THE EFFECTS OF DROUGHT AND HIGH TEMPERATURE STRESS ON REPRODUCTION, PHYSIOLOGY, AND YIELD OF SPRING AND WINTER WHEAT

by

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B.S., Kansas State University, 2008
M.S., Kansas State University, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Agronomy
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Abstract

Drought and high temperature are major detriments to global wheat production. Wheat varies in its susceptibility to drought and high temperature stress. Three experiments were performed to address the challenges of drought and high temperature stress in wheat. The first experiment consisted of 256 genotypes of spring wheat and 301 genotypes of winter wheat, field screened for yield traits related to drought tolerance, in irrigated and dryland experiments. The experimental designs for the first experiment were both augmented incomplete block designs with one-way or row-column blocking. This experiment was performed at the Ashland Bottom Research Farm, south of Manhattan, KS, between 2011-2013. From this experiment, three conclusions were made: wheat genotypes vary widely in their responses between dryland and irrigated treatments and this variation can be used in future experiments or breeding tolerant genotypes. The number of seeds per unit of area, total biomass per unit area, and the average weight of one thousand seeds, were the best yield traits for predicting yield in both irrigated and dryland environments. Twenty genotypes were selected for future research based on their susceptibility or tolerance to drought. The second experiment was performed in the greenhouse facilities to observe the source-sink relationship of spring wheat genotype Seri 82 under drought and defoliation. The experiment was a randomized complete block design with a split-plot treatment arrangement. Post-anthesis cessation of watering and defoliation were the treatments. Both water stress and defoliation affected seed yield and total biomass. The major effect of post-anthesis water stress was a decrease in single seed weight. Defoliation affected the source-sink relationship by reducing the source strength of the leaves. This caused the stem to contribute more to overall yield. The defoliation also caused the remaining leaves to compensate for the removed leaves. The final experiment evaluated the changes in seed-filling rate and duration of three winter wheat genotypes during high temperature stress. High temperature stress reduced the duration of seed fill and increased the rate, differently in each genotype. Higher yields in the winter wheat growing regions, susceptible to post-anthesis high temperature stress, may be possible through selection of cultivars with faster seed-filling rates and/or duration of seed filling.

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Table of Contents

List of Figures

List of Tables

Chapter 1 - Introduction

With an ever increasing population and the possible risk of food scarcity due to climate change, the need for improved crop production per unit of land is of necessity (IPCC, 2013). In arid and semi-arid regions of the world, food supply is already at risk due to high temperatures and low rainfall. Both high temperature and low rainfall can be detrimental to crop plants growth and development (Boyer, 1982). Of the two, drought stress may be the most important stress for these regions (Curtis, 2002; Condon et al., 2004; Fischer et al., 2009; Mirbahar et al., 2009). In some areas and years, the crop damage caused by high temperature stress is similar, if not greater than, the damage due to drought stress (Gibson and Paulsen, 1999; Shah and Paulsen, 2003). One of the major crops grown in the arid and semi-arid regions of the world is wheat (*Triticum aestivum* L., FAO, 2012).

Wheat is the 3rd most important food crop in the world. It was estimated that 670 million Mg of wheat were produced in 2012 (FAO, 2012). Wheat is a cool-season annual grown for its grain (Frederick and Bauer, 1999). All grain crops are sensitive to drought and high temperature stress; some are more sensitive than others (Fischer et al., 2009). Wheat has adapted to withstand environmental stress, but it is still susceptible during certain growth stages (Blum, 1996; Frederick and Bauer, 1999; Curtis, 2002). The most sensitive growth stages to both high temperature and drought stress are those in which yield components are formed (Saini and Aspinall, 1982; Stone and Nicolas, 1995; Blum, 1996; Frederick and Bauer, 1999; Gibson and Paulsen, 1999). These yield components are: plants per unit area, reproductive units per plant, seeds per reproductive unit, and weight per seed. The most sensitive growth stages to stress are germination/emergence, tillering, jointing, booting, anthesis, and seed fill (Shah and Paulsen, 2003; Mirbahar et al., 2009). Stress during germination and emergence will negatively affect the potential number of plants per unit of land. Stress during tillering will affect the number of potential reproductive units per plant (Saini and Aspinall, 1982; Giunta et al.,1993; Abayomi and Wright, 1999). Stress during jointing, boot, and/or anthesis will affect the potential size of the reproductive unit, the maximum number of seeds, and/or the number of seeds pollinated, respectively (Stone and Nicolas, 1995; Frederick and Bauer, 1999; Mirbahar et al., 2009). Stress during seed fill will affect the final weight of individual seeds (Nicolas et al., 1984; Gibson and Paulsen, 1999; Chmielewski and Kohn, 2000; Shah and Paulsen, 2003). Of the growth stages mentioned, stress during germination/emergence, anthesis, and seed-fill tend to cause the greatest loss in potential yield (Frederick and Bauer, 1999; Shah and Paulsen, 2003; Mirbahar et al., 2009; Nouri et al., 2011). The goal for future wheat research should be to improve tolerance to drought and high temperature stress.

How does stress affect wheat and in what ways can wheat develop tolerance? To improve stress tolerance, we first need to better understand it (Reddy et al., 2004; Zhao et al., 2008). Once the mechanism is understood, production can be improved by modifying management, such as timing of irrigation and nutrient application or hormonal/chemical treatments applied during sensitive growth stages. Possibly the best way to improve productivity is breeding (Kirigwi et al., 2004; Leilah et al., 2005; Sinclair, 2011). Due to genotypic and phenotypic differences, not all genotypes will have the same level of sensitivity to stress. Statistics of populations would lead us to believe that plants could vary in their tolerance and susceptibility to stress (Kirigwi et al., 2004; Singh et al., 2007;

Nouri et al., 2011; Sinclair, 2011). When these desirable traits are identified, selection, improvement, and introduction of these traits into elite lines could have the greatest effect on global productivity (Singh et al., 2007; Sinclair, 2011). For any of the aforementioned possibilities to be realized, mechanisms of tolerance must be identified, diversity/ heritability of the trait within the population characterized, and finally the trait needs to be introduced into already high-yielding genotypes (Sinclair, 2011). To continue this process, two studies were conducted based on the following objectives: (i) characterize phenotypic variability of yield traits in genetic mapping populations; (ii) compare the variability and correlations of yield traits in different water regimes; and (iii) identify high yielding genotypes under irrigated and dryland conditions.

One of the ways in which wheat has adapted to stress is in the ability to use pre-anthesis carbon, stored in the stem and leaf sheaths, to fill seed when stress has reduced the ability to photosynthesize (Shah and Paulsen, 2003; Ji et al., 2010). This stored reserve is not a perfect mechanism. With an increase in respiration and rapid leaf senescence cause by drought stress, the stored carbon is divided between two strong sinks, the seed and metabolic demands to keep the plant alive (Cook and Evans, 1978; Ahmadi and Baker, 2001). If the drought stress continues, this process is a race against the clock and there will be a reduction in the yield compared to what it could have been (Cook and Evans, 1978; Yang et al., 2001). Yield produced from stored reserves is not typically as high as when it is produced through photosynthesis (Kruk et al., 1997; Inoue et al., 2004). Because photosynthesis is so important for yield and there are numerous ways in which field plants can lose leaves, from drought stress leaf senescence to damage from foliar diseases, maintaining leaf area is important. At the very least, maintaining productive leaf area is important. So, this begs the questions: How do the leaves and stem reserves interact under drought stress and how do they contribute to yield? And, which leaves are the most productive? To answer these questions, a series of three experiments were performed with the following objectives: (i) characterize the relationship in photosynthetic area and stored reserves during seed-filling to yield and yield components in irrigated and limited moisture environments; and (ii) characterize contributions of leaves and stems to yield.

As mentioned previously, post-anthesis high temperature stress is a major problem. Since not much is known about post-anthesis high temperature stress, it is often overlooked as it is not overtly obvious. There is an increase in the senescence rate, or perceived senescence, during post-anthesis and this often compounds symptoms of high temperature stress (Al-Khatib and Paulsen, 1984; Ristic et al., 2007; Farooq et al., 2011). Major yield damage of post-anthesis high temperature stress is caused by a decline in the seed-filling period. Plants can partially overcome the shorter duration by increasing the rate at which photosynthates and stored carbon are translocated to the seed (Stone and Nicolas, 1994; Shah and Paulsen, 2003). But what are the effects of post-anthesis high temperature stress and how do cultivars differ in their responses? To answer these questions, an experiment was performed with the following objectives: (i) quantify the effects of terminal post-anthesis, high temperature stress on yield and yield components of three cultivars; and (ii) quantify and observe any cultivar differences in seed-filling rate and duration due to high temperature stress on a finer time interval in winter wheat cultivars.

Each of the aforementioned experiments will be examined independently in chapters 2, 3, and 4 to follow this introduction. Chapter 2 will focus on two experiments related to characterizing spring and hard winter wheat: Association mapping panels for yield traits in differing water regimes. Chapter 3 will focus on source-sink interactions with limited moisture and varying levels of defoliation in post-anthesis wheat. Chapter 4 will focus on the effect of high temperature stress on the seed-filling rate and duration of three winter wheat cultivars. All experiments were conducted at Kansas State University Agronomy Department's research farm, greenhouses, and growth chamber facilities, from 2010 through 2015.

Each chapter will include its own introduction, methods and materials, results, discussion, and conclusions. These three chapters will be followed by a set of overall conclusions related to the effects of water and high temperature stress on reproduction, physiology, and yield of spring and winter wheat.

