.6\pm0.09$	0.1	12.5	0.7	0.6

Table 3. Analysis of variance and broad-sense heritability assuming source of variations as random, and mean performance corresponding traits across environments.

<sup>a</sup>Abbreviations of Traits YLD: Yield from a combine harvester, TKW: Thousand Kernel Weight, SPM: Spikes m<sup>-2</sup>, KPS: Kernels Spike<sup>-1</sup>, HI: Harvest Index, HD: Heading Date, PH: Plant Height, BMYLD; Biomass Grain Yield from 0.5-meter inner row, BM: Biomass, HeadWt: Head Weight, KA; Kernel Area, KLEN: Kernel Length, KWID: Kernel Width, PERI: Perimeter, SHDW: Single Head Dry Weight, SSHW: Single Stem Head Weight, SHGW: Single Head Grain Weight, <sup>b</sup>σ<sup>2</sup>Gen: Genotypic Variance, <sup>c</sup>σ<sup>2</sup>G X E: Genotype-by-Environment Variance, <sup>d</sup>σ<sup>2</sup>Env: Environmental Variance, <sup>e</sup>σ<sup>2</sup>Res Pooled Residual Variance, <sup>f</sup>H<sup>2</sup>: Broad Sense Heritability. <sup>g</sup>SD: Standard Deviation, <sup>h</sup>LSD: Least Significant Difference for genotype effect <sup>i</sup>CV: Coefficient of Variation, ns: non significant \*, \*\*, \*\*\*, significant at the 0.05, 0.01, and 0.001 probability levels, respectively. Figure 1. Histogram and Phenotypic distributions of the predicted (BLUP) values for a total of 16 traits of recombinant inbreed lines (RIL) across all environments.



#### 4.2. Phenotypic Correlation Among Traits

Pearson's correlation coefficients were calculated to understand the relationships among all traits (Table 4). The correlation coefficient could be categorized into three groups: low ( $\leq 0.3$ ), moderate (0.4 - 0.6), and high ( $\geq 0.6$ ). Grain yield had the highest positive correlation with HI (r =0.7, *P* < 0.001), while the correlation between yield and HeadWt, SHDW, SHGW, BMYLD, KPS were moderate (r = 0.40 - 0.57, *P* < 0.001). Correlation between HD and all traits except BM, PH, SPM, and KPS was negative. PH was only negatively correlated with SPM, and HeadWt, whereas it was positively correlated with KPS, YLD, HI, KA, PERI, KLEN, TKW, SHDW, SSHW, and SHGW. One of the major yield components, SPM, had significant correlations with all traits except HD and HI.

Seed-related traits showed a higher correlation among each other (r = 0.81 - 0.96, P < 0.001), except the correlation between KWID and KLEN (r = 0.37, P < 0.001) and PERI (r = 0.58 P < 0.001). KWID was highly correlated with TKW (r = 0.91, P < 0.001). Similarly, head-related traits SHDW, SSHW, and SHGW had high positive correlations among each other (r = 0.71 - 0.92, P < 0.001). Regarding the phenotypic correlation of all traits from individual environments (Table 8), GYLD had a higher positive correlation with harvest index from 0.56 to 0.65 (P < 0.001) at 19BSP, 20 EMN, and 21BD, respectively. PH only significantly correlated with HD (r = 0.33 P < 0.001), BM (r = 0.32 P < 0.01), KLEN (r = 0.17 P < 0.05), and HI (r = -0.19 P < 0.05)at different significant levels at 19BSP. HD significantly correlated with KPS in 19BPS and 21BD while there was no significant correlation between HD and KPS in overall environment. Additionally,

individual environments showed similar trends for the majority of the traits as overall correlation.

Traits <sup>a</sup>	HD	PH	HeadWt	BM	KA	PERI	KLEN	KWID	SHDW	SSHW	SHGW	BMYLD	HI	TKW	KPS	SPM
PH	0.10															
HeadWt	-0.10	-0.01														
BM	0.08	0.13	0.79***													
KA	-0.37***	0.24***	0.30***	0.13												
PERI	-0.25***	0.26***	0.29***	0.16*	0.93***											
KLEN	-0.17*	0.28***	0.25***	0.17*	0.81***	0.96***										
KWID	-0.43***	0.11	0.26***	0.05	0.84***	0.59***	0.37***									
SHDW	-0.18*	0.17*	0.51***	0.24***	0.57***	0.50***	0.39***	0.53***								
SSHW	-0.07	0.30***	-0.03	0.00	0.40***	0.35***	0.28***	0.38***	0.75***							
SHGW	-0.27***	0.20**	0.47***	0.25***	0.59***	0.49***	0.38***	0.59***	0.92***	0.71***						
BMYLD	-0.18*	0.05	0.89***	0.72***	0.36***	0.30***	0.26***	0.34***	0.51***	0.05	0.64***					
HI	-0.29***	0.04	0.67***	0.26***	0.40***	0.30***	0.22**	0.44***	0.59***	0.09	0.68***	0.76***				
TKW	-0.45***	0.20**	0.30***	0.10	0.94***	0.79***	0.63***	0.91***	0.60***	0.43***	0.66***	0.40***	0.47***			
KPS	0.12	0.07	0.37***	0.27***	-0.18*	-0.17*	-0.17*	-0.14	0.61***	0.47***	0.59***	0.42***	0.47***	-0.15*		
SPM	0.09	-0.24***	0.46***	0.53***	-0.28***	-0.24***	-0.17*	-0.28***	-0.46***	-0.70***	-0.44***	0.32***	0.06	-0.30***	-0.21**	
YLD	-0 30***	0.14*	0 40***	0.16*	0.23**	0.10	0.04***	0 34***	0 41***	0.10	0 54***	0 54***	0 70***	0 33***	0 40***	0.00

Table 4. Simple Spearman correlation coefficients among traits across environments calculated using best linear unbiased predictor means (BLUPs).

<sup>a</sup>Abbreviations of Traits HD: Heading Date, PH: Plant Height, SPM: Spikes m<sup>-2</sup>, HeadWt: Head Weight, BMYLD; Biomass Grain Yield from 0.5-meter inner row, KA; Kernel Area, PERI: Perimeter, KLEN: Kernel Length, KWID: Kernel Width, TKW: Thousand Kernel Weight, YLD: Yield from combine harvester, HI: Harvest Index, KPS: Kernels Spike<sup>-1</sup>, SHDW: Single Head Dry Weight, SSHW: Single Stem Head Weight, SHGW: Single Head Grain Weight, BM: Biomass

\*, \*\*, \*\*\*, significant at 0.05, 0.01, and 0.001 probability levels, respectively.
#### **4.3. Genetic Linkage Map Construction**

A set of 8,075 SNP markers were used to construct 25 genetic linkage groups (LGs), covering all 21 wheat chromosomes (Table 5). The length of linkage groups (LGs) ranged from 1D (67.7cM) to 4A (394.4 cM) with an average of 193.8 cM. The total length of the genetic map was 4,844.0 cM with an average of marker interval at 0.6. Besides, the physical length of all groups was 14,753.1Mbp, and the average distance between two SNP markers was 1.8 Mbp. Markers distribution by genome was not equal for all genomes. Genome A (3,106) and genome B (3,206) had more SNPs than genome D (1,763). The total length of A, B, and D genomes were 1,851.4, 1,789.5, and 1,203.1 cM, respectively. SNP per cM for A, B, and D genomes were 0.6, 0.6, and 0.7, while SNP per Mbp were 1.7, 2.2, and 3.8, respectively.

Chromosome	25LGs	No. Markers	Genetic Distance	Cumulative Genetic cM Matching	CSS Mb Length Based on Markers with Consistent Genetic and Physical Locations	No. of SNPs/cM	No. of SNPs/Mb
1A	1	514	240.7	240.7	593.2	0.5	1.2
1B	2	210	104.1	344.7	688.8	0.5	3.3
1D	3	147	67.7	171.7	436.2	0.5	3.0
2A	4	426	229.1	296.7	770.1	0.5	1.8
2B	5	597	284.0	513.1	799.5	0.5	1.3
2D	6	412	248.2	532.2	650.5	0.6	1.6
3A	7	403	226.1	474.3	743.5	0.6	1.8
3B	8	542	342.0	568.1	808.7	0.6	1.5
3D	9	146	147.5	489.4	603.7	1.0	4.1
4A	10	596	394.4	541.8	744.4	0.7	1.2
4B	11	632	376.1	770.5	673.1	0.6	1.1
4D	12	157	88.1	464.2	497.5	0.6	3.2
5A	13	204	196.9	285.0	680.7	1.0	3.3
5B1	14	496	214.2	411.1	511.7	0.4	1.0
5B2	15	231	137.5	351.7	713.0	0.6	3.1
5D1	16	29	44.9	182.4	338.0	1.5	11.7
5D2	17	82	107.7	152.6	565.7	1.3	6.9
6A1	18	418	236.4	344.0	600.5	0.6	1.4
6A2	19	18	10.3	246.7	18.7	0.6	1.0
6B	20	203	149.9	160.2	719.7	0.7	3.5
6D1	21	205	115.3	265.1	463.8	0.6	2.3
6D2	22	89	24.9	140.2	12.8	0.3	0.1
7A	23	527	317.6	342.5	736.7	0.6	1.4
7B	24	295	181.8	499.4	744.1	0.6	2.5
7D	25	496	358.9	540.7	638.5	0.7	1.3
Total		8,075.0	4,844.0		14,753.1		
Genome A		3,106.0	1,851.4				
Genome B		3,206.0	1,789.5				
Genome D		1,763.0	1,203.0				
Average		323.0	193.8	373.2	590.1	0.7	2.6

Table 5. Distribution of markers across all genomes and all 21 chromosomes (25 Linkage groups) of the recombinant inbreed line (RIL) population

# 4.4. QTL Identification

### 4.4.1. QTL for yield and yield components

A total of 21 QTL were detected for yield based on individual and across environment analyses (Table A2). There were three consistent QTL that appeared in at least two individuals and across six environments (Table 6). The QTL on chromosome 1B at 566.9 Mbp explained total yield variations from 8.4 to 14.7% and increased yield up to 23.7 g m<sup>-2</sup> under high yielding environment 20MCG (Figure A1). Its additive effects explained yield variations by 7.3% with favorable alleles from Gallagher. The QTL on chromosome 2D at 36.8 Mbp explained up to 26.9% of total yield variations and increased yield by 37g m<sup>-2</sup> with the allele from Gallagher under low yielding environment 20CS (Figure A1). The QTL on chromosome 7D at 52.3 Mbp explained up to 12.9% of total yield variations but the additive effect only explained 5.3% of that yield variations. It increased yield by 24.2 g m<sup>-2</sup> with an allele from TAM 113 under medium yielding environment 19CS (Figure A1). Twelve QTL were only identified from single environments or across six environments. Six QTL were identified from one individual environment and across all six environments on chromosomes 1A at 11.3 Mbp, 2B at 64.0 and 571.4 Mbp, on 2D at 34.4 Mbp, and on 4A at 75.9 and 483.8 Mbp. Those QTL with a Gallagher allele increased yield by 37.6 g m<sup>-2</sup> in low yielding environment 20CS while those QTL from TAM 113 alleles increased yield by 17.4 g m<sup>-2</sup> in low yielding environment 20CS (Figure A1).

Only two QTL were mapped for kernels spike<sup>-1</sup> from individual or across three environment analyses (Table A2). The QTL on chromosome 5A at 12.8 Mbp increased

kernel spike <sup>-1</sup> by 0.88 with Gallagher allele int 20EMN while the QTL on 6A at 582.2 Mbp increased kernel spike <sup>-1</sup> by 0.94 with TAM 113 allele in 19BSP.

A total of ten QTL were detected for thousand kernel weight based on individual or across environmental analyses (Table A2). No consistent QTL was identified from more than one individual environment. Six QTL were only identified from a single environment or across the three environments. Among these six QTL, Gallagher allele increased thousand kernel weight by 0.81 g under 20EMN, while TAM 113 allele increased thousand kernel weigh by 1.14 g in 19BSP. Four QTL were identified from one environment and across all three environments on chromosome 2D at 34.4 and 37.24 Mbp, on 4D at 18.8 Mbp on 6A at 160.6 Mbp. These QTL with a Gallagher allele increased thousand kernel weight by 1.33 g in 19BSP.

For harvest index, eight QTL were identified from individual or across environmental analyses (Table A2). There was no consistent QTL detected from more than one individual environment. Four QTL were only detected from single environment or across the three environments, and all QTL were from TAM 113 allele that increased harvest index by 4% in 21BD. The other four QTL were detected from one environment or across all three environments on chromosome 2D at 106.6, 34.42, and 99.2 Mbp, on chromosome 7D at 52.3 Mbp. Those QTL with a Gallagher allele increased harvest index by 10% in 21BD, whereas QTL from TAM 113 alleles increased harvest index up to 8% in 21BD.

# 4.4.2. QTL of agronomic traits

A total of ten QTL were detected for heading date based on individual and across environment analyses (Table A2). There were three consistent QTL that appeared in more than two or more individual environments out of six environments (Table 6). The first consistent QTL on chromosome 2B at 57.6 Mbp explained total heading date variation from 3.12 to 11.63% and increased heading day by 1.07 days in 20CS. Its additive effect explained heading date variation by 1.85% with Gallagher allele. The second QTL on chromosome 2D colocalized within Ppd-D1 locus at 34.4 Mbp and explained total heading date variation from 34.5 to 64.45% that increased heading date by 3.1 when analyzed across six environments. Its additive effect explained heading date variation by 54.05% with Ppd-D1 sensitive allele from TAM 113. The last QTL on chromosome 7D at 70 Mbp explained up to 15.91% heading date variation, but the additive effect only explained 2.24% of heading date variation. It increased the heading date by 0.96 days with Gallagher allele in 20CS. Four QTL were only found from single environments or across environmental analyses. The Gallagher allele increased heading date up to 1.39 days in 19MCG while TAM 113 allele increased heading date by 0.73 days in 21BD (Table A2). Three QTL were detected from one environment and across environments on chromosomes 2B at 63.9 Mbp, on 6B at 3.5 Mbp, and on 7D at 607.8 Mbp. Those QTL from TAM 113 alleles increased heading date by 3.7 days in 20CS while Gallagher allele increased heading date up to 0.72 days in 19BSP (Table A1).