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Chapter 2 - Characterizing Spring and Hard Winter Wheat (*Triticum aestivum* L.) Association Mapping Panels for Yield Traits in Differing Water Regimes

Wheat (*Triticum aestivum* L.) is the 3rd most important food crop in the world (FAO, 2012). It was estimated that 670 million Mg of wheat were produced in 2012 (FAO, 2012). With an ever increasing population and the potential risk of food scarcity due to climate change, the need for improved production per unit of land is of necessity (IPPC, 2013). It was estimated that wheat production will have to increase by about 60% to meet the food demands by 2050. In 2012 the average yield was 3.2 Mg ha^{-1}, so the average yield will have to increase by 1.9 to 5.3 Mg ha^{-1} in just 35 years (Fischer et al., 2009; FAO 2012). That is an increase in wheat production similar to what was observed during the green revolution, in less time (Fischer et al., 2009). Wheat production could be improved in several ways: improved crop management and intensification; improving light, water, and nutrient use efficiency; and breeding higher yielding cultivars or hybrids, just to name a few.

Another major area of improvement could be in tolerance to adverse environmental conditions and stresses. For wheat the most important abiotic stresses are primarily water and high temperatures (Nicolas et al., 1984; Shah and Paulsen, 2003). Because wheat is traditionally grown in arid and semi-arid regions, water stress is arguably the most important abiotic stress (Condon et al., 2004; Fischer et al., 2009; Mirbahar et al., 2009). Wheat is most sensitive to drought stress at the growth stages in which yield components are formed (Frederick and Bauer, 1999). Yield components being: plants per unit area, reproductive units per plant, seeds per reproductive unit, and weight per seed. The most sensitive growth stages are germination/emergence, tillering, jointing, booting, anthesis, and seed fill (Shah and Paulsen, 2003; Mirbahar et al., 2009). Drought during germination and emergence will negatively affect the potential number of plants per unit of land. Stress during tillering will affect the number of potential reproductive units per plant (Giunta et al.,1993; Simane et al., 1993; Abayomi and Wright, 1999). Stress during jointing, boot, and/or anthesis will affect the potential size of the reproductive unit, the maximum number of seeds, and/or the number of seeds pollinated, respectively (Frederick and Bauer, 1999; Mirbahar et al., 2009). Stress during seed fill will affect the final weight of individual seeds (Nicolas et al., 1984; Chmielewski and Kohn, 2000; Shah and Paulsen, 2003). Of the growth stages mentioned, stress during germination/emergence and anthesis tend to cause the greatest loss in potential yield (Frederick and Bauer, 1999; Mirbahar et al., 2009; Nouri et al., 2011). The reasons are if you don't have plants, you have no yield and no matter how many potential reproductive units or flowers, without pollination you have no seed and thus no yield.

Due to genotypic and phenotypic differences, not all genotypes will have the same level of sensitivity to drought stress. Population statistics would lead us to believe that plants could vary, and possibly vary widely, in their tolerance and susceptibility to drought stress (Kirigwi et al., 2004; Singh et al., 2007; Nouri et al., 2011). The mode of this tolerance could be known or yet undiscovered. The only way to know would be to develop, screen, and characterize populations of genotypes for tolerance or traits related to tolerance. Populations developed for genetic mapping may be the one of the best options for at least three reasons: the population is already being screened for markers and their associated alleles, additional phenotypic data could be associated with new markers, and some of the included genotypes could be elite lines in which minimal backcrossing would be needed to maintain a satisfactory yield potential if they are found to be tolerant. Because drought stress affects components of yield, with plant number and seed number the most affected, screening populations for changes in these components, across water limiting environments, could be a method for finding tolerant genotypes (Kirigwi et al., 2004; Nouri et al., 2011; Sinclair, 2011). These genotypes could be further studied to find the exact mode of tolerance.

To improve stress tolerance, we first need to better understand it (Reddy et al., 2004; Zhao et al., 2008). How does stress affect wheat and in what way or ways can wheat develop tolerance? Once the mechanism is understood, production can be improved by modifying management, like timing of irrigation and nutrient application or hormonal/chemical sprays applied during sensitive growth stages. Possibly the best way to improve productivity is breeding (Kirigwi et al., 2004; Leilah et al., 2005; Sinclair, 2011). When desirable traits are identified; selection, improvement, and introduction of these traits into elite lines could have the greatest affect on global productivity (Singh et al., 2007; Sinclair, 2011). For any of the aforementioned possibilities to be realized, mechanisms of tolerance must be identified, diversity/ heritability of the trait within the population characterized, and finally the trait needs to be introduced into already high yielding genotypes (Sinclair, 2011). To continue this process, two studies were conducted based on the following objectives.

Objectives

1. Characterize phenotypic variability of yield traits in genetic mapping populations
2. Compare the variability and correlations of yield traits in different water regimes
3. Identify high yielding genotypes under irrigated and dryland treatments

Materials and Methods

Association Mapping Panels

Two germplasm collections were used in this experiment. Both were developed by the Triticeae Coordinated Agricultural Project (http://www.triticeaecap.org) or TCAP. The collections are association mapping panels for spring and winter wheat. The Spring Wheat Association Mapping Panel (SWAMP) consisted of 256 genotypes and the Hard Winter Wheat Association Mapping Panel (HWWAMP) consisted of 300 genotypes. A local genotype, 'Everest' (http://kswheatalliance.org/varieties/everest/), was added due to its productivity in Kansas, for a total of 301 genotypes. Both germplasms included recent cultivars, experimental breeding lines, and a few genotypes derived prior to the Green Revolution. Public and private breeding programs developed the genotypes and contributed to the TCAP AM panels. The AM panels were designed to include genotypes that represent the prevalent germplasm of the wheat growing regions of the United States and Canada (Narayanan and Prasad, 2014; Gorgon et al., 2016).

Locations and Experimental Design

Both AM panels were planted at the Ashland Bottoms research farm, south of Manhattan, KS (39.137615, -96.640046) for the 2011-2012 and 2012-2013 growing season. The grounds are owned and maintained by the Agronomy Department, Kansas State University. Due to the large spatial size of the experiment, large number of experimental observations, and limitations to available seed, augmented designs where used (Federer and Raghavarao, 1975). With the use of augmented designs, replicated checks are used as the source of experimental error and also, when arranged appropriately, can be used to correct for the potential spatial variability present in large fields (Federer and Raghavarao, 1975; Robinson, 1991). The designs are based around a single replication of experimental units, but true replication was also used when seed was available as in the HWWAMP. Using both the experimental error and the spatial correction of checks, Empirical Best Linear Unbiased Predictors (eBLUPs or BLUPs) and Least-squares means (or Best Linear Unbiased Estimators, BLUEs) can be created. Both BLUPs and BLUEs can be used to adjust observed values so as to establish genotypic rank free of field and possibly less environmental variability (Federer and Raghavarao, 1975; Robinson, 1991).

In the Spring 2012 and 2013, 256 genotypes from the SWAMP were planted in two fields as an unreplicated augmented block design with 5 blocks and 6 check genotypes; one field was fully irrigated and the other was dryland. With the augmented design, 250 genotypes were randomly assigned a position in the field and separated into 5 blocks. Each block was randomly assigned the same 6 check genotypes. Blocking was only conducted in one direction.

In the Fall of 2011 and 2012, 301 genotypes from the HWWAMP were planted in four fields as a replicated augmented row/column incomplete block design with 30 checks (15 of Settler Cl and Everest) in 2011, and 60 checks (30 of Settler CL and

Everest) in 2012. Two of the fields where randomly assigned as irrigated and the remaining two as dryland. With this design, each water regime had two replications. The 299 genotypes were randomly assigned a position in each field, then the check genotypes where laid out in blocks in a row/column fashion (across all four fields). In each row/column block both checks where present at least three times, with some up to six times, when viewed across fields.

Field Preparation, Planting, and Maintenance

The SWAMP and HWWAMP fields were tilled with an offset disk and sprayed with broad spectrum non-residual herbicides, preplant. Nitrogen fertilizer was applied in the spring so as to be non-limiting. The 2012 SWAMP was planted on 5 March as single row plots, 1 m long, with a cone-metered push planter, at a density of 300 seeds m^{-2}. In 2013 the SWAMP was planted on 7 March with a self-propelled cone drill, that can plant two 3-row plots at once. Each plot was 0.9 m wide by 1.27 m long and planted at a density of 300 seeds m^{-2}.

In 2011 and 2012 the HWWAMP was planted on 18 and 6 November, respectively, with a cone drill that can plant two 3-row plots at once. Each plot was 0.9 m wide by 3.7 m long and was planted at a density of 280 seeds m^{-2}. After wheat emergence all weed species were controlled manually. Due to the variable susceptibility to rust (*Puccinia* spp.) in the AM Panels, all plots were sprayed after flowering with a foliar fungicide. Irrigation water was applied using a solid-set linear sprinkler system, installed at spring green up. Water was applied when the soil surface was visibly dry.

Weather Data and Harvest

Weather stations were positioned in fields in both years, to provide rainfall, leaf wetness, and solar radiation during the growing season (WatchDog 1650 Micro Station, Spectrum Technologies, 3600 Thayer Court, Aurora, IL 60504). Weather station data were supplemented with weather data from the Kansas Weather Data Library (http://mesonet.k-state.edu/).

Plots were harvested by cutting all above ground biomass from the entire plot, or one meter of the center row, from each plot when the plots were larger then a one-meter row. The SWAMP was harvested on 2 and 18 July in 2012 and 2013, respectively. The HWWAMP was harvested 3 and 15 July in 2012 and 2013, respectively. Total biomass was weighed, spikes counted, spikes threshed, seeds weighed, and seeds counted. From these measurements seeds per spike, thousand kernel weight, and harvest index were derived.