For plant height, a total of 29 QTL were identified from individual and across environment analyses (Table A1). Only one consistent QTL on 2D at 34.4 Mbp was detected from two individual environments, explained plant height variations from 15.46 to 28.79%, and increased plant heigh by 3.48 cm with TAM 113 allele in 20MCG. Fifteen QTL were only identified from single environments or across environment analyses. Eight QTL with Gallagher allele increased plant height up to 1.8 cm, while seven QTL from TAM 113 allele increased plant height up to 1.75 cm. Thirteen QTL were detected from one environment and across all six environments on chromosome 1A at 349.3 Mbp, on 2D at 68.8 Mbp, and on 4B at 423.5, 484.6, 505.4, 50.39, 614.9, and 645.9 Mbp, on 6A at 102.01, 174.78, 397.3, 318.03, and 86.4 Mbp. Eleven QTL from Gallagher alleles increased plant height by 2.62 cm in 20CS while four QTL from TAM 113 alleles increased plant height up to 1.54 cm in 20CS.

## 4.4.3. QTL for Kernel-related traits

A set of 35 QTL regions were associated with kernel-related traits (kernel area, length, width, and perimeter) from individual and across environment analyses. A total of five QTL were identified for kernel area from individual environments or across three environments (TableA2). The only consistent QTL, *Qkarea.tamu.2D.37* detected from two single environments and across three environments, explained total kernel area variation from 14.9 to 32.6% and increased kernel area by 0.29 mm<sup>2</sup> in 20EMN. Its additive effect explained kernel area variation by 18.72% with a favorable allele from Gallagher. Two QTL detected from single environment or across environmental analyses. One of these QTL with Gallagher allele increased kernel area by 0.19 mm<sup>2</sup> in 20EMN. The other QTL with a favorable allele from TAM 113 increased kernel area by 0.16 mm<sup>2</sup> in 19BSP. Two QTL were identified for kernel area from one environment and across all three environments. *Qkarea.tamu.6A.572* has Gallagher allele, and it increased kernel area

up to 0.22 mm<sup>2</sup> in 19BSP while the *Qkarea.tamu.6D.172* from TAM 113 allele increased kernel area by 0.21 mm<sup>2</sup> in 20EMN.

For kernel length, seven QTL were identified based on single and across three environment analyses (Table A2). The only consistent QTL, *Qklen.tamu.5B.497* identified from two individual environments and across all environments (Table 6), explained total kernel length variations from 4.9 to 12.4%. Its additive effects explained kernel length variation by 10.68% with a favorable allele from TAM 113 and increased kernel length up to 0.06 mm in 19BSP. Two QTL were detected from one single environment or across all environmental analyses. *Qklen.tamu.7A.639* with Gallagher allele increased kernel area by 0.05 mm across environmental analyses while *Qklen.tamu.2D.41* with TAM 113 allele increased kernel area 0.003 mm in 19BSP. Four QTL were identified from one single environment and across all three environments on chromosome 3D at 585.35 Mbp, on chromosome 4A at 29.33 Mbp, and on 6A at 98.33 and 113.23 Mbp, with favorable alleles from Gallagher that increased kernel length by 0.1 mm with *Qklen.tamu.6A.98* in 20EMN.

A total of 18 QTL for kernel width were mapped from single or across environmental analyses. There was no consistent QTL detected from more than one environment. Fifteen QTL appeared at only one single environment or across three environments (Table A2). Eight QTL from Gallagher increased kernel up to 0.04 mm with *Qkwid.tamu.2D.37* in 19BSP while seven QTL from TAM 113 increased kernel width up to 0.03 mm with *Qkwid.tamu.7D.66* in 19BSP. Three QTL were detected from one single environment and across three environmental analyses on chromosome 2D at 34.42 Mbp and 37.24 Mbp and on 3B at 431.27 Mbp. Those QTL from Gallagher increased kernel width up to 0.03 mm in 21BD and 20 EMN, while the QTL from TAM 113 allele increased kernel width by 0.02 mm in 21BD.

For kernel perimeter, a total of five QTL were identified from single and across all environmental analyses (Table A2). There was only one consistent QTL on chromosome 6A at 98.3 Mbp detected from 19BSP, 20EMN, and across the three environments, and it explained kernel perimeter variations ranging from 11.07 to 19.74%. The additive effect explained 11.8% of perimeter variations and increased kernel perimeter by 0.18 and 0.19 mm with a favorable allele from Gallagher in 19BSP and 20EMN, respectively. Two QTL were identified from an individual environment and two QTL were detected from one single environment and across the three environmental analyses. *Qperi.tamu.2D.33* increased kernel perimeter by 0.16 mm with Gallagher allele under 19BSP. *Qperi.tamu.5B.497* increased kernel perimeter by 0.15 mm with a TAM 113 allele in 20EMN.

QTL name	Chr.	Trait	Peak Pos (Mbp)	Env.	Threshold	LOD	LOD (A)	LOD (AbyE)	Total PVE Ranges	PVE (A)	PVE (AbyE)	Add	Parental alleles	Position (cM)	QTL CI (cM)	LeftMarker	Alleles	Plei.
Qyld.tamu.1B.567	1B	YLD	566.9	AcrossEnv, 19CS, 20CS	3.5 - 6.4	8.6 - 19.47	9.55	9.16	5.78 - 14.68	7.37	7.31	(-21.3) - (-8.38)	Gallagher	9	8.5 - 9.5	chr1B_ 566956619	G/A	
Qhd.tamu.2B.58	2B	HD	57.61	AcrossEnv, 21BD, 20CS	3.5 - 5.8	4.91 - 16.11	7.18	8.92	2.16 - 11.63	1.85	1.27	(-1.07) - (-0.58)	Gallagher	101	100.5 - 101.5	chr2B_ 57657606	T/A	р
Qhd.tamu.2D.34	2D	HD	34.42	AcrossEnv, 19BSP, 19MCG, 20CS, 20MCG, 21BD	3.5 - 5.8	22.30 - 157.95	103.9	54.06	34.50 - 64.65	54.05	10.6	3.15 - 4.86	TAM 113	61	60.5 - 61.5	chr2D_ 32901354	C/T	р
Qyld.tamu.2D.37	2D	YLD	36.9	AcrossEnv, 20MCG,20CS	3.59	9.13-33.40	11.37	22.03	11.70 - 26.90	22.3	17.6	(-9.0) - (-37.0)	Gallagher	63	62.5 - 64.5	chr2D_ 36584261	T/G	р
Qph.tamu.2D.34	2D	РН	34.42	19BSP, 20MCG	3.47 - 5.8	11.35 - 19.85	-	-	15.46 - 28.79	-	-	2.12 - 3.48	TAM 113	61	58.5 - 61.5	chr2D_ 32901354	C/T	р
Qkarea.tamu.2D.37	2D	KA	36.89	AcrossEnv, 19BSP, 20EMN	4.85	8.67 - 17.81	12.42	5.38	14.90 - 32.60	18.72	13.95	(-0.29) - (-0.17)	Gallagher	63	62.5 - 64.5	chr2D_ 36584261	T/G	р
Qklen.tamu.5B.497	5B	KLEN	496.6	AcrossEnv, 19BSP, 20EMN	3.4 - 4.8	3.92 - 8.42	6.5	1.91	4.91 - 12.45	10.69	1.76	0.04 - 0.06	TAM 113	211	210.5 - 211.5	chr5B_ 489969825	A/G	
Qperi.tamu.6A.98	6A	PERI	98.33	AcrossEnv, 19BSP, 20EMN	3.4 - 4.8	5.43 - 12.38	7.31	5.07	11.07 - 19.74	11.86	7.88	(-0.19) - (-0.11)	Gallagher	77	76.5 - 77.5	chr6A_ 98982341	C/T	
Qyld.tamu.7D.52	7D	YLD	52.31	AcrossEnv, 19BSP, 19CS	3.4 - 6.4	9.69 - 21.59	7.26	14.32	12.13 - 16.87	5.28	7.59	7.08 - 24.16	TAM 113	66	65.5 - 66.5	chr7D_ 51735477	A/G	р
Qhd.tamu.7D.70	7D	HD	70.03	AcrossEnv, 19BSP, 20CS	3.4 - 5.8	3.78 - 15.91	8.79	7.19	1.73 - 2.42	2.24	0.18	(-0.96) - (-0.57)	Gallagher	94	90.5 - 95.5	chr7D_ 63208599	G/A	

Table 6. Consistent QTL associated with yield and yield-related traits detected from individual and across environments.

Chr: Chromosome, Abbreviation of traits: YLD: Grain Yield from combine harvester, HD: Heading Date, PH: Plant Height, KA: Kernel Area, KLEN: Kernel Length, PERI: Perimeter, Env: Environment, AcrossEnv: Across Environments, 19CS: College Station 2019, 20CS: College Station 2020, 21BD: Bushland Dryland 2021, 19BSP: Bushland South Pivot 2019, 19MCG: McGregor 2019, 20MCG: McGregor 2020, 20EMN: Emeny Land 2020, LOD: Logarithm of the Odds, PVE: Phenotypic Variation Explained, AbyE: Additive by Environment Effect, Add: Additive Effect, cM: centimorgan, CI: Confidence Interval, Plei: Pleiotropic, p: affecting more than one trait.

## 4.4.4. Pleiotropic QTL

A set of 12 QTL regions were identified as pleiotropic QTL affecting more than one trait (Table 7, Figure 2). The first pleiotropic QTL at 57.6 Mbp on 2B was associated with yield and one of the consistent heading date QTL. It increased yield by  $16.56 \text{ g m}^{-2}$ with TAM 113 allele in 20MCG and increased heading date by 1.73 days with Gallagher allele in 20CS. Another QTL at 63.96 Mbp increased heading date 0.29 day with Gallagher allele across environments and increased grain yield by 14.5 g with TAM 113 allele in 21BD. The pleiotropic QTL at 69.34 Mb on 2B increased yield by 37.04 g m<sup>-2</sup> with a TAM 113 allele in 21BD, increased harvest index by 1 %, and single head grain weight by 0.02 mg head-1 with TAM 113 allele across all environments. The QTL at 76.4 Mbp on 2B increased harvest index by 4 % with a TAM 113 allele in 21BD and increased single head grain weight by 0.06 mg head<sup>-1</sup> with a TAM 113 allele in 21BD. A QTL detected on chromosome 2B at 84.91 Mbp was associated with yield and kernel width. TAM 113 allele increased yield 12.96 g m<sup>-2</sup> in 19CS and kernel width 0.01 mm across all environments. For the QTL at 31.5 Mbp on 2D, TAM 113 allele increased plant height by 1.01 cm in 21BD, while Gallagher allele increased single stem head weight 0.1 mg head<sup>-1</sup> in 21BD. A QTL on chromosome 2D at 34.43 Mbp was associated with yield, heading date, harvest index, kernel width, kernel diameter, plant height, single head grain weight, and thousand kernel weight. The favorable allele from Gallagher increased yield, harvest index, kernel width, kernel diameter, single head grain weight, and thousand kernel weight by up to 30.4 g m<sup>-2</sup>, 1 %, 0.02 mm, 0.07 mm, 0.03 mg head<sup>-1,</sup> and 1.33 g, respectively. In contrast, TAM 113 allele increased heading date, kernel hardness index, plant height by up to 4.86 days, 5.71 %, and 3.48 cm, respectively. Another QTL at 36.9 Mbp on 2D was associated with multiple traits, including kernel area, yield, kernel width, single kernel weight, biomass grain yield, single head dry weight, and thousand kernel weight. A Gallagher allele increased all these traits by up to 0.17mm, 37.6 g m<sup>-2</sup>, 0.04 mm, 1.02 mg, 20 g m<sup>-2</sup>, 0.09 mg head<sup>-1.</sup> and 0.38 g, respectively. Biomass, grain yield, and harvest index were linked to QTL on chromosome 4B at 441.13 Mbp. A TAM 113 allele increased biomass grain yield and harvest index by 13.29 g m<sup>-2</sup> and 1%, respectively. A QTL at 171.52 Mbp on 6D was associated with kernel area and single kernel weight. It increased kernel area by 0.21 mm and single kernel weight by 0.86 mg with TAM 113 alleles. A QTL at 52 Mbp on 7D was linked to harvest index by 1% and yield by 24.16 g m<sup>-2</sup>. A pleiotropic QTL on 7D at 66.02 Mbp increased kernel diameter by 0.03 mm under 19MCG and yield by 22.21 g m<sup>-2</sup> with a TAM 113 allele in 20MCG.

QTL name	Chr.	Trait	Peak Position (Mbp)	Env.	Thr.	LOD	LOD (A)	PVE	PVE (A)	PVE (AbyE)	Add	Parental alleles	Pos (cM)	QTL CI (cM)	Left Marker	All.	Right Marker	All.	Cons.
Qyld.tamu.2B.58	2B	YLD	57.6	20MCG	3.59	3.68	-	4.34	-	-	16.52	TAM 113	101	99.5 - 101.4	chr2B_ 57657606	T/A	chr2B_ 57282937	T/C	
Qhd.tamu.2B.58	2B	HD	57.6	AcrossEnv, 21BD, 20CS	5.85	4.91 - 16.11	7.18	2.16 - 11.63	1.85	1.27	(-1.07) - (-0.58)	Gallagher	101	100.5 - 101.5	chr2B_ 57657606	T/A	chr2B_ 57282937	T/C	у
Qyld.tamu.2B.64	2B	YLD	63.96	AcrossEnv, 21BD	3.4 - 6.4	6.18 - 7.77	3.04	4.26 - 13.12	2.19	2.06	4.58 - 14.47	TAM 133	105	104.5 - 105.5	chr2B_ 63428577	C/T	chr2B_ 64952887	G/A	y?
Qhd.tamu.2B.64	2B	HD	63.96	AcrossEnv, 19BSP	3.4 - 5.8	9.16 - 10.22	1.81	1.05 - 8.12	0.44	0.6	(-0.29) - (-0.07)	Gallagher	105	104.5 - 105.5	chr2B_ 63428577	C/T	chr2B_ 64952887	G/A	y?
Qbmyld.tamu.2B.69	2B	BMYLD	69.34	21BD	3.4	4.24	4.50	10.34	-	-	37.04	TAM 133	108	107.5 - 110.5	chr2B_ 68426788	G/A	chr2B_ 89540772	C/T	
Qhi.tamu.2B.69	2B	ні	69.34	AcrossEnv	4.9	6.19	5.40	5.19	1.97	3.21	0.01	TAM 133	108	107.5 - 110.5	chr2B_ 68426788	G/A	chr2B_ 89540772	C/T	
Qshgw.tamu.2B.69	2B	SHGW	69.34	AcrossEnv	4.7	5.12	4.50	12.88	5.65	7.22	0.02	TAM 133	108	107.5 - 110.5	chr2B_ 68426788	G/A	chr2B_ 89540772	C/T	
Qhi.tamu.2B.76	2B	ні	76.4	21BD	3.4	6.09	-	1.80	-	-	0.04	TAM 133	109	107.5 - 110.5	chr2B_ 68426788	G/A	chr2B_ 89540772	C/T	
Qshgw.tamu.2B.76	2B	SHGW	76.4	21BD	3.5	4.86	-	10.68	-	-	0.06	TAM 133	109	107.5 - 110.5	chr2B_ 68426788	G/A	chr2B_ 89540772	C/T	
Qyld.tamu.2B.85	2B	YLD	84.91	19CS	3.6	3.67	-	3.46	-	-	12.96	TAM 133	113	112.5 - 114.5	chr2B_ 76076511	#N/A	chr2B_ 98844071	T/C	
Qkwid.tamu.2B.85	2B	KWID	84.91	AcrossEnv	4.8	4.29	3.40	3.94	2.67	1.25	0.01	TAM 133	113	112.5 - 114.5	chr2B_ 76076511	#N/A	chr2B_ 98844071	T/C	
Qph.tamu.2D.31	2D	РН	31.5	21BD	3.4	6.11	-	9.52	-	-	1.01	TAM 133	58	57.5 - 59.5	chr2D_ 31103643	A/G	chr2D_ 32901354	C/T	
Qsshw.tamu.2D.31	2D	SSHW	31.5	21BD	3.5	13.84	5.14	26.43	-	-	-0.10	Gallagher	58	57.5 - 59.5	chr2D_ 31103643	A/G	chr2D_ 32901354	C/T	

Table 7. Pleiotropic QTL associated with yield and yield-related traits detected from individual and across environment.

Chr: Chromosome, Abbreviation of traits; YLD: Grain Yield from combine harvester, HD: Heading Date, BMYLD: Biomass Grain Yield from 0.5-meter inner row, HI: Harvest Index, SHGW: Single Head Grain Weight, KWID; Kernel Width, PH: Plant Height, SSHW: Single Stem Head Weight, DIAM: Kernel Diameter, KHI: Kernel Hardness Index, TKW: Thousand Kernel Weight, KA: Kernel Area, SHDW: Single Head Dry Weight, SKW: Single Kernel weight, Env: Environment, AcrossEnv: Across Environments, 19CS: College Station 2019, 20CS: College Station 2020, 21BD: Bushland Dryland 2021, 19BSP: Bushland South Pivot 2019, 19MCG: McGregor 2019, 20MCG: McGregor 2020, 20EMN: Emeny Land 2020, Thr: threshold, LOD: Logarithm of the Odds, PVE: Phenotypic Variation Explained, AbyE: Additive by Environment Effect, Add: Additive Effect, cM: centimorgan, CI: Confidence Interval, Cons: Consistent, y: identified at least two single environment, y?: identified one individual and across environment.

Tab	le 7.	continued
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QTL name	Chr.	Trait	Peak Position (Mbp)	Env.	Thr.	LOD	LOD (A)	PVE	PVE (A)	PVE (AbyE)	Add	Parental alleles	Pos (cM)	QTL CI (cM)	Left Marker	All.	Right Marker	All.	Cons.
Qsshw.tamu.2D.31	2D	SSHW	31.5	AcrossEnv	4.8	14.0	-	3.04	1.31	1.72	-0.04	Gallagher	58	54.5 - 59.5	chr2D_ 31103643	A/G	chr2D_ 32901354	C/T	
Qyld.tamu.2D.34	2D	YLD	34.43	AcrossEnv, 19BSP	3.6 - 6.4	17.5 - 21.12	9.21	17.57 - 21.1	6.90	10.67	(-30.4) - (-8.11)	Gallagher	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	y?
Qhd.tamu.2D.34	2D	HD	34.43	AcrossEnv, 19BSP, 19MCG, 20CS, 20MCG, 21BD	3.4 - 5.8	22.3 - 157.95	103.90	34.50 - 64.65	54.05	10.6	3.15 - 4.86	TAM 133	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	у
Qhi.tamu.2D.34	2D	ні	34.43	AcrossEnv, 19BSP	3.4 - 4.9	10.96 - 15.78	2.19	0.80 - 21.81	0.78	0.02	0	Gallagher	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	y?
Qkwid.tamu.2D.34	2D	KWID	34.43	AcrossEnv, 21BD	3.4 - 4.8	5.17 - 5.19	-	1.78 8.62	0.68	1.09	(-0.02) - (-0.01)	Gallagher	61	59.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	y?
Qdiam.tamu.2D.34	2D	DIAM	34.43	20MCG	3.5	23.51	-	35.05			-0.07	Gallagher	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	
Qkhi.tamu.2D.34	2D	КНІ	34.43	20MCG	3.5	23.12	-	29.85	-	-	5.71	TAM 133	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	
Qph.tamu.2D.34	2D	РН	34.43	19BSP, 20MCG	3.4	11.35 - 19.85	-	15.46 - 28.79	-	-	2.12 - 3.48	TAM 133	61	58.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	у
Qshgw.tamu.2D.34	2D	SHGW	34.43	AcrossEnv, 19BSP	3.5 - 4.7	5.64 - 7.68	4.70	6.45 - 10.55	5.83	0.62	(-0.03) - (-0.02)	Gallagher	61	60.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	y?
Qtkw.tamu.2D.34	2D	TKW	34.43	AcrossEnv, 19BSP	3.4 - 4.6	12.18 - 13.52	5.40	9.12 - 17.46	7.15	10.28	(-1.33) - 22.27	TAM 133	61	59.5 - 61.5	chr2D_ 32901354	C/T	chr2D_ 34562299	T/C	y?
Qkarea.tamu.2D.37	2D	KA	36.9	AcrossEnv, 19BSP, 20EMN	4.8	8.67 - 17.81	12.42	14.90 - 32.60	18.72	13.95	(-0.29) - (-0.17)	Gallagher	63	62.5 - 64.5	chr2D_ 36584261	T/G	chr2D_ 37211804	A/G	у
Qyld.tamu.2D.37	2D	YLD	36.9	AcrossEnv, 20CS	3.5 - 6.4	30.09 - 33.4	11.37	26.14 - 26.99	8.53	17.61	(-37.6) - (-9.00)	Gallagher	63	62.5 - 63.5	chr2D_ 36584261	T/G	chr2D_ 37211804	A/G	y?
Qkwid.tamu.2D.37	2D	KWID	36.9	19BSP	4.7	12.48	-	17.49	-	-	-0.04	Gallagher	63	62.5 - 64.5	chr2D_ 36584261	T/G	chr2D_ 37211804	A/G	

Chr: Chromosome, Abbreviation of traits; YLD: Grain Yield from combine harvester, HD: Heading Date, BMYLD: Biomass Grain Yield from 0.5-meter inner row, HI: Harvest Index, SHGW: Single Head Grain Weight, KWID; Kernel Width, PH: Plant Height, SSHW: Single Stem Head Weight, DIAM: Kernel Diameter, KHI: Kernel Hardness Index, TKW: Thousand Kernel Weight, KA: Kernel Area, SHDW: Single Head Dry Weight, SKW: Single Kernel weight, Env: Environment, AcrossEnv: Across Environments, 19CS: College Station 2019, 20CS: College Station 2020, 21BD: Bushland Dryland 2021, 19BSP: Bushland South Pivot 2019, 19MCG: McGregor 2019, 20MCG: McGregor 2020, 20EMN: Emeny Land 2020, Thr: threshold, LOD: Logarithm of the Odds, PVE: Phenotypic Variation Explained, AbyE: Additive by Environment Effect, Add: Additive Effect, cM: centimorgan, CI: Confidence Interval, Cons: Consistent, y: identified at least two single environment, y?: identified one individual and across environment.

Tab	le 7.	continued
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QTL name	Chr.	Trait	Peak Position (Mbp)	Env.	Thr.	LOD	LOD (A)	PVE	PVE (A)	PVE (AbyE)	Add	Parental alleles	Pos (cM)	QTL CI (cM)	Left Marker	All.	Right Marker	All.	Cons.
Qskw.tamu.2D.37	2D	SKW	36.9	20MCG	3.4	8.41	-	12.56	-	-	-1.02	Gallagher	63	62.5 - 64.5	chr2D_ 36584261	T/G	chr2D_ 37211804	A/G	
Qbmyld.tamu.2D.37	2D	BMYLD	37.25	AcrossEnv, 19BSP	4.8	4.96 - 6.35	2.40	2.35 - 8.53	1.90	0.45	(-20.00) - (-12.43)	Gallagher	64	63.5 - 64.5	chr2D_ 37211804	A/G	chr2D_ 37257093	A/G	y?
Qkwid.tamu.2D.37	2D	KWID	37.25	AcrossEnv, 20EMN	.35 - 4.8	5.30 - 17.37	14.00	12.68 - 18.20	11.69	6.5	(-0.03) - (-0.02)	Gallagher	64	63.5 - 64.5	chr2D_ 37211804	A/G	chr2D_ 37257093	A/G	y?
Qshdw.tamu.2D.37	2D	SHDW	37.25	AcrossEnv, 21BD	3.5 - 4.9	10.33 - 11.56	10.41	22.16 - 23.95	12.40	11.5	(-0.09) - (-0.04)	Gallagher	64	63.5 - 64.5	chr2D_ 37211804	A/G	chr2D_ 37257093	A/G	y?
Qtkw.tamu.2D.37	2D	TKW	37.25	AcrossEnv, 20EMN	3.5 - 4.6	5.62 - 6.86	3.30	8.41 - 12.11	4.20	4.9	(-0.96) - 21.43	Gallagher	64	63.5 - 64.5	chr2D_ 37211804	A/G	chr2D_ 37257093	A/G	y?
Qbmyld.tamu.4B.441	4B	BMYLD	441.13	AcrossEnv	4.8	10.65	2.79	3.68	2.18	1.5	13.29	TAM 133	160	158.5 - 160.5	chr4B_ 449765851	G/A	chr4B_ 414396615	G/A	
Qhi.tamu.4B.441	4B	ні	441.13	AcrossEnv	4.9	9.75	0.80	0.46	0.31	0.15	0.01	TAM 133	160	158.5 - 160.5	chr4B_ 449765851	G/A	chr4B_ 414396615	G/A	
Qkarea.tamu.6D.172	6D	KA	171.52	AcrossEnv, 20EMN	3.5 - 4.8	4.71 - 5.27	3.77	8.24 - 9.97	5.46	4.5	0.09 - 0.21	TAM 133	28	27.5 - 28.5	chr6D_ 172603833	C/A	chr6D_ 170544597	C/T	y?
Qskw.tamu.6D.172	6D	SKW	171.52	20MCG	3.4	6.14	-	8.96	-	-	0.86	TAM 133	28	27.5 - 28.5	chr6D_ 172603833	C/A	chr6D_ 170544597	C/T	
Qyld.tamu.7D.52	7D	YLD	52.32	AcrossEnv, 19BSP, 19CS	3.4 - 6.4	9.69 - 21.59	7.2	12.13 - 16.87	5.28	7.59	7.08 - 24.16	TAM 133	66	65.5 - 66.5	chr7D_ 51735477	A/G	chr7D_ 52399452	G/A	у
Qhi.tamu.7D.52	7D	ні	52.32	AcrossEnv, 19BSP	3.4 - 4.9	4.89 - 6.47	2.09	0.90 - 9.81	0.71	0.2	0.01	TAM 133	66	65.5 - 66.5	chr7D_ 51735477	A/G	chr7D_ 52399452	G/A	y?
Qdiam.tamu.7D.66	7D	DIAM	66.02	19MCG	3.56	5.5	-	7.60	-	-	0.03	TAM 113	89	86.5 - 95.5	chr7D_ 63208599	G/A	chr7D_ 71584239	A/G	
Qyld.tamu.7D.66	7D	YLD	66.02	20MCG	3.59	5.6	-	7.80	-	-	22.20	TAM 113	89	84.5 - 94.5	chr7D_ 63208599	G/A	chr7D_ 71584239	A/G	

Chr: Chromosome, Abbreviation of traits; YLD: Grain Yield from combine harvester, HD: Heading Date, BMYLD: Biomass Grain Yield from 0.5-meter inner row, HI: Harvest Index, SHGW: Single Head Grain Weight, KWID; Kernel Width, PH: Plant Height, SSHW: Single Stem Head Weight, DIAM: Kernel Diameter, KHI: Kernel Mardness Index, TKW: Thousand Kernel Weight, KA: Kernel Area, SHDW: Single Head Dry Weight, SKW: Single Kernel weight, Env: Environment, AcrossEnv: Across Environments, 19CS: College Station 2019, 20CS: College Station 2019, 20CS: McGregor 2020, 21BD: Bushland Dryland 2021, 19BSP: Bushland South Pivot 2019, 19MCG: McGregor 2020, 20EMN: Emeny Land 2020, Thr: threshold, LOD: Logarithm of the Odds, PVE: Phenotypic Variation Explained, AbyE: Additive by Environment Effect, Add: Additive Effect, cM: centimorgan, CI: Confidence Interval, Cons: Consistent, y: identified one individual and across environment.