Data Analysis

Histogram plots were created to observe shape and distribution of all dependent variables using SigmaPlot 11.0 (Systat Software, San Jose, CA). Correlations were created to look for relationships between all pairs of dependent variables. Variance component analysis for all variables was performed to estimate genotypic (G), environmental (E), and GxE variability by water regime (Trt), with type 1 sum of squares. Any negative variances were assumed to be zero. Analysis of variance using a Mixed model was performed for all variables with genotype and water-regime nested within water-regime and environment, respectively (G(Trt) and Trt(E)). Replication

(Block) nested within year for the SWAMP and replication nested within year and row-column effects for the HWWAMP were used as random effects. Each trait was plotted by water regime. This plot is divided by perpendicular lines on the mean of each water regime to form a quadrate plot where each quadrate represents the yield trait as either above or below the mean in dryland, irrigated, or both. Regression by seed yield was performed against all other yield traits, to estimate impact and contribution of traits to overall yield. Statistical analyses were performed using the Corr, Varcomp, Mixed, and Reg procedures of SAS 9.2 (SAS Institute, Cary, NC). All graphs were created using SigmaPlot 11.0. For all analyses and graphs, only the uncorrected data for each of the dependent variables were used.

Results

Environmental Conditions

In Ashland Bottoms, Manhattan, KS, total seasonal precipitation for 2011-2012 and 2012-2013 were 497 mm and 377 mm, respectively (Figures 2-1 and 2-2). Of this, 242 mm and 292 mm of precipitation occurred during the 2012 and 2013 spring wheat growing season, respectively. Maximum temperatures were 40.6°C and 41.7°C in July 2011-2012 and July 2012-2013, respectively. Minimum temperatures for spring wheat were -0.6°C March 2012 and -10.0°C April 2013. For winter wheat, the minimum temperatures were observed in February and were -14.4°C in 2011-2012 and -18.3°C in 2012-2013. The winter wheat had similar seasonal growth except during the early spring. In 2012, the early spring (March) temperature was warmer and stayed warm for the rest of the season. In 2013, the spring was cooler and didn't warm up until late April, early

May. This didn't seem to affect, perceptibly, the winter wheat, except delayed maturity; but cooler temperatures may be a reason for the reduced overall performance of the spring wheat in 2013. Rust was present both seasons but was controlled and it is not believed to have caused any major yield reductions. In 2013, glyphosate was sprayed too close to the irrigated spring wheat field. This killed 1/16 of the plots and caused reduced growth and vigor in another 1/16. The destroyed and damaged plots were not included in any analysis.

Yield Trait Characteristics

Overall, irrigated winter wheat was higher in all yield traits (Table 2-1). This is true for all yield traits except thousand seed weights which was similar to the spring wheat results. Within spring wheat, total biomass and spike number were greater in dryland than irrigated fields. Seed yield, seed number, seeds per spike, thousand seed weights, and harvest index were all greater in irrigated wheat. In the winter wheat, only harvest index was higher in the dryland. When spring and winter wheat were combined, a similar trend as with the spring wheat was observed; total biomass and spike number were higher in the dryland fields. All other yield traits were higher in irrigated fields.

All histograms of yield demonstrate roughly normally distributed data with a few histograms having slight off center means and/or tails (Figures 2-3 through 2-9). The big difference is between spring and winter wheat and a smaller difference between dryland and irrigated wheat. With spring versus winter wheat, the winter wheat data tend to be more normally distributed along with a higher mean. Spring wheat data also tend to have more yield traits with tails. When comparing dryland versus irrigated wheat, the major difference seems to be that dryland wheat tended to have more variability. Total biomass data were normally distributed with a slight tail above the mean in the spring wheat (Figure 2-3). Data related to spike number is normally distributed except that it has more genotypes above or below the mean in the winter wheat and spring wheat, respectively (Figure 2-4). Winter wheat seed yield data has a small tail below the mean and the spring wheat data has a small tail above the mean (Figure 2-5). Seed number data is normally distributed with dryland winter wheat data having a sharp peak at the mean and spring wheat data having tails above the mean. Seeds per spike data were normally distributed and, due to the nature of its distributions, the bins of the histogram are larger than the rest of the yield traits. Seeds per spike spring wheat data has a tail above the mean as well. The histograms for thousand seed weights were the most normally distributed and similar among wheat types and water regime except spring dryland where the mean had a sharp peak and the irrigated wheat had a small tail above the mean. Harvest index is the least normally distributed data with a strong drop off at above 0.35 in all except the dryland spring wheat (Figure 2-9). From these histograms it is clear that all yield traits roughly fit a normal (Gaussian) distribution with some yield traits having outliers either above or below the mean.

Figure 2-10 is a correlation matrix of the spring and winter wheat, in both seasons, for all yield traits. This matrix visually shows correlations between all combinations of yield traits. The most notable correlations are between seed yield vs. seed number (r=0.93) and seed yield vs. total biomass (r=0.92). Spike number and harvest index also were highly correlated with seed yield, with correlations of r=0.82 and r=0.85, respectively. Other high correlations were between spike number and seed number at r=0.81; total biomass and seed number at r=0.88; total biomass and spike number at r=0.89; seeds per spike and seed number at r=0.62; and harvest index and seed number at r=0.71. Thousand seed weights had low to no correlations with any other yield traits, with seed yield being the highest correlations at r=0.33. Also of note is the shape of the scatter plots of harvest index and the other yield traits; the plots all tend to plateau at a harvest index of roughly 0.30-0.35. The correlation combinations hint at which yield traits are important and some of the underlying relationships between traits.

Table 2-2 presents the variance component analysis by wheat type and water regime. Variance component analysis is used to look for partitioning of variance within the experiment. For spring wheat, the average experimental error is 80388 and ranges from 0.01 to 682141. Genotype had lower variance as a percent of experimental error, with an average of 5.22 and the highest two variances being dryland total biomass at 10.29 and dryland seed yield at 13.23. Variance components for environment were higher with an average of 26 percent and the five highest variances are irrigated spike number at 61.22, irrigated seed number at 42.44, dryland thousand seed weights at 54.95; irrigated thousand seed weights at 55.54; and dryland harvest index at 41.78. The genotype by environment interaction had the highest variance with an average of 31 and the three highest variances being irrigated seed number at 34.10, irrigated thousand seed weights at 383.84, and dryland seeds per head at 13.05. Winter wheat average experimental error is 116483 and ranges from 0.003 to 834328.8. Genotype variance averaged 13 and the four highest variances were dryland seeds per head at 15.04, irrigated seeds per head at 12.97, dryland harvest index at 44.40, and irrigated harvest index at 33.33. Environment variance is the highest with an average of 282 and only four yield traits with variances below 100 and 10 yield traits with variances above 100 percent. The highest three variances are irrigated total biomass at 505.96, dryland seed yield at 613.37, and irrigated seed yield at 645.33. The genotype by environment interaction has a variance lower than genotype with an average of 11. The highest three yield traits are irrigated seed weights at 18.19, dryland harvest index at 18.75, and irrigated harvest index at 26.64. Overall, the highest average variability for both spring and winter wheat were observed in E and GxE interaction. Genotype alone typically had a variance percent similar to the replication or blocking terms.

Overall analysis of variance (ANOVA) was used to establish differences between genotype and water regime main effects for each yield trait. With the ANOVA of spring and winter wheat for genotype, spring wheat had only three yields traits different at an Pr< 0.10 and one at Pr<0.05 (Table 2-3). These three traits are total biomass at 0.0853, seed yield at 0.0637, and harvest index at 0.0304. All winter wheat yield traits are different at the Pr<0.05 level. For the ANOVA of water regime, all spring wheat and all but two winter wheat traits were different at an alpha of 0.05. These two traits are thousand seed weights with a probability greater than F (Pr > F) of 0.2320 and harvest index at 0.0726.

Water Regime Effects on Yield Traits

Quadrate plots are made up of four quadrants created by plotting dryland vs. irrigated wheat and dividing genotypes into quadrants separated by perpendicular lines plotted at the treatment means. With this separation, genotypes in each quadrant represent: I, genotypes that are above average under irrigated and dryland treatments; II, genotypes that are above average under irrigated and below average under dryland treatments; III, genotypes that are below average under irrigated and above average under dryland treatments; and VI, genotypes that are below average under irrigated and dryland treatments. Across all graphs (Figures 2-11 to 2-17), the distribution of genotypes is mostly equal between the four quadrants. Another commonality amongst quadrate plots is the increased variability or spread of genotypes in the spring wheat as compared to the winter wheat. Data related to total biomass (Figure 2-11), spike number (Figure 2-12), seed yield (Figure 2-13), and seed number (Figure 2-14) have the greatest spread as well as the largest differences between spring and winter wheat means. Data related to seeds per spike (Figure 2-15), thousand seed weights (Figure 2-16), and harvest index (Figure 2-17) have the least spread and the lowest differences between means, with thousand seed weight having the smallest of both. These plots show that, in all yield traits, there are distributions of genotypes in the potentially beneficial quadrants (I, II, and III), that could be used for future selection and breeding based on the yield trait and quadrant of greatest interest.

Table 2-4, shows the paired yield trait correlations between water regimes. This table has each yield component correlation paired by water regime. Several correlations show a change in magnitude between dryland and irrigated wheat; seeds per spike and total biomass, seeds per spike and seed yield, seeds per spike and seed number, thousand seed weights and seeds per spike, harvest index and seeds per spike, and harvest index and thousand seed weights. All of these correlation differences decrease from dryland to irrigation environments. These differences ranged from 0.11 to 0.19. Four correlation combinations stay relatively close between water regimes; they are spike number and total biomass, seed yield and total biomass, seed number and total biomass, and seed number and seed yield, with none of the differences being more than 0.04. This shows that the relationships between seed number and total biomass and yield are consistent in both water regimes; while other traits fluctuate based on water regime. Both the consistent and variable traits may be useful for future research.

Importance of Observed Yield Traits

Seed yield was regressed against all of the yield traits to observe their effect and predictive power (Figure 2-18). This determines the relationship (positive or negative) and visually demonstrates the strength of the relationship. The regression R^2 ranged from 0.11 to 0.87 for all yield traits. The regression between seed number and seed yield is positive and also has the highest R^2 of 0.87. The total biomass and seed yield regression is also positive with an R^2 of 0.85. The R^2 of spike number and harvest index, when regressed against seed yield, are moderately high with 0.67 and 0.56, respectively. The regressions with seed yield with the lowest R^2 are seeds per spike and thousand seed weights, with 0.28 and 0.11, respectively.

Multiple linear regressions were performed to observe which yield traits could be used to best predict the changes in seed yield (Table 2-5). Using adjusted R^2, root mean squared error (RMSE), and variance inflation factor (VIF for each variable and this data is not shown) as selection criteria, with the goal to maximize R^2 and minimize both RMSE and VIF. Table 2-5 shows the results of these regressions with the 12 models. Three models were included for the 1 yield trait, three were included with 2 yield traits, three were included with 3 yield traits, and 1 model each was included for the 4, 5, and all 6 yield traits models. The best single parameter model was seed number with an adjusted R^2 of 0.87, an RMSE of 15.12, and the parameter VIF of 1. The best 2 parameter model was total biomass and harvest index with an adjusted R^2 of 0.97, RMSE of 7.88, and the highest parameter VIF of 1.33. Finally, the best three parameter model was seed number, total biomass, and thousand seed weights, with an adjusted R^2 of 0.97, RMSE of 7.45, and the highest parameter VIF of 5.05. The 4, 5, and 6 parameter models do not increase adjusted R^2 or RMSE by a large enough amount (R^2 0.98 and RMSE of 6.26) to justify the more complex and much higher VIF for the variables, with 19.12 as the highest parameter VIF in the 6 parameter model (VIF>10 was used as a cut off criteria). For all the models tested, it was observed that total biomass and seed number had the greatest effect on increasing the VIF scores, which hints to some multicollinearity between the two traits.

Tolerant and Susceptible Genotypes

Using the quadrate plot for seed yield, 5 genotypes were selected from each quadrant to be identified for future research or breeding. These genotypes are listed on Table 2-6 and 2-7. From the 20 genotypes, analysis was performed on the yield traits to look for commonalities between each quadrant (data not shown). No data were found to contribute to the first objective of this study. The genotypes selected do have similarities in seed yield. For quadrant I, the seed yields range from 50-105 g m row^{-1} in spring wheat and 90-104 g m row^{-1} in winter wheat with an average yield of 76 and 98 g m row^{-1}, respectively. In quadrant II, seed yield values ranged from 32-108 g m row^{-1} with an average dryland yield of 22 and 49 g m row^{-1} and an average irrigated yield of 84 and 92 g m row^{-1}, for spring and winter wheat, respectively. Quadrant III ranged in values from 22-68 g m row^{-1} for spring wheat and 49-102 g m row^{-1} for winter wheat. The average irrigated yields were 31 g m row^{-1} for spring wheat and 60 g m row^{-1} for winter wheat. The average dryland yields were 66 g m row^{-1} for spring wheat and 96 g m row^{-1} for winter wheat. In quadrant VI, the seed yields ranged from 4-23 g m row^{-1} in spring wheat and 21-55 g m row^{-1} in the winter wheat. The spring wheat averaged 31 and 66 g m row^{-1} for irrigated and dryland wheat, respectively. For the winter wheat seed yield averaged 49 and 41 g m row^{-1} for irrigated and dryland wheat, respectively.

Discussion

Winter wheat, overall, performed better than the spring wheat in this experiment and, within water regime, irrigated was the higher performer for most yield traits. Looking at the precipitation over the season, the dryland plots would have been slightly stressed compared to the irrigated, but not to the level of causing extreme yield loss. This is seen in the magnitude of yield differences between water regimes. When comparing winter wheat to spring wheat, there are possibly two major reasons why the winter wheat preformed better: longer growing season and better cold temperature tolerance. The extra growing season that winter wheat has allows more time to develop biomass and tillers, and allows more precipitation to fall during the plants' growing season. Both of these factors can be observed in the data. The other potential reason was observed in 2013 when the spring temperatures stayed cold until late April. Winter wheat seems to tolerate cold temperatures better than spring wheat. It was observed that winter wheat continued to grow, although slowly, when temperatures stayed above 0°C. The same cannot be said for the spring wheat, which didn't appear to grow at all until the temperatures rose above approximately 10°C. All analysis were originally preformed on a per year basis to observe the differences caused by the two years (data not shown), as they were moderately dissimilar in temperature and rainfall patterns (Figures 2-1 and 2-2). The years were later combined for analysis with the goal of making observations and conclusions more robust against year to year variability.

Most of the yield traits examined in this study seemed to roughly fit a normal distribution with some yield traits having outliers either above or below the mean. The big difference was variability. Both the spring wheat and the dryland regime showed higher variability. This can also be observed in the variance component analysis where environment and GxE interaction dominated the variance portioning, in some cases actually being greater than the experimental error. The spring wheat seems to have been affected more by environment and water regime than the winter wheat. Looking at the means between yield traits and water regime, spring wheat has a greater difference. Also in the ANOVA, spring wheat yield traits were highly significant by water regime but only mildly significant by genotype. The reason for this may be because the environmental effects (water regime included) caused enough stress that they limited yield traits more than genotype could.

The quadrate plots show the variability of yield traits by water regime. The variability was quite large for all yield traits; although, some traits like thousand seed weights had less variability than the rest. The data shows that genotypes seem to be mostly equally spaced in a circle around the intersection of the two means. These plots also show that, in all yield traits, there are distributions of genotypes in the potentially beneficial quadrants (I, II, and III). The genotypes in these quadrants are high yielding in either irrigated, dryland, or both environments and could be used in a breeding program with the quadrant chosen to be most similar to the program's needs. The top or bottom 5 genotypes from each quadrant are reported for posterity in Table 2-6 and 2-7.

The changes of yield traits across water regimes is not very obvious or intuitive. Interestingly, the yield trait changes are different depending on water regime. The only yield traits that decreased in the dryland regime in both spring and winter wheat are seed yield and seed number (Giunta et al.,1993; Simane et al., 1993; Abayomi and Wright, 1999). The other traits increase or decrease differently according to the different water regimes across spring and winter wheat. With the correlation table by water regime, the changes in correlations are now more stable; spike number and total biomass, seed yield and total biomass, and seed number and seed yield now do not change with water regime (Table 2-4). These are also the combinations of yield traits that have the highest correlations in the combined matrix (Figure 2-10). The yield traits that change in the correlation table are those correlated with seeds per spike and they all increase in the dryland treatment. This finding may lead one to think that seed per spike is an important yield trait, even though its overall correlation with seed yield is only 0.53 in the combined correlation matrix (Figure 2-10).

Multiple linear regressions demonstrate a trend similar to the stable correlations; the two most prominent yield traits in the models on Table 2-5 are seed number and total biomass. Both yield traits had high R^2, above 0.85 (Frederick and Bauer, 1999). Seed number and total biomass are in 7 and 9, of the 12 models, respectively. Another observation was that any time seed number and total biomass are in the same model, they both have higher VIF scores than the other factors. Consequently, these two traits may have some level of multicollinearity. Another point to be made is that although both harvest index and thousand seed weights don't have very high correlations with yield, they are present in half of the 12 models in Table 2-5.

With this experiment, no new modes of tolerance have been discovered. It would seem, however, that more questions have been generated. In particular, how important is seeds per spike to wheat? The good news is that the genotypes of this experiment have a large amount of variability and include many genotypes that have yield traits that perform well (or poorly) in irrigated, dryland, and combined environments. In these mapping populations, the potential exist to use these genotypes for future stress research, in a breeding program, or to develop QTLs for desired traits. Another potential outcome of this experiment is to use the results to develop models to predict wheat growth and development (or at least add to the existing models).

Conclusions

In this experiment, winter wheat had higher seed yield in Kansas than spring wheat. The spring wheat and the winter wheat both had lower values for measured yield traits in dryland as compared to irrigated environments. Both wheat types also demonstrated a large amount of variability within genotypes. This variability provides good potential for future scientific endeavors.

Overall, the spring and winter wheat responded similarly to the water regimes. Unfortunately, no clear cut compensation to differing water treatments was observed other than the increase in correlation between seeds per spike and the other yield traits.

Seed number, spike number, and total biomass were found to have the greatest relationship with seed yield, regardless of water regime and may be useful selection criteria to focus on in a breeding program. Because total biomass was so highly correlated with seed yield it may be a good surrogate end point to yield if it can be harvested more efficiently (time, equipment, etc) than yield.

Using multiple linear regressions, total biomass and harvest index was the best 2 parameter model for predicting seed yield, regardless of water regime. These linear regressions also indicated seed number, total biomass, and thousand seed weights were the best 3 parameter model for predicting seed yield, regardless of water regime. This tells us, that when it comes to wheat, these variables might be the most important yield components and that the growth stages at which they form might be the most sensitive to stress.

Finally, using quadrate plots, where seed yield was graphed by water regime, 20 genotypes were identified, 5 from each quadrant, for future research or breeding purposes (Table 2-6 and 2-7). Five genotypes had above average yields in both dryland and irrigated environments, 5 were above average in irrigated but below average in dryland environments, 5 were below average in irrigated and above average in dryland environments, and 5 were below average in both irrigated and dryland environments.