	1B	2B	2D	4B	5B	6A 6D	7D
0 20 20 40 40 40 40 40 40 40 40 40 4		0 220 0 220 0 0 20 0 0 0 0 0 0 0 0 0 0 0 0 0	Gitw.tamu.20.37 Qshwid.tamu.20.37 Qshwid.tamu.20.37 Qshwid.tamu.20.37 Qyid.tamu.20.37 Qyid.tamu.20.37 Qistw.tamu.20.37 Qistw.tamu.20.34 Qph.tamu.20.34 Qph.tamu.20.34 Qohritamu.20.34 Qohritamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.34 Qistw.tamu.20.31 Qistw.tamu.20.31	Ohitany 48.441 Obny/d.tanu.48.441	0 1 20 1 1 1 1 1 1 1 1 1 1 1 1 1	Gskw.tamu.60.172 Okaros.tamu.60.172 Operi.tamu.64.98	Ohd.tamu.7D.70 Ohd.tamu.7D.52 Oyld.tamu.7D.52 Oyld.tamu.7D.52

Figure 2. Consistent and pleiotropic QTL detected from single and multi-environment analysis.

### 4.4.5. Epistasis, epistasis-by-environment, and additive-by-environment interactions

Epistatic interactions with total LOD > 5 were summarized for yield and yieldrelated traits collected from multiple Texas locations (Table A3). For yield, there were 109 epistatic interactions with overall LOD scores > 5, but none of them had LOD > 10. Four previously identified yield QTL from individual and across environmental additive analyses were also identified across environmental epistasis analysis. The first QTL, Qyld.tamu.2B.64 had epistatic interaction with Qyld.tamu.5B.1. Their epistasis interactions increased yield by 4.56 g m<sup>-2</sup> with favorable alleles from Gallagher and the epistasis-by-environment interaction increased grain yield by 4.59 g m<sup>-2</sup> in 20CS. The QTL Qyld.tamu.2D.34 interacted with Qyld.tamu.5B.21, increased grain yield by 4.17 g m<sup>-2</sup> with favorable alleles from Gallagher, and epistasis-by-environment interaction increased grain yield by 8.59 g m<sup>-2</sup> with favorable alleles from TAM113 in 19BSP. The third major QTL Qyld.tamu.6D.10 had epistatic interactions with two QTL, Qyld.tamu.4B.11 and Qyld.tamu.4B.13, and increased yield by 5.1 and 3.62 g m<sup>-2</sup> with favorable alleles from TAM 113 and Gallagher, respectively. Epistasis-by-environment interaction of Qyld.tamu.6D.10 and Qyld.tamu.4B.11 increased grain yield 8.0 g m<sup>-2</sup> with TAM 113 allele under 19CS while the epistasis-by-environment interaction of Qyld.tamu.6D.10 and Qyld.tamu.4B.13 increased grain yield 8.13 g m<sup>-2</sup> with Gallagher The fourth major QTL Qyld.tamu.7D.66 interacting allele in19CS. with Qyld.tamu.6A.596, had an epistatic interaction that increased grain yield by 6.36 g m<sup>-2</sup> with TAM 113 allele. Their epistasis-by-environment effect increased yield by 4.18 g m<sup>-2</sup> in 19CS.

For plant height, a total of 212 epistatic interactions with total LOD scores > 5were identified, and only two had overall LOD scores > 10, but none of them had a major effect. There were three plant height QTL associated with epistatic interactions. The first QTL Qph.tamu.3B.564 interacted with Qph.tamu.3B.625. Their epistasis interaction increased plant height by 1.07 cm with the favorable allele from TAM 113 while epistasisby-environment interaction increased plant height by 1.69 cm with TAM 113 allele in 19CS. The second QTL Qph.tamu.2D.30 interacted with Qph.tamu.6A.596, and their epistasis interactions increased plant height by 0.2 cm with the favorable allele from Gallagher while the epistasis-by-environment interaction increased plant height by 0.78 cm under 19CS. Qph.tamu.2D.30 also interacted with Qph.tamu.6D.458, and its epistasis interaction increased plant height by 0.39 cm with a TAM 113 allele while the epistasisby-environment interaction increased plant height up to 0.64 cm with a Gallagher allele in 20MCG. The last QTL, Qph.tamu.4B.646 interacted with Qph.tam.7D.33. Their epistatic interaction increased plant height by 0.42 cm with a Gallagher allele, and their epistaticby-environment interaction increased higher plant height by up to 0.43 cm with a TAM 113 allele in 20EMN.

A total of 251 epistatic interactions were detected with total LOD scores > 5 for heading date, and 22 had total LOD score >10. There were four QTL involved with these interactions. One QTL *Qhd.tamu.1A.566* interacted with *Qhd.tam.4A.714*. Their epistasis increased heading date by 0.46 days with a Gallagher allele, whereas epistasis-by-environment interaction increased heading date by up to 0.71 days with a Gallagher allele in 19CS. *Qhd.tamu.7A.709* interacted with two QTL, *Qhd.tamu.3D.603* and

*Qhd.tamu.1B.620.* Their epistatic interactions increased heading date by 0.61 and 0.77 days with the Gallagher allele. Epistasis-by-environment interactions increased heading date by 0.34 and 0.38 days with TAM 113 allele in 20EMN and 19CS, respectively. *Qhd.tamu.7D.608* interacted with *Qhd.tamu.6B.660* and their epistasis increased heading date by 0.51 days with a TAM 113 allele while epistasis-by-environment interactions increased heading date by 0.43 days with a Gallagher allele in 21BD. The last QTL, *Qhd.tamu.2D.34* interacted with *Qhd.tamu.2B.106* and their epistasis increased heading date by 0.67 days with a Gallagher allele, while epistasis-by-environment interactions increased heading date up to 0.52 with a TAM 113 allele. No other major QTL showed epistatic interactions for rest of the traits.

Figure 3. Epistatic interactions between QTL associated with yield and yield-related traits at LOD value > 5.0 and LOD value > 10.0.







#### 5. DISCUSSION

Improving yield is the primary objective of all wheat breeding programs. Understanding genetic bases of high yielding ability and components is critical in accelerating genetic gain in wheat improvement.

BLUP values were used to conduct statistical analyses. Combined ANOVA results indicate that the genotypic variation was higher than GbyE and environmental variances for all traits except biomass, grain yield, and head weight. Environmental and genotypeby-environmental interaction were also highly significant for most traits in our study. Genotypic variation and GbyE interaction for seed-related traits were highly significant (P < 0.001), but environmental variation was not significant, indicating that the contribution of genetic effect is higher than the environmental effect. Genotypic variation for harvest index was significant (P < 0.01), whereas GbyE and environmental variations were not significant for the same traits (Table 3).

Heritability is described as the ratio of genotypic variation over phenotypic variation, and it is a crucial parameter affecting selection response (Piepho & Mohring, 2007). The broad sense heritability ( $H^2$ ) varied from 0.02 to 0.9 for all traits (Table 3). Heritability values for agronomic and kernel-related traits were over 0.9, indicating that genotypic factors played a significant role in the phenotypic expression of these traits. Xin, Zhu, Wei, Han, and Zhao (2020) also reported high heritability estimates for kernel-related traits. However, broad sense heritability for yield and yield-related traits ranged

from low to high, suggesting that some traits could be affected by environmental factors, as it was reported by Garcia et al. (2019) and Al-Tabbal &Al-Fraihat, (2012).

Simple Pearson correlation coefficients among traits based on best linear unbiased estimates (BLUE) calculated across environments indicated that grain yield showed a negative correlation with deading date, consistent with what has been reported by Ali, Zhang, Rashed, Wang, and Zhang (2020). Gonfa and Tesfaye (2016) have reported different correlations of biomass and grain yield at different irrigation conditions. Similarly, we observed a significant positive correlation between grain yield and biomass under non-irrigated conditions but no correlation under irrigated conditions.

In this research, 156 QTL were mapped on all chromosomes except 1D and 3A (Table A2). Ten QTL were identified in more than two individual environments, and twelve genomic regions affect two or more traits. Several QTL detected for plant height in this study overlapped with previous reports, and some were located near previously identified QTL regions (Semang et al. 2021; Yang et al., 2020; Cao, Xu, Hanif, Xia, & He, 2020; Ma, Zhang, Li, Zou, & Li, 2019). Plant height QTL was found at 614.9 Mbp on chromosome 4B, explained 5.48 to 7.18% of the phenotypic variation. Semang et al. (2021) reported a plant height QTL located at a similar region at 611.1 Mbp on 4B, explaining 16% of the phenotypic variation. Another plant height QTL on chromosome 4B, *Qph.tamu.4B.485*, was also located very close to QTL detected by Semagn et al. (2021) on 4B at 474.9 Mbp.

The yield QTL on 1B at 571.4 Mbp was very close to previously reported QTL on 1B at 573 Mbp (Smith et al., 2021). Additionally, two more yield QTL were detected on

6D at 10.3 Mbp and 7B at 4.2 Mbp. Similarly, Yang et al. (2020) found two yield QTL on 6D and 7B around 10 Mbp away from our results. Recently, Semang et al. (2021) also reported the same yield QTL on 6D at 15.6 Mbp. Rabbi et al. (2021) also reported yield QTL near 7 Mbp at 6D. One consistent yield QTL was identified at 58 Mbp on 2B with 11.6 phenotypic variations. Semagn et al. (2021) found a similar genetic region between 55-62 Mbp on the same chromosome.

Ten genomic regions for heading date were detected on chromosomes 1A, 2B, 2D, 6B, 7A, and 7D. One consistent heading date QTL was mapped at 70 Mbp on 7D. Isham, Wang, Zhao, Wheeler, and Klassen (2021) mapped two heading date QTL at 68 Mbp and 71 Mbp on 7D, and this region could be co-localized with major flowering time gene *FT-D1*. Furthermore, another heading date QTL was detected on 7D in this study (*Qhd.tamu.7D.65*), and this genomic region is a few Mbp away from one major vernalization gene *Vrn3- on chromosome 7D* (Cao, Xu, Hanif, Xia, & He, 2020)

Liu et al. (2020) reported several thousand kernel weight QTL, one of which, (qTgw.nwipb-6AL), was mapped at 573 Mbp on 6A, which is also found in our present study. Moreover, another QTL was mapped near 28 Mbp on 2D, 7 Mb far away from our findings.

Multiple QTL were detected for seed related traits, some of them matching with previous reports; For instance, one kernel width QTL was mapped at 34 Mbp on 2D, which is close to a previously reported QTL region at 32 Mbp on the same chromosome (Ma, Zhang, Li, Zou, & Li, 2019). They also mapped kernel length QTL close to 48 Mbp on 2D, and we detected the same QTL 7 Mbp away from his findings. One kernel length QTL on 7A at

638.6 was close to a previously reported QTL region on 7A between 624 and 639 Mb (Cao, Xu, Hanif, Xia, & He, 2020).

Twelve pleiotropic QTL were identified from individual and across environmental analyses. One cluster QTL region was located between 51.2 to 70 Mbp on 7D, affecting multiple yield and yield-related traits. Similarly, Yan et al. (2020) also reported that the physical interval between 64 to 68 Mb was associated with yield and kernel-related traits using the RIL population derived from TAM 112 and TAM 111 hard red winter wheat.

There was two QTL cluster on 2D, one of which was located at 34.4 Mbp on 2D, affecting yield and kernel-related traits. This QTL region was co-localized with one of the photoperiod gene *Ppd-D1* that has pleiotropic effects on heading date, plant height, grain yield, thousand kernel weight, kernel width, and kernel diameter. (Basavaraddi, Savin, Wingen, Bencivenga, & Przewieslik-Allen, 2021; Vitale, Fania, Esposito, Pecorella, & Pecchioni, 2021). Another cluster QTL was located at 37 Mbp on 2D and was associated with thousand kernel weight, kernel width, biomass grain yield, and yield. Those six traits were significantly correlated to each other (Table 4). This suggests that traits with higher correlation could be under similar genotypic controls. Cluster QTL region can be used to design markers for MAS selection to understand the genetic basis of targeted traits (Lv et al., 2016).

Breeding progress is made through accumulating incremental gains for yield and related traits while maintaining quality, adaptation traits, and tolerance to biotic and abiotic stresses. This process utilizes the additive genetic variance for fixing these yieldassociated traits. The ICIM-EPI approach was performed to reveal genotype-by-environment and epistatic interactions between traits. Some QTL were involved with epistatic interactions. For example, four yield QTL (*Qyld.tamu.2B.64*, *Qyld.tamu.2D.34*, *Qyld.tamu.6D.10 and Qyld.tamu.7D.66*) involved in epistatic interactions and additive-by-additive interactions increased grain yield by 3.79, 6.23, 5.1 and 6.36 g m<sup>-2</sup>. In some environments, epistasis-by-environment interaction had higher grain yield increment than epistasis *per se*.

#### 6. CONCLUSION

This research used a population of 191 recombinant inbred lines (RIL) derived from a cross between TAM 113 and Gallagher hard red winter wheat to evaluate yield, yield components, and kernel traits in three different environments in Texas. A set of 8075 SNP markers covering all 21 Chromosomes was used to construct a high-density gene linkage map. We found a total of 156 QTL associated with 20 different traits, of which ten QTL were consistent in at least more than two individual environments, and 12 genomic regions had pleiotropic effect affecting more than one trait. Among those pleiotropic and consistent QTL, four were common at 57.61 on 2B, 34.3 Mb and 36.9 on 2D, 69.9 Mb on 2B, and 52.3 7D.

One QTL region at 2D overlapped with one of the significant photoperiod gene *Ppd-D1*. Another QTL region on 7D could be sharing the same genetic region with flowering time gene *FT-D1*. Among consistent or pleiotropic QTL, three yield, three heading date, two kernel width, one kernel length, one perimeter, one kernel area, one kernel length, one biomass grain yield, one single head grain weight, and one single head dry weight QTL had larger additive than additive-by-environment variation (Table 6, Table 7), that can be used in wheat breeding.

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## APPENDIX A

Table A1. Simple Spearmann correlation coefficients among traits collected in Bushland, TX 2020-2021. Values calculated using predicted means (BLUPs). - 21BD

TRAIT <sup>a</sup>	HD	PH	BM	SPM	HeadWt	BMGYLD	AREA	PERI	KLEN	KWIDTH	TKW	YLD	HI	KPS	SHW	SSHW
PH	0.01															
BM	0.05	0.35***														
SPM	0.29***	0.09	0.71***													
HeadWt	-0.19**	0.35***	0.84***	0.61***												
BMGYLD	-0.30***	0.34***	0.74***	0.45***	0.93***											
AREA	-0.07	0.20*	0.17*	-0.11	0.08	0.05										
PERI	0.10	0.23*	0.17*	-0.06	0.02	-0.04	0.90***									
KLEN	0.09	0.20*	0.16*	-0.03	0.02	-0.04	0.79***	0.96***								
KWIDTH	-0.19**	0.07	0.07	-0.06	0.07	0.05	0.70***	0.35***	0.18*							
TKW	0.14	-0.02	-0.13	-0.04	-0.15*	-0.15*	-0.08	-0.03	-0.05	-0.07						
YLD	-0.42***	0.47***	0.40***	0.16*	0.63***	0.68***	-0.02	-0.12	-0.11	0.00	-0.14					
HI	-0.44***	0.23**	0.27**	0.12	0.66***	0.82***	-0.04	-0.16*	-0.16*	0.02	-0.19**	0.65***				
KPS	0.14*	-0.02	-0.14	-0.04	-0.15*	-0.16*	-0.09	-0.04	-0.06	-0.08	1.00***	-0.14	-0.19**			
SHW	-0.48***	0.36***	0.43***	-0.12	0.69***	0.74***	0.22**	0.10	0.08	0.16*	-0.18*	0.65***	0.72***	-0.18*		
SSHW	-0.29***	0.32***	0.37***	-0.38***	0.28***	0.34***	0.38***	0.31***	0.26**	0.20**	-0.14	0.30***	0.17*	-0.14*	0.71***	
SHGW	-0.47***	0.34***	0.43***	-0.04	0.69***	0.85***	0.13	0.01	-0.01	0.11	-0.18**	0.66***	0.86***	-0.18*	0.91***	0.61***

<sup>a</sup>Abbreviations of Traits HD: Heading Date, BM: Biomass PH: Plant Height, SPM: Spikes m<sup>-2</sup>, HeadWt: Head Weight, BMYLD; Biomass Grain Yield from 0.5-meter inner row , KA; Kernel Area, PERI: Perimeter, KLEN: Kernel Length, KWID: Kernel Width, TKW: Thousand Kernel Weight, YLD from combine harvester: Yield, HI: Harvest Index, KPS: Kernels Spike<sup>-1</sup>, SHDW: Single Head Dry Weight, SSHW: Single Stem Head Weight, SHGW: Single Head Grain Weight

 $\ast,$   $\ast\ast,$   $\ast\ast\ast,$  significant at 0.05, 0.01, and 0.001 probability levels, respectively.

TRAIT <sup>a</sup>	PH	BM	SPM	HeadWt	BMGYLD	AREA	PERI	KLEN	KWIDTH	TKW	YLD	HI	KPS	SHW	SSHW
BM	0.16*														
SPM	-0.26***	0.60***													
HeadWt	0.12	0.79***	0.52**												
BMGYLD	0.22**	0.74***	0.39**	0.84***											
AREA	0.42***	0.16*	-0.25*	0.28***	0.23**										
PERI	0.36***	0.12	-0.24*	0.20**	0.15*	0.92***									
KLEN	0.30***	0.11	-0.20*	0.15*	0.11	0.81***	0.96***								
KWIDTH	0.38***	0.17*	-0.19*	0.30***	0.26**	0.83***	0.57***	0.35***							
TKW	0.45***	0.19**	-0.26*	0.30***	0.28***	0.93***	0.77***	0.62***	0.89***						
YLD	0.46***	0.28***	0.0	0.45***	0.55***	0.26**	0.16*	0.10	0.31***	0.34***					
HI	0.24**	0.23**	0.0	0.63***	0.65***	0.28***	0.20**	0.14	0.32***	0.34***	0.68***				
KPS	0.26**	0.33***	-0.15	0.50***	0.60***	-0.01	-0.02	-0.02	0.00	0.02	0.55***	0.72***			
SHW	0.36***	0.31***	-0.33**	0.63***	0.55***	0.54***	0.45***	0.36***	0.51***	0.57***	0.48***	0.61***	0.68***		
SSHW	0.46***	0.31***	-0.56**	0.18**	0.28***	0.45***	0.40***	0.36***	0.39***	0.49***	0.24**	0.11	0.50***	0.71***	
SHGW	0.41***	0.35***	-0.29**	0.51***	0.76***	0.42***	0.34***	0.28***	0.41***	0.48***	0.56***	0.61***	0.73***	0.81***	0.70***

Table A1. Simple Spearmann correlation coefficients among traits collected in Bushland, TX 2020-2021. Values calculated using predicted means (BLUPs) – 20EMN

<sup>a</sup>Abbreviations of Traits PH: Plant Height, BM: Biomass, SPM: Spikes m<sup>-2</sup>, HeadWt: Head Weight, BMYLD; Biomass Grain Yield from 0.5-meter inner row, KA; Kernel Area, PERI: Perimeter, KLEN: Kernel Length, KWID: Kernel Width, TKW: Thousand Kernel Weight, YLD: Yield from combine harvester, HI: Harvest Index, KPS: Kernels Spike<sup>-1</sup>, SHDW: Single Head Dry Weight, SSHW: Single Stem Head Weight, SHGW: Single Head Grain Weight

\*, \*\*, \*\*\*, significant at 0.05, 0.01, and 0.001 probability levels, respectively.

TRAIT <sup>a</sup>	HD	PH
PH	0.16*	
YLD	-0.58***	0.13

Table A1. Simple Spearmann correlation coefficients among traits collected in Bushland, TX 2020-2021. Values calculated using predicted means (BLUPs) - 20CS

TRAIT <sup>a</sup>	HD	PH	BM	SPM	HeadWt	BMGYLD	AREA	PERI	KLEN	KWIDTH	TKW	YLD	HI	KPS	SHW	SSHW
PH	0.33***															
BM	0.11	0.32**														
SPM	0.06	0.06	0.67***													
HeadWt	-0.23**	0.07	0.86***	0.64***												
BMGYLD	-0.41***	0.01	0.75***	0.50***	0.91***											
AREA	-0.58***	0.08	0.02	-0.28**	0.22**	0.41***										
PERI	-0.45***	0.12	0.09	-0.19*	0.26**	0.38***	0.93***									
KLEN	-0.32**	0.17*	0.11	-0.11	0.25**	0.33**	0.82***	0.96***								
KWIDTH	-0.62***	-0.05	-0.07	-0.34***	0.14	0.37***	0.84***	0.61***	0.38***							
TKW	-0.65***	0.01	-0.01	-0.30**	0.21*	0.44***	0.95***	0.82***	0.65***	0.92***						
YLD	-0.36***	-0.16	0.09	-0.04	0.27**	0.44***	0.34***	0.24**	0.18*	0.38***	0.40***					
HI	-0.65***	-0.19*	0.39***	0.25**	0.71***	0.89***	0.58***	0.49***	0.39***	0.57***	0.64***	0.56***				
KPS	0.20*	-0.13	0.21*	-0.19*	0.20*	0.19*	-0.31**	-0.29**	-0.26**	-0.26**	-0.30**	0.15	0.12			
SHW	-0.32**	-0.01	0.13	-0.51***	0.32**	0.40***	0.59***	0.53***	0.43***	0.56***	0.60***	0.36***	0.48***	0.46***		
SSHW	-0.01	0.13	-0.20*	-0.85***	-0.25**	-0.13	0.38***	0.32**	0.23**	0.39***	0.39***	0.13	-0.05	0.42***	0.78***	
SHGW	-0.48***	-0.05	0.14	-0.43***	0.33***	0.56***	0.69***	0.58***	0.45***	0.70***	0.74***	0.49***	0.68***	0.39***	0.92***	0.68***

Table A1. Simple Spearmann correlation coefficients among traits collected in Bushland, TX 2020-2021. Values calculated using predicted means (BLUPs) – 19BSP

<sup>a</sup>Abbreviations of Traits HD: Heading Date, PH: Plant Height, BM: Biomass, SPM: Spikes m<sup>-2</sup>, HeadWt: Head Weight, BMYLD; Biomass Grain Yield from 0.5-meter inner row , KA; Kernel Area, PERI: Perimeter, KLEN: Kernel Length, KWID: Kernel Width, TKW: Thousand Kernel Weight, YLD: Yield from combine harvester, HI: Harvest Index, KPS: Kernels Spike<sup>-1</sup>, SHDW: Single Head Dry Weight, SSHW: Single Stem Head Weight, SHGW: Single Head Grain Weight

\*, \*\*, \*\*\*, significant at 0.05, 0.01, and 0.001 probability levels, respectively.

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
BMYLD	Qbmyld.tamu.2B.69	21BD	3.48	2B	69.34	108	chr2B_68426788	4.24			10.34			37.04	TAM 113		р
BMYLD	Qbmyld.tamu.7D.51	19BSP	3.47	7D	51.34	64	chr7D_47632974	4.28			7.28			18.53	TAM 113		
BMYLD	Qbmyld.tamu.2B.19	19BSP	3.47	2B	18.82	26	chr2B_18656478	3.76			6.65			17.66	TAM 113		
BMYLD	Qbmyld.tamu.4B.441	AcrossEnv	4.85	4B	441.13	160	chr4B_449765851	10.65	2.8	7.86	3.68	2.18	1.5	13.29	TAM 113		р
BMYLD	Qbmyld.tamu.4B.551	AcrossEnv	4.85	4B	551.23	237	chr4B_541365812	18.76	2.06	16.71	6.91	1.73	5.18	-11.87	Gallagher		
BMYLD	Qbmyld.tamu.2D.37	AcrossEnv	4.85	2D	37.25	64	chr2D_37211804	6.35	2.48	3.87	2.36	1.9	0.45	-12.43	Gallagher	y?	р
BMYLD	Qbmyld.tamu.2D.37	19BSP	4.85	2D	37.25	64	chr2D_37211804	4.96			8.53			-20.03	Gallagher	y?	р
DIAM	Qdiam.tamu.7D.66	19MCG	3.56	7D	66.02	89	chr7D_63208599	5.55			7.69			0.03	TAM 113		р
DIAM	Qdiam.tamu.2B.149	20MCG	3.56	2B	149.26	120	chr2B_145617210	5.53			6.69			0.03	TAM 113		
DIAM	Qdiam.tamu.6A.565	20MCG	3.56	6A	564.98	179	chr6A_566172088	5.67			6.83			-0.03	Gallagher		
DIAM	Qdiam.tamu.2D.34	20MCG	3.56	2D	34.43	61	chr2D_32901354	23.51			35.05			-0.07	Gallagher		р
HARD	Qhard.tamu.1A.584	20MCG	3.56	1A	583.86	235	chr1A_583256428	3.92			7.22			2.49	TAM 113		
HD	Qhd.tamu.2D.34	20MCG	3.48	2D	34.43	61	chr2D_32901354	32.91			53.52			4.86	TAM 113	у	р
HD	Qhd.tamu.2D.34	20CS	3.5	2D	34.43	61	chr2D_32901354	48.67			38.55			4.55	TAM 113	у	р
HD	Qhd.tamu.7D.608	20CS	3.5	7D	607.85	330	chr7D_611166154	37.22			25.55			3.7	TAM 113	y?	
HD	Qhd.tamu.2D.34	19MCG	3.47	2D	34.43	61	chr2D_32901354	22.34			38.31			3.21	TAM 113	у	р
HD	Qhd.tamu.2D.34	AcrossEnv	5.85	2D	34.43	61	chr2D_32901354	157.96	103.9	54.06	64.66	54.05	10.6	3.15	TAM 113	у	р
HD	Qhd.tamu.2D.34	21BD	3.48	2D	34.43	61	chr2D_32901354	23.43			34.51			1.66	TAM 113	у	р
HD	Qhd.tamu.2D.34	19BSP	3.47	2D	34.43	61	chr2D_32901354	30.61			35.52			1.51	TAM 113	у	р
HD	Qhd.tamu.7A.709	20MCG	3.48	7A	709.16	285	chr7A_701123987	3.62			4.4			1.39	TAM 113		
HD	Qhd.tamu.6B.4	20CS	3.5	6B	3.56	1	chr6B_2202189	4.18			1.85			0.99	TAM 113	y?	
HD	Qhd.tamu.7D.608	AcrossEnv	5.85	7D	607.85	330	chr7D_611166154	38.02	6.88	31.14	14.77	1.829	12.94	0.58	TAM 113	y?	

Table A2. QTL detected for all traits in individual and across environments.