Acknowledgements

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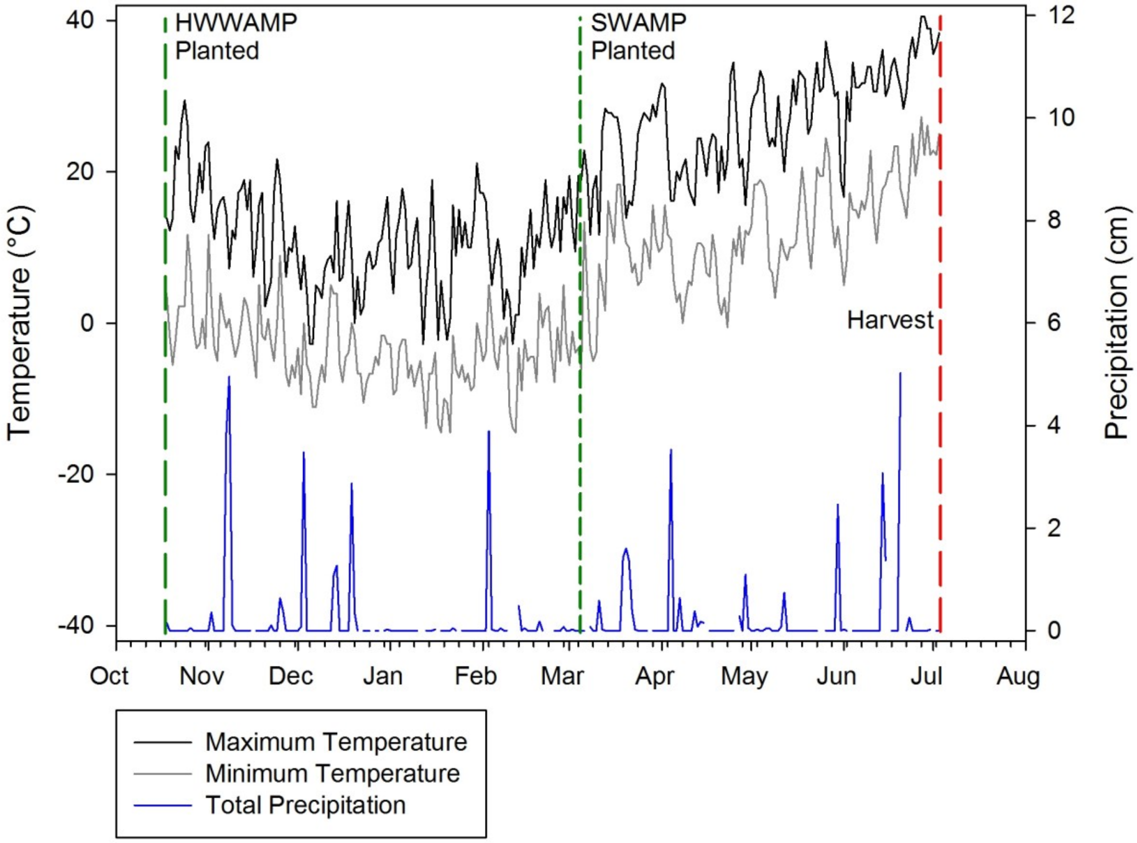

Figure 2-1. Manhattan KS, weather data for the 2011-2012 growing season showing daily maximum temperature, minimum temperature, and precipitation. Also shown are the planting and harvest dates for spring and hard winter wheat association mapping panels.

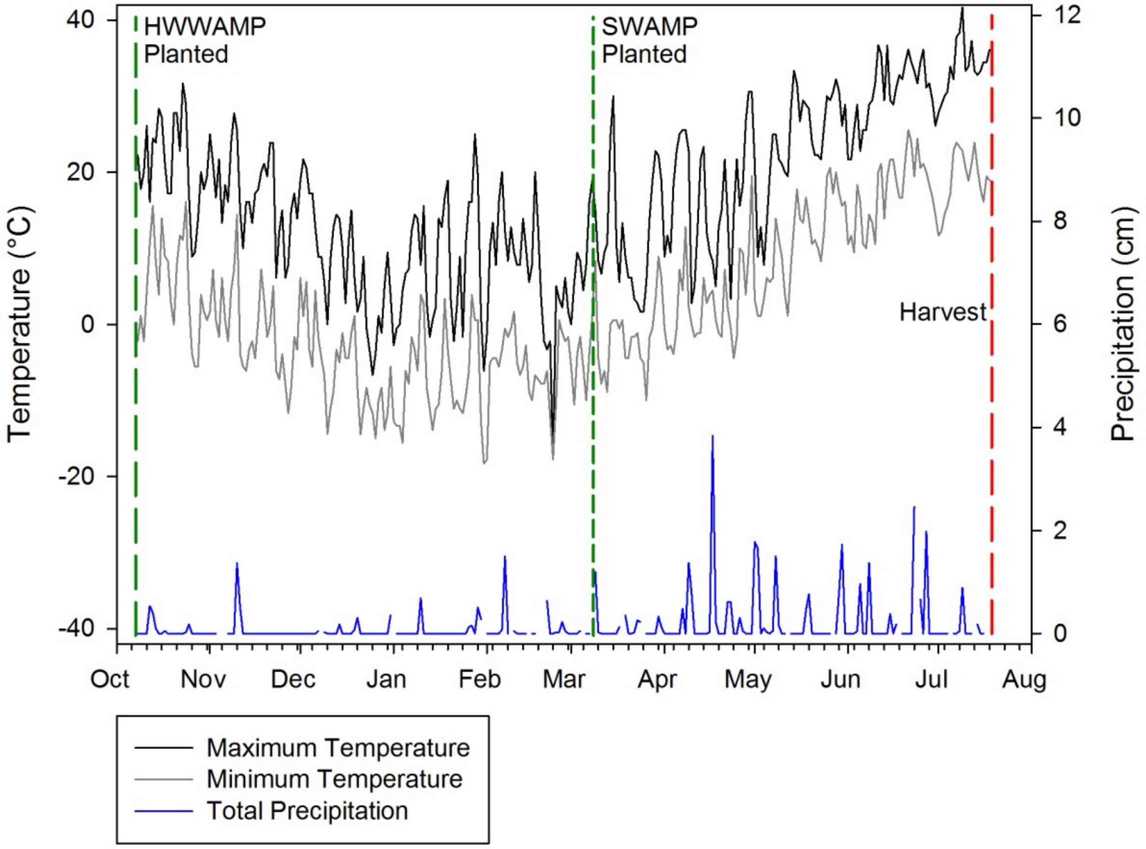

Figure 2-2. Manhattan KS, weather data for the 2012-2013 growing season showing daily maximum temperature, minimum temperature, and precipitation. Also shown are the planting and harvest dates for spring and hard winter wheat association mapping panels.

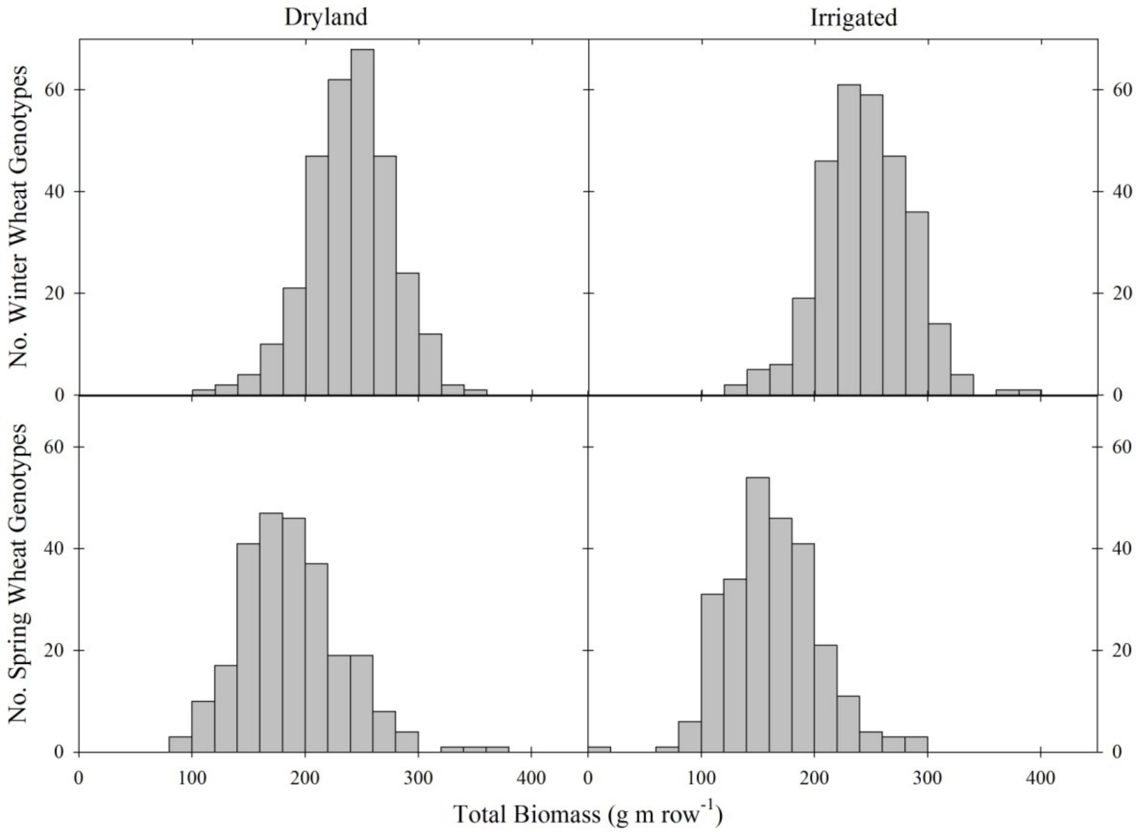

Figure 2-3. Histogram of total biomass, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