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
HD	Qhd.tamu.1A.566	AcrossEnv	4.91	1A	566.29	205	chr1A_565388907	5.87	4.12	1.75	1.18	1.045	0.14	0.44	TAM113		
HD	Qhd.tamu.6B.4	AcrossEnv	5.85	6B	3.56	1	chr6B_2202189	7.79	6.39	1.39	2.14	1.603	0.54	0.54	TAM113	y?	
HD	Qhd.tamu.2B.64	AcrossEnv	5.85	2B	63.96	105	chr2B_63428577	10.22	1.81	8.41	1.06	0.447	0.61	-0.29	Gallagher	y?	р
HD	Qhd.tamu.7D.70	19BSP	3.47	7D	70.03	94	chr7D_63208599	5.55			5.11			-0.57	Gallagher	у	
HD	Qhd.tamu.2B.58	AcrossEnv	5.85	2B	57.61	101	chr2B_57657606	16.11	7.19	8.93	3.12	1.849	1.27	-0.58	Gallagher	у	р
HD	Qhd.tamu.7D.70	AcrossEnv	5.85	7D	70.03	94	chr7D_63208599	15.92	8.8	7.12	2.42	2.238	0.18	-0.64	Gallagher	у	
HD	Qhd.tamu.2B.64	19BSP	3.47	2B	63.96	105	chr2B_63428577	9.16			8.12			-0.72	Gallagher	y?	р
HD	Qhd.tamu.7D.65	21BD	3.48	7D	65.22	88	chr7D_63208599	5.28			6.71			-0.73	Gallagher		
HD	Qhd.tamu.7D.71	20CS	3.5	7D	70.83	95	chr7D_63208599	3.78			1.73			-0.96	Gallagher	у	
HD	Qhd.tamu.2B.58	21BD	3.48	2B	57.61	101	chr2B_57657606	9.48			11.63			-0.96	Gallagher	у	р
HD	Qhd.tamu.2B.58	20CS	3.5	2B	57.61	101	chr2B_57657606	4.91			2.16			-1.07	Gallagher	у	р
HD	Qhd.tamu.2B.63	19MCG	3.47	2B	63.25	104	chr2B_56732564	3.97			5.49			-1.22	Gallagher		
HI	Qhi.tamu.2D.99	21BD	3.48	2D	99.25	112	chr2D_96540686	23.86			8.78			0.08	TAM113	y?	
HI	Qhi.tamu.2B.76	21BD	3.48	2B	76.4	109	chr2B_68426788	6.09			1.8			0.04	TAM113		р
HI	Qhi.tamu.2D.99	AcrossEnv	4.91	2D	99.25	112	chr2D_96540686	23.95	20.09	3.86	25.7	8.261	17.44	0.03	TAM113	y?	
HI	Qhi.tamu.2B.69	AcrossEnv	4.91	2B	69.34	108	chr2B_68426788	6.19	5.45	0.74	5.19	1.975	3.22	0.01	TAM113		р
HI	Qhi.tamu.7D.52	AcrossEnv	4.91	7D	52.32	66	chr7D_51735477	6.47	2.09	4.38	0.91	0.707	0.2	0.01	TAM113	y?	р
HI	Qhi.tamu.7D.52	19BSP	3.47	7D	52.32	66	chr7D_51735477	4.89			9.81			0.01	TAM113	y?	р
HI	Qhi.tamu.4B.441	AcrossEnv	4.91	4B	441.13	160	chr4B_449765851	9.75	0.83	8.91	0.46	0.308	0.15	0.01	TAM113		р
HI	Qhi.tamu.4B.603	AcrossEnv	4.91	4B	603.4	258	chr4B_603463167	16.04	0.49	15.55	0.48	0.171	0.31	0	Gallagher		
HI	Qhi.tamu.2D.34	AcrossEnv	4.91	2D	34.43	61	chr2D_32901354	15.79	2.2	13.59	0.81	0.779	0.03	-0.01	Gallagher	y?	р
HI	Qhi.tamu.2D.34	19BSP	3.47	2D	34.43	61	chr2D_32901354	10.96			21.81			-0.01	Gallagher	y?	р

Table A2. QTL detected for all traits in individual and across environments.

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
HI	Qhi.tamu.2D.107	AcrossEnv	4.91	2D	106.64	114	chr2D_104650607	33.36	30.84	2.51	41.3	14.28	27.02	-0.03	Gallagher	y?	
HI	Qhi.tamu.2D.107	21BD	3.48	2D	106.64	114	chr2D_104650607	33.2			14.28			-0.1	Gallagher	y?	
HeadWt	Qhw.tamu.1A.10	21BD	3.48	1A	10.02	5	chr1A_9877409	3.73			6.2			-52.53	Gallagher		
KA	Qkarea.tamu.6D.172	AcrossEnv	3.52	6D	171.52	28	chr6D_172603833	4.71			8.24			0.21	TAM113	у?	р
KA	Qkarea.tamu.6D.351	19BSP	3.47	6D	350.82	43	chr6D_362479513	3.73			6.05			0.16	TAM113		р
KA	Qkarea.tamu.6D.172	AcrossEnv	4.85	6D	171.52	28	chr6D_172603833	5.28	3.77	1.51	9.97	5.456	4.52	0.09	TAM113	у?	р
KA	Qkarea.tamu.6A.572	AcrossEnv	4.85	6A	572.4	188	chr6A_571690944	6.19	2.05	4.14	9.08	2.855	6.23	-0.07	Gallagher	y?	
KA	Qkarea.tamu.2D.37	AcrossEnv	4.85	2D	36.9	63	chr2D_36584261	17.81	12.42	5.39	32.68	18.72	13.95	-0.17	Gallagher	у	р
KA	Qkarea.tamu.6A.562	20EMN	3.52	6A	562.27	174	chr6A_562265727	4.29			7.44			-0.2	Gallagher		р
KA	Qkarea.tamu.6A.572	19BSP	3.47	6A	572.4	188	chr6A_571690944	6.1			10.77			-0.22	Gallagher	y?	
KA	Qkarea.tamu.2D.37	19BSP	4.85	2D	36.9	63	chr2D_36584261	8.67			14.9			-0.25	Gallagher	у	р
KA	Qkarea.tamu.2D.37	20EMN	4.85	2D	36.9	63	chr2D_36584261	8.85			16.23			-0.29	Gallagher	у	р
KHI	Qkhi.tamu.2D.34	20MCG	3.56	2D	34.43	61	chr2D_32901354	23.12			29.85			5.71	TAM113		р
KHI	Qkhi.tamu.4B.665	20MCG	3.56	4B	664.95	361	chr4B_664910777	4.73			4.81			-2.28	Gallagher		
KHI	Qkhi.tamu.5D.8	20MCG	3.56	5D	7.77	2	chr5D_6333523	4.78			4.87			-2.31	Gallagher		
KHI	Qkhi.tamu.2B.65	20MCG	3.56	2B	65.44	106	chr2B_64954626	8.28			8.84			-3.11	Gallagher		
KLEN	Qklen.tamu.5B.497	19BSP	3.47	5B	496.62	211	chr5B_489969825	3.92			7.71			0.06	TAM113	у	р
KLEN	Qklen.tamu.5B.497	20EMN	3.52	5B	496.62	211	chr5B_489969825	4.17			4.91			0.05	TAM113	у	р
KLEN	Qklen.tamu.5B.497	AcrossEnv	4.85	5B	496.62	211	chr5B_489969825	8.42	6.5	1.92	12.45	10.69	1.77	0.04	TAM113	у	р
KLEN	Qklen.tamu.2D.41	AcrossEnv	4.85	2D	41.12	70	chr2D_38687722	5.93	0.02	5.91	10.89	0.037	10.86	0	TAM113		р
KLEN	Qklen.tamu.3D.585	AcrossEnv	4.85	3D	585.36	126	chr3D_585018045	6.4	1.33	5.07	9.2	2.062	7.14	-0.02	Gallagher	y?	
KLEN	Qklen.tamu.6A.113	AcrossEnv	4.85	6A	113.23	129	chr6A_105002720	5.91	1.38	4.53	9.74	2.2	7.54	-0.02	Gallagher	y?	

Table A2. QTL detected for all traits in individual and across environments.

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
KLEN	Qklen.tamu.4A.29	AcrossEnv	4.85	4A	29.34	20	chr4A_29303359	5.32	2.84	2.48	7.12	4.477	2.64	-0.03	Gallagher	y?	
KLEN	Qklen.tamu.6A.98	AcrossEnv	4.85	6A	98.34	77	chr6A_98982341	14.28	3.98	10.3	20.8	6.461	14.34	-0.03	Gallagher	y?	р
KLEN	Qklen.tamu.3D.585	20EMN	3.52	3D	585.36	126	chr3D_585018045	3.87			4.54			-0.05	Gallagher	у?	
KLEN	Qklen.tamu.4A.29	20EMN	3.52	4A	29.34	20	chr4A_29303359	4.26			5.11			-0.05	Gallagher	у?	
KLEN	Qklen.tamu.7A.639	19BSP	3.47	7A	638.67	214	chr7A_639295826	3.63			6.93			-0.05	Gallagher		
KLEN	Qklen.tamu.6A.113	19BSP	3.47	6A	113.23	129	chr6A_105002720	5.82			11.49			-0.07	Gallagher	у?	
KLEN	Qklen.tamu.6A.98	20EMN	3.52	6A	98.34	77	chr6A_98982341	14.23			18.91			-0.1	Gallagher	у?	р
KPS	Qkps.tamu.6A.586	19BSP	3.47	6A	586.24	200	chr6A_586202172	6.71			16.17			0.95	TAM113		
KPS	Qkps.tamu.5A.13	20EMN	3.52	5A	12.83	29	chr5A_12691384	4.71			10.03			-0.88	Gallagher		
KWID	Qkwid.tamu.7D.66	19BSP	3.47	7D	66.02	89	chr7D_63208599	8.3			12.64			0.04	TAM113	y?	р
KWID	Qkwid.tamu.7D.67	AcrossEnv	4.85	7D	66.83	90	chr7D_63208599	11.59	9.17	2.43	8.2	6.6	1.6	0.02	TAM113	y?	р
KWID	Qkwid.tamu.2B.703	21BD	3.48	2B	703.26	212	chr2B_696048977	5.21			8.87			0.02	TAM113		
KWID	Qkwid.tamu.3B.431	21BD	3.48	3B	431.27	69	chr3B_427070695	4.75			8.07			0.02	TAM113	y?	
KWID	Qkwid.tamu.6D.351	AcrossEnv	4.85	6D	350.82	43	chr6D_362479513	5.75	5.42	0.33	5.26	4.282	0.98	0.02	TAM113		р
KWID	Qkwid.tamu.2B.85	AcrossEnv	4.85	2B	84.91	113	chr2B_76076511	4.29	3.46	0.83	3.94	2.679	1.26	0.01	TAM113		р
KWID	Qkwid.tamu.3B.431	AcrossEnv	4.85	3B	431.27	69	chr3B_427070695	5.39	2.22	3.17	2.15	1.732	0.42	0.01	TAM113	y?	
KWID	Qkwid.tamu.2B.698	AcrossEnv	4.85	2B	697.55	211	chr2B_696048977	5.56	1.9	3.65	2.13	1.47	0.66	0.01	TAM113		
KWID	Qkwid.tamu.3B.26	AcrossEnv	4.85	3B	26	35	chr3B_25733703	2.85	1.52	1.33	2.45	1.181	1.26	0.01	TAM113		
KWID	Qkwid.tamu.2D.34	AcrossEnv	4.85	2D	34.43	61	chr2D_32901354	5.2	0.86	4.34	1.78	0.681	1.1	-0.01	Gallagher	y?	р
KWID	Qkwid.tamu.6D.463	AcrossEnv	4.85	6D	462.71	111	chr6D_462634429	2.62	1.4	1.22	1.79	1.083	0.7	-0.01	Gallagher		
KWID	Qkwid.tamu.1A.336	AcrossEnv	4.85	1A	335.94	83	chr1A_301162467	2.83	2.52	0.31	2.63	1.947	0.69	-0.01	Gallagher		
KWID	Qkwid.tamu.1A.406	AcrossEnv	4.85	1A	405.71	131	chr1A_46276720	3.19	2.68	0.51	3.06	2.034	1.02	-0.01	Gallagher		

Table A2. QTL detected for all traits in individual and across environments.

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
KWID	Qkwid.tamu.1A.406	AcrossEnv	4.85	1A	405.92	116	chr1A_399489700	3.16	2.84	0.32	2.97	2.204	0.76	-0.01	Gallagher		
KWID	Qkwid.tamu.1A.480	AcrossEnv	4.85	1A	480.28	111	chr1A_485182245	3.2	3.06	0.15	3.13	2.369	0.76	-0.01	Gallagher		
KWID	Qkwid.tamu.6A.562	AcrossEnv	4.85	6A	562.27	174	chr6A_562265727	3.98	3.27	0.71	3.64	2.591	1.05	-0.01	Gallagher		р
KWID	Qkwid.tamu.1B.620	AcrossEnv	4.85	1B	619.99	25	chr1B_619535304	4.48	3.76	0.72	4.81	2.965	1.85	-0.01	Gallagher		
KWID	Qkwid.tamu.2D.34	21BD	3.48	2D	34.43	61	chr2D_32901354	5.17			8.62			-0.02	Gallagher	y?	р
KWID	Qkwid.tamu.2D.37	AcrossEnv	4.85	2D	37.25	64	chr2D_37211804	17.38	14	3.38	18.2	11.69	6.52	-0.02	Gallagher	у?	р
KWID	Qkwid.tamu.2D.37	20EMN	3.52	2D	37.25	64	chr2D_37211804	5.3			12.68			-0.03	Gallagher	у?	р
KWID	Qkwid.tamu.2D.37	19BSP	3.47	2D	36.9	63	chr2D_36584261	12.48			17.49			-0.04	Gallagher		р
PERI	Qperi.tamu.5B.497	20EMN	3.52	5B	496.62	211	chr5B_489969825	3.76			7.64			0.15	TAM113	у?	р
PERI	Qperi.tamu.2D.41	21BD	3.48	2D	41.12	70	chr2D_38687722	3.91			9.7			0.15	TAM113		р
PERI	Qperi.tamu.5B.497	AcrossEnv	4.83	5B	496.62	211	chr5B_489969825	5.87	5.06	0.81	9.89	8.251	1.64	0.1	TAM113	y?	р
PERI	Qperi.tamu.2D.33	AcrossEnv	4.83	2D	33.14	60	chr2D_32901354	5.22	1.29	3.93	6.75	1.904	4.84	-0.05	Gallagher	y?	
PERI	Qperi.tamu.6A.98	AcrossEnv	4.83	6A	98.34	77	chr6A_98982341	12.38	7.31	5.07	19.75	11.86	7.89	-0.11	Gallagher	у	р
PERI	Qperi.tamu.2D.33	19BSP	3.47	2D	33.14	60	chr2D_32901354	5.23			9.04			-0.16	Gallagher	y?	
PERI	Qperi.tamu.2D.37	20EMN	3.52	2D	36.9	63	chr2D_36584261	4.45			8.81			-0.17	Gallagher		р
PERI	Qperi.tamu.6A.98	19BSP	3.47	6A	98.34	77	chr6A_98982341	6.91			11.55			-0.18	Gallagher	у	р
PERI	Qperi.tamu.6A.98	20EMN	3.52	6A	98.34	77	chr6A_98982341	5.43			11.07			-0.19	Gallagher	у	р
PH	Qph.tamu.2D.34	20MCG	3.48	2D	34.43	61	chr2D_32901354	19.85			28.79			3.48	TAM113	у	р
PH	Qph.tamu.4B.424	19MCG	3.47	4B	423.5	105	chr4B_430792975	16.32			10.36			2.5	TAM113	y?	
PH	Qph.tamu.2D.34	19BSP	3.47	2D	34.43	61	chr2D_32901354	11.36			15.46			2.12	TAM113	у	р
PH	Qph.tamu.2D.28	20CS	3.5	2D	28.26	51	chr2D_22290058	6.95			10.09			1.75	TAM113		
PH	Qph.tamu.5B.490	20CS	3.5	5B	490.39	208	chr5B_489384278	7.21			7.79			1.55	TAM113		

Table A2. QTL detected for all traits in individual and across environments.

Table A2.	Continued
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Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
PH	Qph.tamu.2D.69	19MCG	3.47	2D	68.81	93	chr2D_68797075	5.78			3.19			1.38	TAM113	y?	
PH	Qph.tamu.2D.32	AcrossEnv	6.51	2D	32.27	59	chr2D_31103643	43.91	34.77	9.14	36.3	20.82	15.49	1.36	TAM113		
PH	Qph.tamu.2B.646	19BSP	3.47	2B	645.72	175	chr2B_645610956	3.7			4.62			1.16	TAM113		
PH	Qph.tamu.2D.31	21BD	3.48	2D	31.5	58	chr2D_31103643	6.11			9.52			1.01	TAM113		р
PH	Qph.tamu.3B.564	21BD	3.48	3B	563.95	110	chr3B_563291707	3.65			5.51			0.77	TAM113		
PH	Qph.tamu.5B.489	AcrossEnv	3.52	5B	488.95	207	chr5B_488397473	9.29	3.77	5.51	5.37	2.13	3.24	0.43	TAM113		
PH	Qph.tamu.2D.69	AcrossEnv	6.51	2D	68.81	93	chr2D_68797075	6.99	3.14	3.85	4.29	1.789	2.5	0.4	TAM113	y?	
PH	Qph.tamu.4B.424	AcrossEnv	6.51	4B	423.5	105	chr4B_430792975	17.6	2.65	14.95	12.19	1.503	10.69	0.36	TAM113	y?	
PH	Qph.tamu.6A.318	AcrossEnv	6.51	6A	318.04	100	chr6A_383955363	8.57	1.04	7.53	3.72	0.552	3.16	-0.22	Gallagher	y?	
PH	Qph.tamu.6A.89	AcrossEnv	6.51	6A	88.63	67	chr6A_100368136	9.67	1.5	8.17	6.34	0.86	5.48	-0.28	Gallagher		
PH	Qph.tamu.6A.397	AcrossEnv	6.51	6A	397.39	88	chr6A_369369749	12.1	1.5	10.59	4.11	0.87	3.24	-0.28	Gallagher	y?	
PH	Qph.tamu.6A.102	AcrossEnv	6.51	6A	102.01	82	chr6A_102090552	6.93	2.14	4.79	6.69	1.219	5.47	-0.33	Gallagher	y?	
PH	Qph.tamu.4B.615	AcrossEnv	6.51	4B	614.94	265	chr4B_612610190	7.19	2.26	4.93	3.12	1.267	1.86	-0.33	Gallagher	y?	
PH	Qph.tamu.6A.175	AcrossEnv	6.51	6A	174.79	123	chr6A_184344892	9.5	2.88	6.62	6.91	1.622	5.29	-0.38	Gallagher	y?	
PH	Qph.tamu.4B.50	AcrossEnv	6.51	4B	50.4	91	chr4B_56298857	7.52	3.06	4.46	4.33	1.74	2.59	-0.39	Gallagher	y?	
PH	Qph.tamu.1A.349	AcrossEnv	4.84	1A	349.34	97	chr1A_265556603	6.67	3.25	3.42	4.14	1.83	2.31	-0.4	Gallagher	y?	
PH	Qph.tamu.6A.86	AcrossEnv	6.51	6A	86.43	70	chr6A_86557461	17.97	3.54	14.43	12.77	2.021	10.74	-0.42	Gallagher	y?	
PH	Qph.tamu.1A.85	AcrossEnv	6.51	1A	84.79	81	chr1A_62276029	9.59	3.61	5.98	4.5	2.044	2.46	-0.42	Gallagher		
PH	Qph.tamu.4B.505	AcrossEnv	6.51	4B	505.5	66	chr4B_508667019	7.19	3.96	3.23	4.35	2.207	2.14	-0.44	Gallagher	y?	
PH	Qph.tamu.4A.36	AcrossEnv	6.51	4A	35.68	24	chr4A_35060935	6.72	5.77	0.95	4.92	3.254	1.66	-0.54	Gallagher		
PH	Qph.tamu.4B.646	AcrossEnv	6.51	4B	645.96	285	chr4B_645618725	8.5	6.34	2.16	6.89	3.609	3.28	-0.56	Gallagher	y?	
PH	Qph.tamu.4B.485	AcrossEnv	6.51	4B	484.67	188	chr4B_475417745	25.54	8.67	16.87	19.6	4.915	14.68	-0.66	Gallagher	y?	

Table A2.	Continued
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Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
PH	Qph.tamu.1A.392	21BD	3.48	1A	391.69	101	chr1A_385940529	3.85			5.74			-0.78	Gallagher		
PH	Qph.tamu.3D.558	20CS	3.5	3D	558.14	90	chr3D_558034362	3.53			3.72			-1.06	Gallagher		
PH	Qph.tamu.4B.615	20EMN	3.52	4B	614.94	265	chr4B_612610190	5.48			8.29			-1.11	Gallagher	y?	
PH	Qph.tamu.2A.385	19BSP	3.47	2A	384.67	125	chr2A_271026277	4.43			5.57			-1.27	Gallagher		
PH	Qph.tamu.1A.349	20CS	3.5	1A	349.34	97	chr1A_265556603	5.43			5.94			-1.35	Gallagher	y?	
PH	Qph.tamu.4B.505	19BSP	3.47	4B	505.5	66	chr4B_508667019	4.99			6.52			-1.37	Gallagher	y?	
PH	Qph.tamu.1A.60	20EMN	3.52	1A	59.87	80	chr1A_45627022	8.42			13.33			-1.41	Gallagher		
PH	Qph.tamu.4B.50	20CS	3.5	4B	50.4	91	chr4B_56298857	6.08			6.49			-1.41	Gallagher	y?	
PH	Qph.tamu.6A.318	20EMN	3.52	6A	318.04	100	chr6A_383955363	8.4			13.92			-1.44	Gallagher	y?	
PH	Qph.tamu.6A.397	21BD	3.48	6A	397.39	88	chr6A_369369749	11.82			19.43			-1.45	Gallagher	y?	
PH	Qph.tamu.4B.646	20MCG	3.48	4B	645.96	285	chr4B_645618725	5.77			7.17			-1.74	Gallagher	y?	
PH	Qph.tamu.6A.89	19MCG	3.47	6A	88.63	67	chr6A_100368136	9.62			5.65			-1.85	Gallagher		
PH	Qph.tamu.6A.102	20MCG	3.48	6A	102.01	82	chr6A_102090552	6.66			8.44			-1.88	Gallagher	y?	
PH	Qph.tamu.6A.175	19BSP	3.47	6A	174.79	123	chr6A_184344892	9.25			12.9			-1.93	Gallagher	y?	
PH	Qph.tamu.6A.86	20CS	3.5	6A	86.43	70	chr6A_86557461	17.95			22.36			-2.62	Gallagher	y?	
PH	Qph.tamu.4B.485	19MCG	3.47	4B	484.67	188	chr4B_475417745	24.05			17.25			-3.22	Gallagher	y?	
SHDW	Qshdw.tamu.2A.747	19BSP	3.51	2A	746.93	36	chr2A_746960172	5.04			10.43			0.03	TAM113	y?	р
SHDW	Qshdw.tamu.2A.747	AcrossEnv	4.9	2A	746.93	36	chr2A_746960172	5.92	3	2.93	4.09	3.418	0.67	0.02	TAM113	y?	р
SHDW	Qshdw.tamu.1A.74	AcrossEnv	4.9	1A	74.22	118	chr1A_74644136	6.15	4.55	1.6	5.22	5.164	0.06	-0.02	Gallagher	y?	р
SHDW	Qshdw.tamu.1A.74	19BSP	3.51	1A	74.22	118	chr1A_74644136	3.72			7.58			-0.03	Gallagher	y?	р
SHDW	Qshdw.tamu.2D.264	19BSP	3.51	2D	263.59	129	chr2D_267421652	3.83			7.78			-0.03	Gallagher		
SHDW	Qshdw.tamu.2D.37	AcrossEnv	4.9	2D	37.25	64	chr2D_37211804	11.56	10.41	1.15	23.96	12.4	11.56	-0.04	Gallagher	y?	р

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
SHDW	Qshdw.tamu.2D.37	21BD	3.51	2D	37.25	64	chr2D_37211804	10.33			22.16			-0.09	Gallagher	у?	р
SHGW	Qshgw.tamu.2B.76	21BD	3.51	2B	76.4	109	chr2B_68426788	4.86			10.68			0.06	TAM113		р
SHGW	Qshgw.tamu.7D.55	21BD	3.51	7D	55.4	71	chr7D_54833302	4.57			10.23			0.06	TAM113		
SHGW	Qshgw.tamu.2A.747	19BSP	3.51	2A	746.93	36	chr2A_746960172	5.43			10.08			0.03	TAM113	у?	р
SHGW	Qshgw.tamu.7D.55	AcrossEnv	4.76	7D	55.4	71	chr7D_54833302	6.17	6.13	0.04	12.4	7.478	4.92	0.03	TAM113		
SHGW	Qshgw.tamu.2B.69	AcrossEnv	4.76	2B	69.34	108	chr2B_68426788	5.12	4.51	0.61	12.88	5.652	7.22	0.02	TAM113		р
SHGW	Qshgw.tamu.7D.68	AcrossEnv	4.76	7D	68.43	92	chr7D_63208599	5.07	2.53	2.54	3.15	3.009	0.14	0.02	TAM113		
SHGW	Qshgw.tamu.2A.747	AcrossEnv	4.76	2A	746.93	36	chr2A_746960172	5.64	1.19	4.45	2.93	1.472	1.46	0.01	TAM113	y?	р
SHGW	Qshgw.tamu.2D.34	AcrossEnv	4.76	2D	34.43	61	chr2D_32901354	7.69	4.78	2.91	6.46	5.83	0.63	-0.02	Gallagher	y?	р
SHGW	Qshgw.tamu.2D.34	19BSP	3.51	2D	34.43	61	chr2D_32901354	5.65			10.55			-0.03	Gallagher	y?	р
SKW	Qskw.tamu.6D.172	20MCG	3.48	6D	171.52	28	chr6D_172603833	6.14			8.96			0.86	TAM113		р
SKW	Qskw.tamu.5A.606	20MCG	3.48	5A	606.28	142	chr5A_604579136	3.99			5.64			0.68	TAM113		
SKW	Qskw.tamu.2D.37	20MCG	3.48	2D	36.9	63	chr2D_36584261	8.41			12.56			-1.02	Gallagher		р
SKW	Qskw.tamu.6A.573	20MCG	3.48	6A	573.08	189	chr6A_571690944	8.37			12.93			-1.03	Gallagher		
SPM	Qspm.tamu.5A.637	AcrossEnv	4.81	5A	637.08	159	chr5A_636992509	5.31	4.15	1.16	6.17	4.758	1.41	-20.88	Gallagher	y?	
SPM	Qspm.tamu.5A.637	20EMN	3.52	5A	637.08	159	chr5A_636992509	4.1			10.67			-36.3	Gallagher	y?	
SSHW	Qsshw.tamu.2B.28	20EMN	3.51	2B	28.1	56	chr2B_28097658	60.92			18.59			0.24	TAM113	y?	
SSHW	Qsshw.tamu.4A.447	19BSP	3.51	4A	447.31	139	chr4A_335786182	25.89			8.85			0.23	TAM113	y?	
SSHW	Qsshw.tamu.4B.224	20EMN	3.51	4B	223.89	116	chr4B_210535748	19.85			3.49			0.1	TAM113	y?	
SSHW	Qsshw.tamu.4A.447	AcrossEnv	4.8	4A	447.31	139	chr4A_335786182	26.44	20.39	6.05	16.57	5.868	10.7	0.08	TAM113	y?	
SSHW	Qsshw.tamu.2B.28	AcrossEnv	4.8	2B	28.1	56	chr2B_28097658	61.19	16.42	44.76	17.03	4.602	12.43	0.07	TAM113	y?	
SSHW	Qsshw.tamu.5A.628	20EMN	3.51	5A	628.13	153	chr5A_626143346	5.49			0.8			0.05	TAM113		