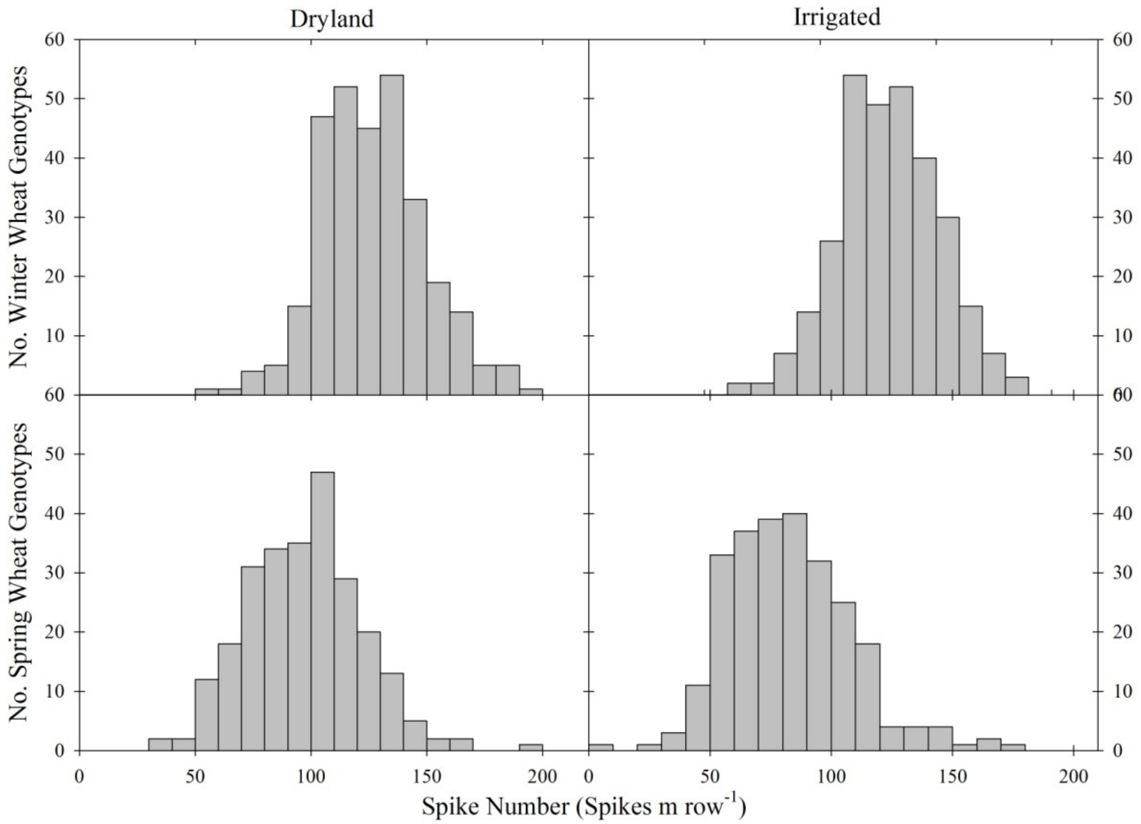

Figure 2-4. Histogram of spike number, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

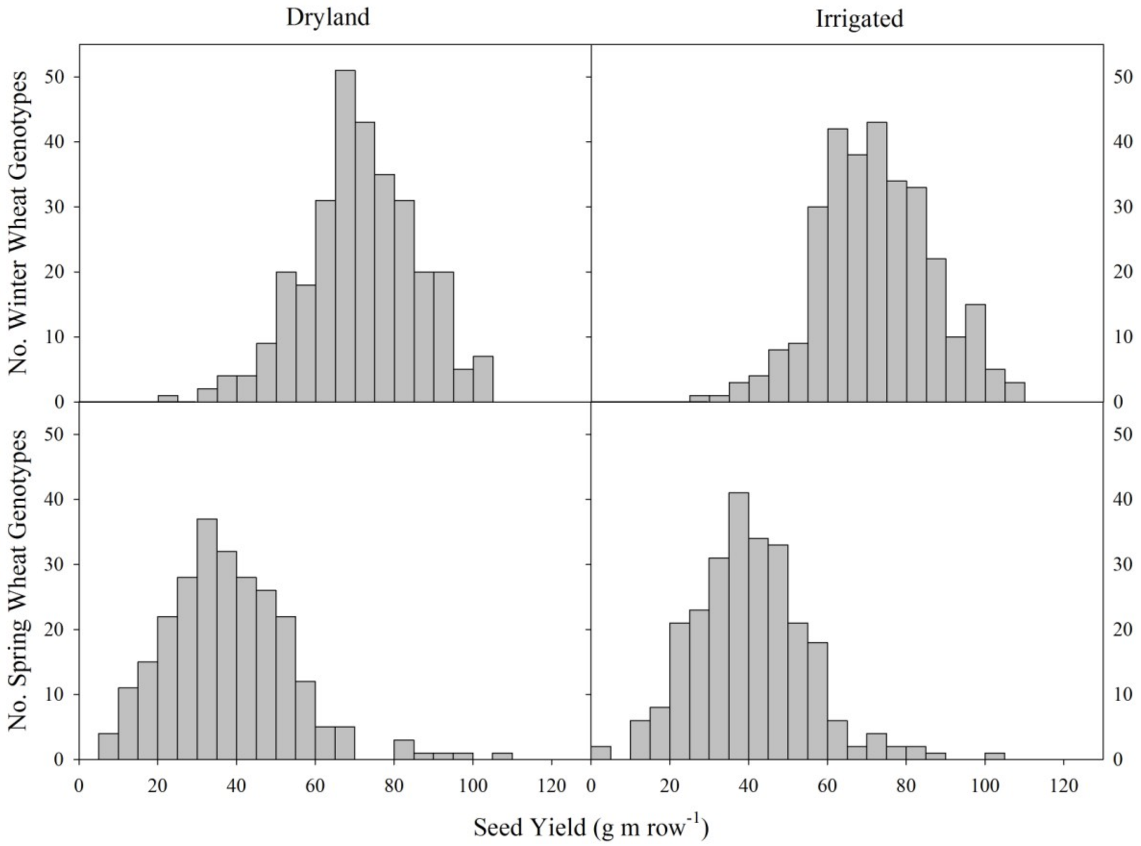

Figure 2-5. Histogram of seed yield, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

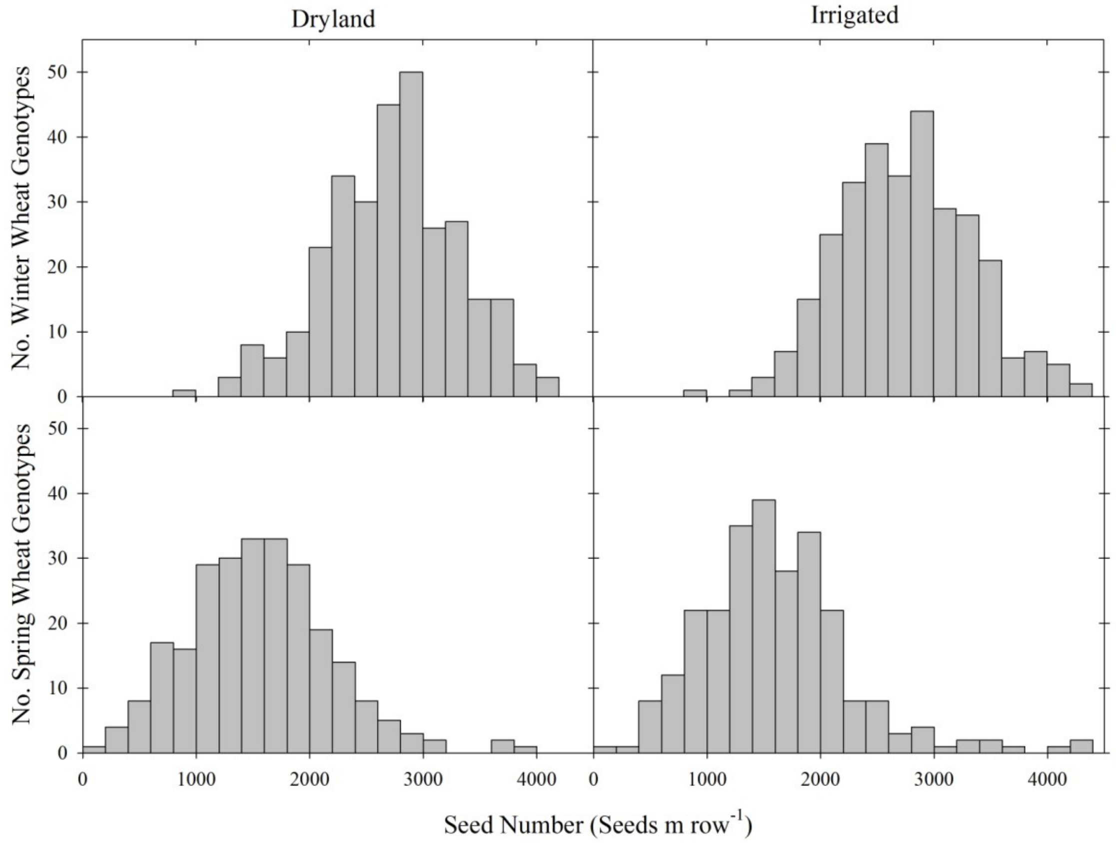

Figure 2-6. Histogram of seed number, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

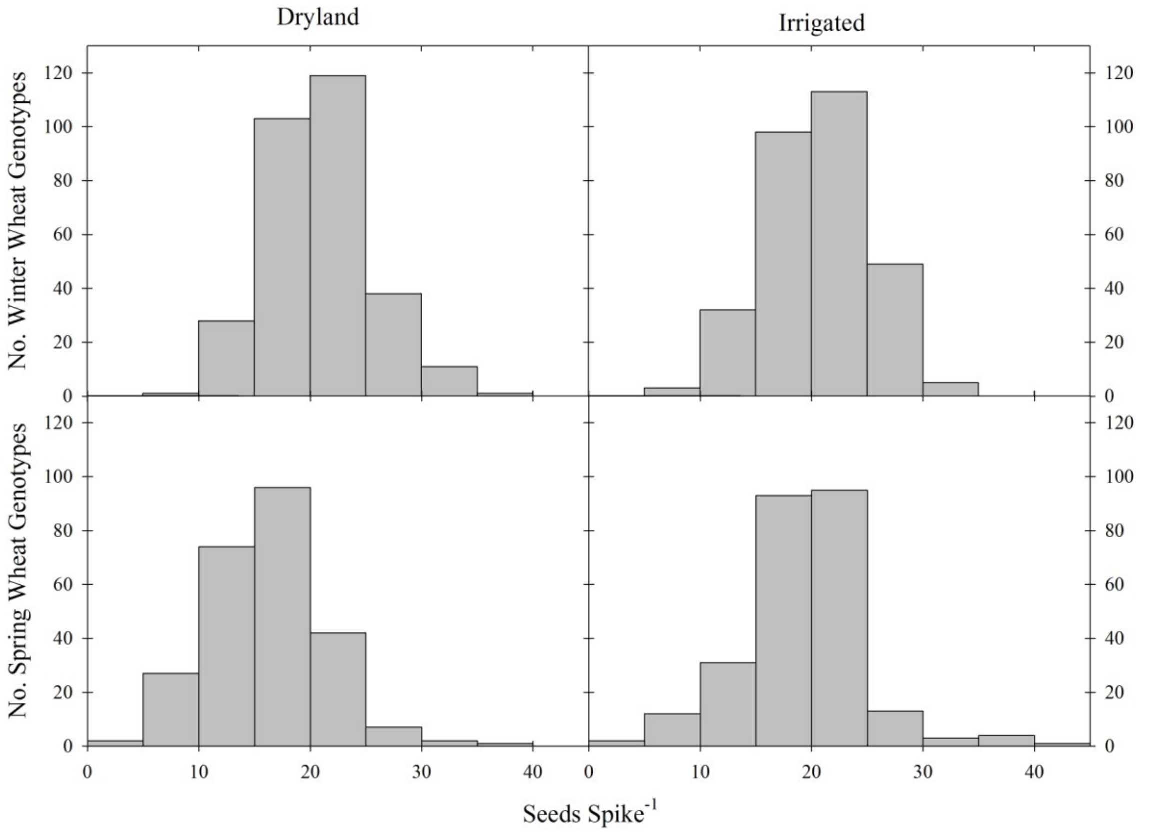

Figure 2-7. Histogram of seeds per spike, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

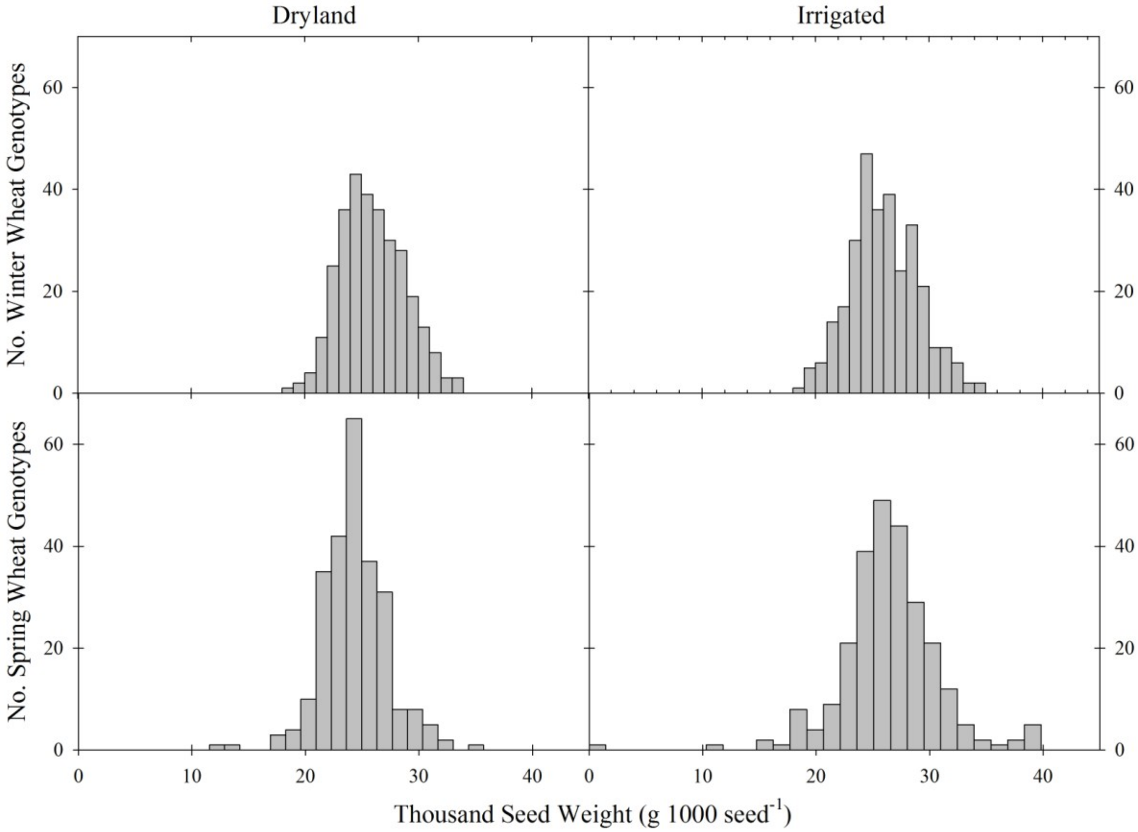

Figure 2-8. Histogram of thousand seed weights, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

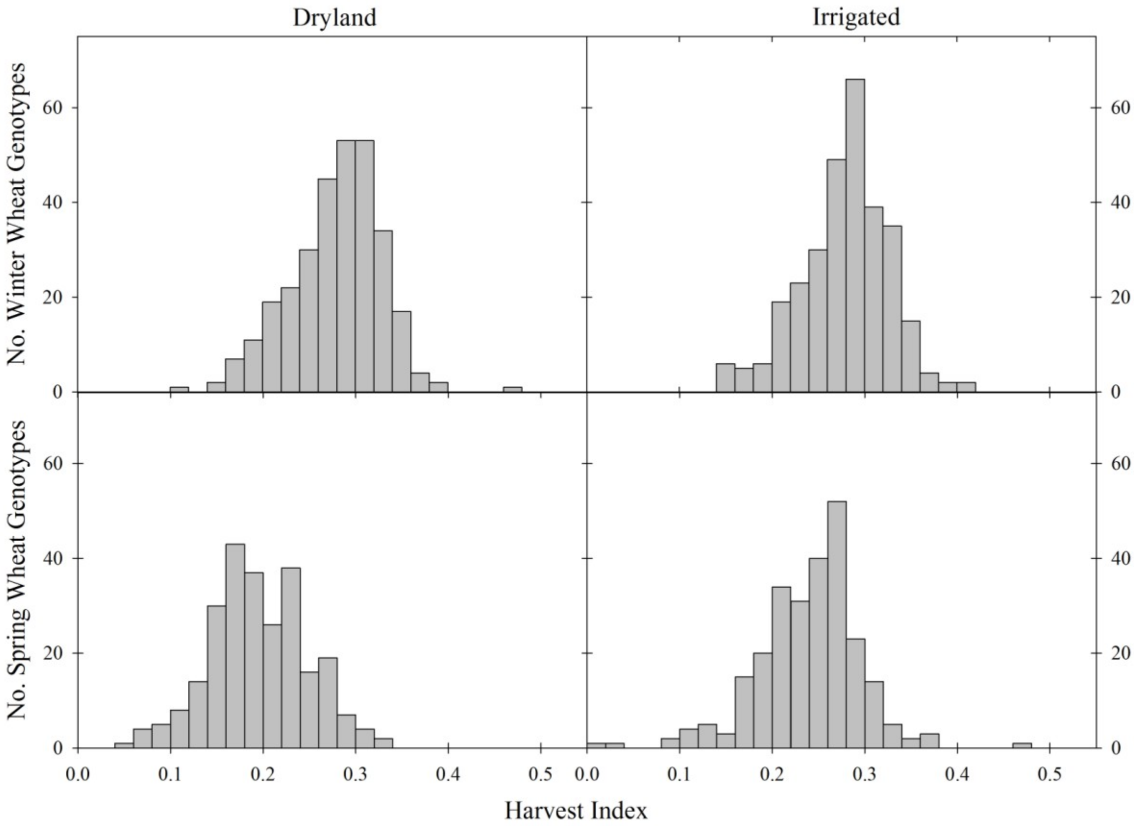

Figure 2-9. Histogram of harvest index, harvested from one meter of row, from spring and hard winter wheat association mapping panels and the combined 2011-2012 and 2012-2013 growing seasons.