Table A2.	Continued
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Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
SSHW	Qsshw.tamu.4B.224	AcrossEnv	4.8	4B	223.89	116	chr4B_210535748	19.91	4.51	15.4	3.15	1.242	1.91	0.04	TAM113	y?	
SSHW	Qsshw.tamu.5A.627	AcrossEnv	4.8	5A	626.72	152	chr5A_626143346	7.2	4.7	2.51	1.46	1.15	0.31	0.04	TAM113		
SSHW	Qsshw.tamu.2D.31	AcrossEnv	4.8	2D	31.5	58	chr2D_31103643	14	5.14	8.86	3.04	1.312	1.73	-0.04	Gallagher		р
SSHW	Qsshw.tamu.4B.238	AcrossEnv	4.8	4B	237.93	131	chr4B_214009418	28.34	6.13	22.21	4.98	1.651	3.32	-0.04	Gallagher	y?	
SSHW	Qsshw.tamu.4D.489	21BD	3.51	4D	488.73	84	chr4D_488578794	3.52			5.85			-0.05	Gallagher		
SSHW	Qsshw.tamu.1A.293	AcrossEnv	4.8	1A	293.1	117	chr1A_332686690	10.48	8.06	2.42	2.62	2.149	0.47	-0.05	Gallagher	y?	
SSHW	Qsshw.tamu.1A.293	20EMN	3.51	1A	293.1	117	chr1A_332686690	6.39			0.93			-0.05	Gallagher	y?	
SSHW	Qsshw.tamu.1A.74	19BSP	3.51	1A	74.22	118	chr1A_74644136	3.77			0.96			-0.08	Gallagher		р
SSHW	Qsshw.tamu.4B.17	19BSP	3.51	4B	16.56	22	chr4B_16480364	4.23			1.11			-0.08	Gallagher		
SSHW	Qsshw.tamu.4A.409	AcrossEnv	4.8	4A	409.3	150	chr4A_493726644	35.55	27.67	7.88	25.63	8.397	17.24	-0.1	Gallagher	y?	
SSHW	Qsshw.tamu.2D.31	21BD	3.51	2D	31.5	58	chr2D_31103643	13.84			26.43			-0.1	Gallagher		р
SSHW	Qsshw.tamu.4B.238	20EMN	3.51	4B	237.93	131	chr4B_214009418	28.26			5.57			-0.13	Gallagher	y?	
SSHW	Qsshw.tamu.4A.409	19BSP	3.51	4A	409.3	150	chr4A_493726644	35.2			13.82			-0.29	Gallagher	y?	
TKW	Qtkw.tamu.7D.65	19BSP	3.47	7D	65.22	88	chr7D_63208599	8.44			12.89			1.14	TAM113		
TKW	Qtkw.tamu.7D.62	AcrossEnv	4.94	7D	62.01	85	chr7D_61665314	9.96	7.7	2.26	13.33	10.02	3.31	0.58	TAM113		
TKW	Qtkw.tamu.6A.161	AcrossEnv	4.6	6A	160.62	116	chr6A_162293239	7.33	2.21	5.13	9.78	2.847	6.94	-0.31	Gallagher	y?	
TKW	Qtkw.tamu.4D.19	AcrossEnv	4.94	4D	18.87	28	chr4D_9929888	5.29	2.76	2.53	6.41	3.556	2.86	-0.35	Gallagher	y?	
TKW	Qtkw.tamu.1B.620	AcrossEnv	4.6	1B	619.6	24	chr1B_619535304	5.02	2.9	2.12	7.25	3.725	3.53	-0.36	Gallagher		
TKW	Qtkw.tamu.2D.37	AcrossEnv	4.6	2D	37.25	64	chr2D_37211804	5.87	3.33	2.54	9.2	4.292	4.9	-0.38	Gallagher	y?	р
TKW	Qtkw.tamu.2D.34	AcrossEnv	4.6	2D	34.43	61	chr2D_32901354	12.41	5.48	6.93	17.44	7.157	10.29	-0.49	Gallagher	y?	р
TKW	Qtkw.tamu.7A.640	19BSP	3.47	7A	639.97	215	chr7A_638247862	3.53			4.57			-0.68	Gallagher		
TKW	Qtkw.tamu.6A.573	21BD	3.53	6A	573.37	190	chr6A_573274893	4.12			8.9			-0.73	Gallagher		

Table A2.	Continued
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Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Troit	Cons.	Plei.
TKW	Otkw tamu 4D 19	21BD	3 53	4D	( <b>NIDP</b> )	28	chr4D 9929888	4 98			10.48			-0.79	Gallagher	v?	
TKW	Otkw.tamu.6A.572	20EMN	3.52	6A	572.01	185	chr6A 572104165	4.06			8.68			-0.81	Gallagher	<u> </u>	
TKW	Otkw.tamu.2D.37	20EMN	3.52	2D	37.25	64	chr2D 37211804	5.62			12.11			-0.96	Gallagher	v?	p
TKW	Otkw.tamu.6A.161	19BSP	3.47	6A	160.62	116	chr6A 162293239	7.15			9.66			-0.99	Gallagher	v?	
TKW	Otkw.tamu.2D.34	19BSP	3.47	2D	34.43	61	chr2D 32901354	12.18			17.46			-1.33	Gallagher	v?	р
YLD	Qyld.tamu.7D.52	19CS	3.63	7D	52.32	66		11.61			12.13			24.16	TAM113	y	p
YLD	Qyld.tamu.7D.66	20MCG	3.59	7D	66.02	89	chr7D_63208599	5.62			7.83			22.21	TAM113		p
YLD	Qyld.tamu.4A.76	20CS	3.5	4A	75.9	40	chr4A_69708392	8.54			5.82			17.44	TAM113	y?	-
YLD	Qyld.tamu.2B.58	20MCG	3.59	2B	57.61	101	chr2B_57657606	3.68			4.34			16.56	TAM113		р
YLD	Qyld.tamu.2B.571	21BD	3.48	2B	571.41	156	chr2B_572204779	7.68			16.6			16.26	TAM113	y?	
YLD	Qyld.tamu.4A.710	19CS	3.63	4A	710.33	352	chr4A_709865490	4.94			4.68			14.99	TAM113		
YLD	Qyld.tamu.2B.64	21BD	3.48	2B	63.96	105	chr2B_63428577	6.18			13.12			14.47	TAM113	y?	р
YLD	Qyld.tamu.7D.52	19BSP	3.47	7D	52.32	66	chr7D_51735477	9.69			16.87			13.17	TAM113	у	р
YLD	Qyld.tamu.7B.4	19CS	3.63	7B	4.22	12	chr7B_4035451	3.8			3.58			13.1	TAM113		
YLD	Qyld.tamu.6D.10	20CS	3.5	6D	10.33	20	chr6D_10311612	4.94			3.21			12.99	TAM113		
YLD	Qyld.tamu.2B.85	19CS	3.63	2B	84.91	113	chr2B_76076511	3.67			3.46			12.96	TAM113		р
YLD	Qyld.tamu.7D.52	AcrossEnv	6.4	7D	52.32	66	chr7D_51735477	21.59	7.27	14.32	12.88	5.282	7.59	7.08	TAM113	У	р
YLD	Qyld.tamu.2B.64	AcrossEnv	6.4	2B	63.96	105	chr2B_63428577	7.77	3.05	4.72	4.26	2.198	2.07	4.58	TAM113	y?	р
YLD	Qyld.tamu.2B.571	AcrossEnv	6.4	2B	571.41	156	chr2B_572204779	8.09	2.11	5.98	4.83	1.531	3.3	3.82	TAM113	y?	
YLD	Qyld.tamu.4A.76	AcrossEnv	6.4	4A	75.9	40	chr4A_69708392	9.62	0.54	9.09	5.87	0.391	5.48	1.92	TAM113	y?	
YLD	Qyld.tamu.1A.11	AcrossEnv	6.4	1A	11.28	8	chr1A_11207721	7.55	0.11	7.44	4.87	0.083	4.79	-0.89	Gallagher	y?	
YLD	Qyld.tamu.4A.484	AcrossEnv	6.4	4A	483.81	91	chr4A_486382996	18.4	4.86	13.55	12.49	3.552	8.94	-5.8	Gallagher	y?	

Table A2.	Continued

Trait	QTL name	Env.	Thres.	Chr.	Peak position (Mbp)	Position (cM)	LeftMarker	LOD	LOD (A)	LOD (AbyE)	PVE	PVE (A)	PVE (AbyE)	Add	Allele Increase Trait	Cons.	Plei.
YLD	Qyld.tamu.7B.728	19BSP	3.47	7B	728.09	162	chr7B_728700316	3.93			6.32			-8.05	Gallagher		
YLD	Qyld.tamu.2D.34	AcrossEnv	6.4	2D	34.43	61	chr2D_32901354	21.12	9.22	11.9	17.58	6.903	10.67	-8.11	Gallagher	y?	р
YLD	Qyld.tamu.1B.567	AcrossEnv	6.4	1B	566.97	9	chr1B_566956619	19.47	9.96	9.52	14.68	7.368	7.32	-8.38	Gallagher	у	
YLD	Qyld.tamu.2D.37	AcrossEnv	6.4	2D	36.9	63	chr2D_36584261	33.4	11.37	22.03	26.15	8.528	17.62	-9	Gallagher	у	р
YLD	Qyld.tamu.1A.564	20CS	3.5	1A	563.99	200	chr1A_563051268	3.59			2.31			-11.02	Gallagher		
YLD	Qyld.tamu.7B.717	20CS	3.5	7B	717.42	153	chr7B_716454686	3.91			2.54			-11.53	Gallagher		
YLD	Qyld.tamu.4B.623	20CS	3.52	4B	623.17	268	chr4B_623071554	4.16			2.66			-11.79	Gallagher		
YLD	Qyld.tamu.1A.11	20CS	3.5	1A	11.28	8	chr1A_11207721	6.97			4.7			-15.7	Gallagher	y?	
YLD	Qyld.tamu.1B.567	20CS	3.5	1B	566.97	9	chr1B_566956619	8.6			5.78			-17.46	Gallagher	у	
YLD	Qyld.tamu.1B.567	19CS	3.63	1B	566.97	9	chr1B_566956619	9.59			9.38			-21.3	Gallagher	у	
YLD	Qyld.tamu.7D.275	20MCG	3.59	7D	275.08	174	chr7D_274379353	6.27			7.63			-21.97	Gallagher		
YLD	Qyld.tamu.1B.567	20MCG	3.59	1B	566.97	9	chr1B_566956619	7.27			8.9			-23.75	Gallagher	Y	
YLD	Qyld.tamu.4A.484	20CS	3.5	4A	483.81	91	chr4A_486382996	17.3			12.87			-25.96	Gallagher	y?	
YLD	Qyld.tamu.2D.37	20MCG	3.59	2D	36.9	63	chr2D_36584261	9.14			11.73			-27.2	Gallagher	у	р
YLD	Qyld.tamu.7B.731	20MCG	3.59	7B	731.14	171	chr7B_732628699	9.37			12.19			-27.69	Gallagher		
YLD	Qyld.tamu.2D.34	19CS	3.63	2D	34.43	61	chr2D_32901354	17.57			19.14			-30.42	Gallagher	y?	р
YLD	Qyld.tamu.2D.37	20CS	3.5	2D	36.9	63	chr2D_36584261	30.09			26.99			-37.64	Gallagher	у	р

Trait	Loci 1	Position (cM) 1	peak Mbp	LeftMarker1	Loci 2	Position (cM) 2	Peak (Mbp) 2	LeftMarker2	LOD	LOD (AA)	LOD (AAbyE)	PVE	PVE (AA)	PVE (AAbyE)	Add1	Add2	AddbyAdd
YLD	Qyld.tamu.4B.11	5	10.6	chr4B_10393064	Qyld.tamu.6D.10	20	10.3	chr6D_10311612	6.0	4.0	2.0	1.2	0.8	0.4	-2.0	1.4	5.2
YLD	Qyld.tamu.4B.13	15	12.8	chr4B_12369792	Qyld.tamu.6D.10	20	10.3	chr6D_10311612	5.4	2.0	3.4	1.0	0.4	0.6	0.8	2.0	-3.6
YLD	Qyld.tamu.2B.64	105	64.0	chr2B_63428577	Qyld.tamu.5B.1	0	1.0	chr5B_978437	5.8	3.6	2.2	0.9	0.6	0.3	0.8	-2.5	-4.6
YLD	Qyld.tamu.2D.34	60	33.1	chr2D_32901354	Qyld.tamu.5B.21	40	21.1	chr5B_20696411	6.0	2.7	3.3	1.1	0.5	0.6	-3.5	-3.3	-4.2
HD	Qhd.tamu.1A.566	205	566.3	chr1A_565388907	Qhd.tamu.4A.714	380	713.7	chr4A_708146969	7.8	4.9	2.9	1.3	0.8	0.5	0.5	0.1	-0.5
HD	Qhd.tamu.2B.106	115	106.1	chr2B_101775233	Qhd.tamu.2D.33	60	33.1	chr2D_32901354	13.5	9.4	4.1	1.6	1.6	0.1	-0.1	3.0	-0.7
HD	Qhd.tamu.3D.603	145	602.6	chr3D_602632145	Qhd.tamu.7A.709	270	702.6	chr7A_701123987	5.5	3.8	1.7	0.8	0.6	0.2	-0.1	0.2	-0.4
HD	Qhd.tamu.1B.620	25	620.0	chr1B_619535304	Qhd.tamu.7A.709	280	707.0	chr7A_701123987	10.6	8.3	2.3	1.4	1.2	0.2	0.1	0.2	0.6
HD	Qhd.tamu.6B.660	65	660.2	chr6B_656922280	Qhd.tamu.7D.608	330	607.8	chr7D_611166154	8.2	4.8	3.4	1.2	0.7	0.5	0.1	0.6	0.5
PH	Qph.tamu.3B.564	110	563.9	chr3B_563291707	Qph.tamu.3B.625	160	625.5	chr3B_625827886	6.5	2.4	4.1	0.1	0.1	0.0	-1.1	1.3	1.1
PH	Qph.tamu.2D.30	55	30.0	chr2D_22290058	Qph.tamu.6A.596	220	595.5	chr6A_595061983	7.1	0.8	6.3	1.0	0.1	0.8	0.5	0.2	-0.2
PH	Qph.tamu.2D.30	55	30.0	chr2D_22290058	Qph.tamu.6D.458	100	457.6	chr6D_457987070	6.3	3.5	2.8	0.9	0.5	0.4	0.5	-0.1	0.4
PH	Qph.tamu.4B.646	285	646.0	chr4B_645618725	Qph.tamu.7D.33	40	33.4	chr7D_28855364	6.1	4.1	2.0	0.8	0.6	0.2	-0.5	-0.1	-0.4

Table A3. Epistatic interactions involved with major QTL

Abbreviation of traits; HD: Heading Date, PH: Plant Height, YLD: Grain Yield from combine harvester. LOD: Logarithm of the Odds, PVE: Phenotypic Variation Explained, AA: additive by additive (Epistasis), AAbyE; Epistasis by environment interaction, AddbyAdd: Additive by Additive, Add: Additive Effect, cM: centimorgan.



Figure A1: Phenotypic distribution of grain yield across six environments in Texas.