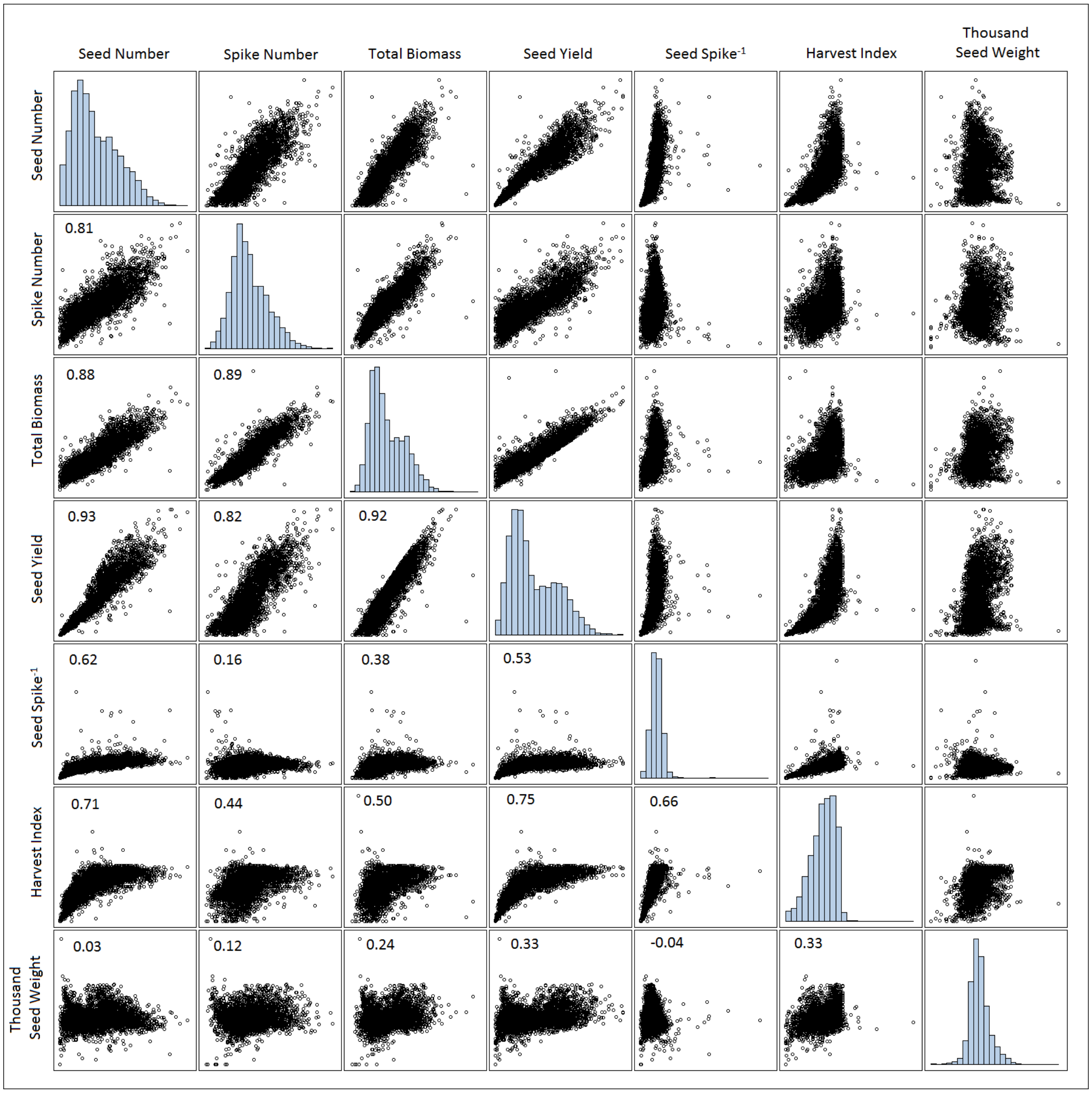

Figure 2-10. Pearson correlation matrix and histograms of yield traits of the combined spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. Yield traits are seed number, spike number, total biomass, seed yield, seeds per spike, harvest index, and thousand seed weights.

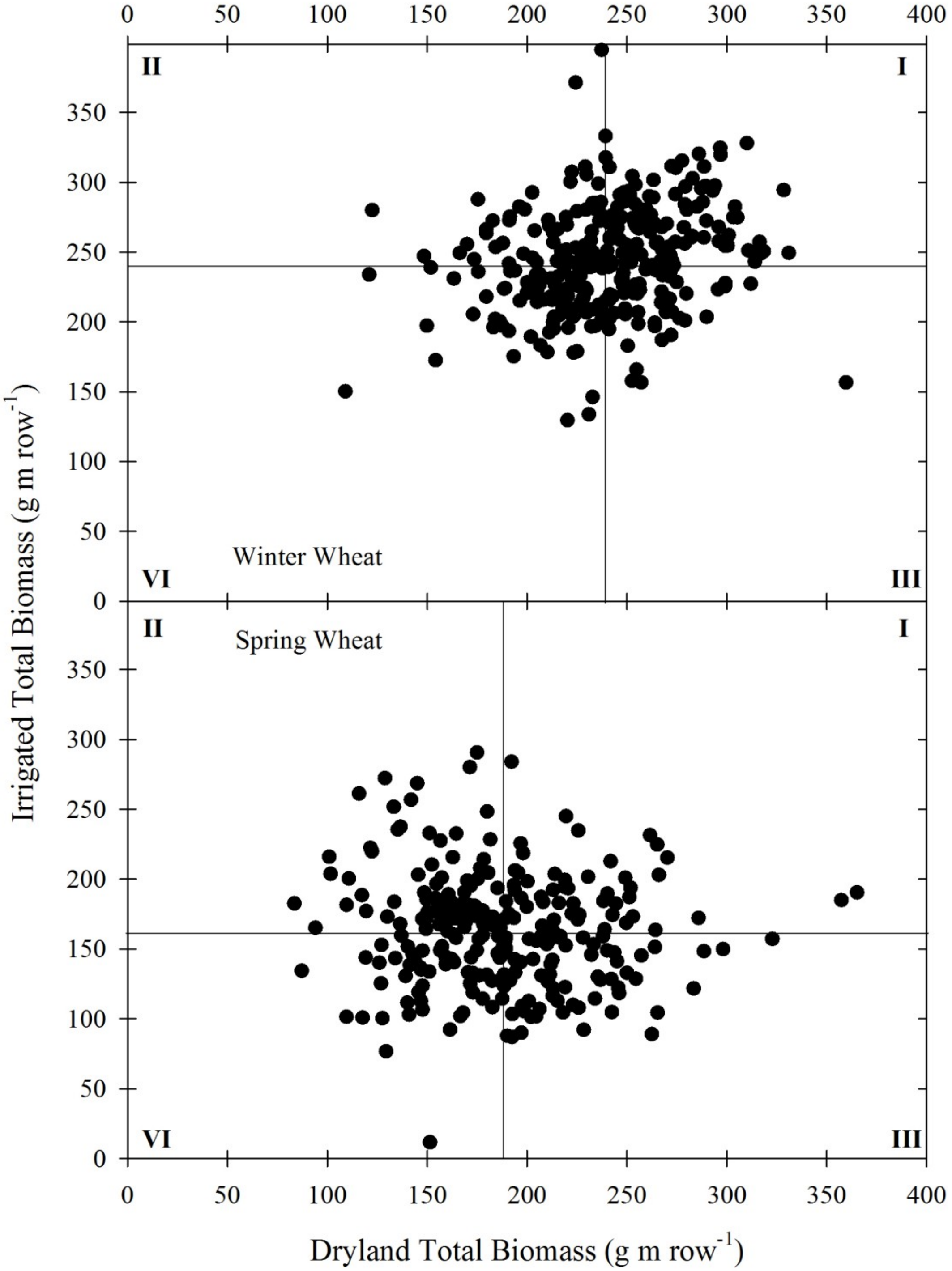

Figure 2-11. Quadrant plot of total biomass when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

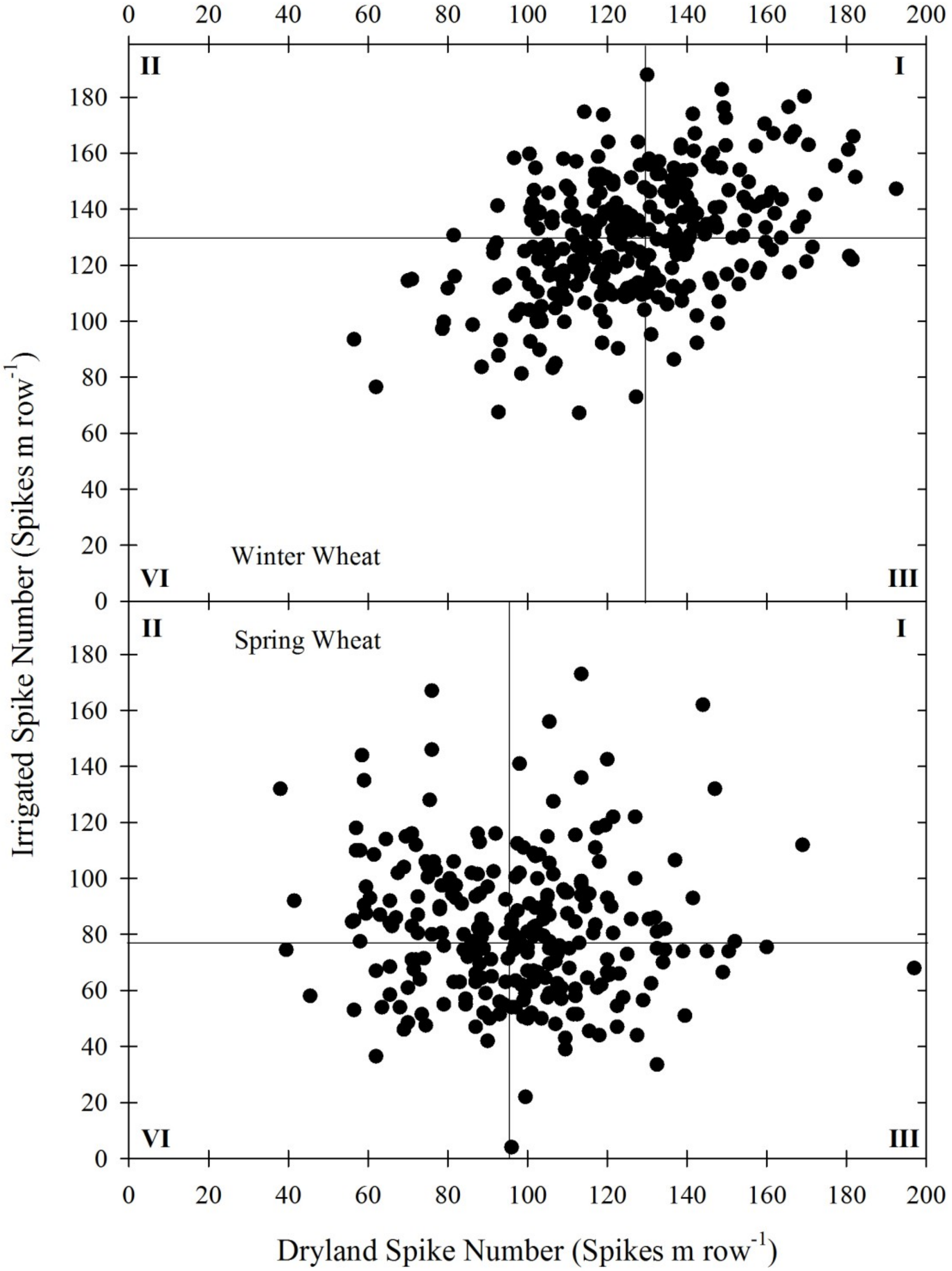

Figure 2-12. Quadrant plot of spike number when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

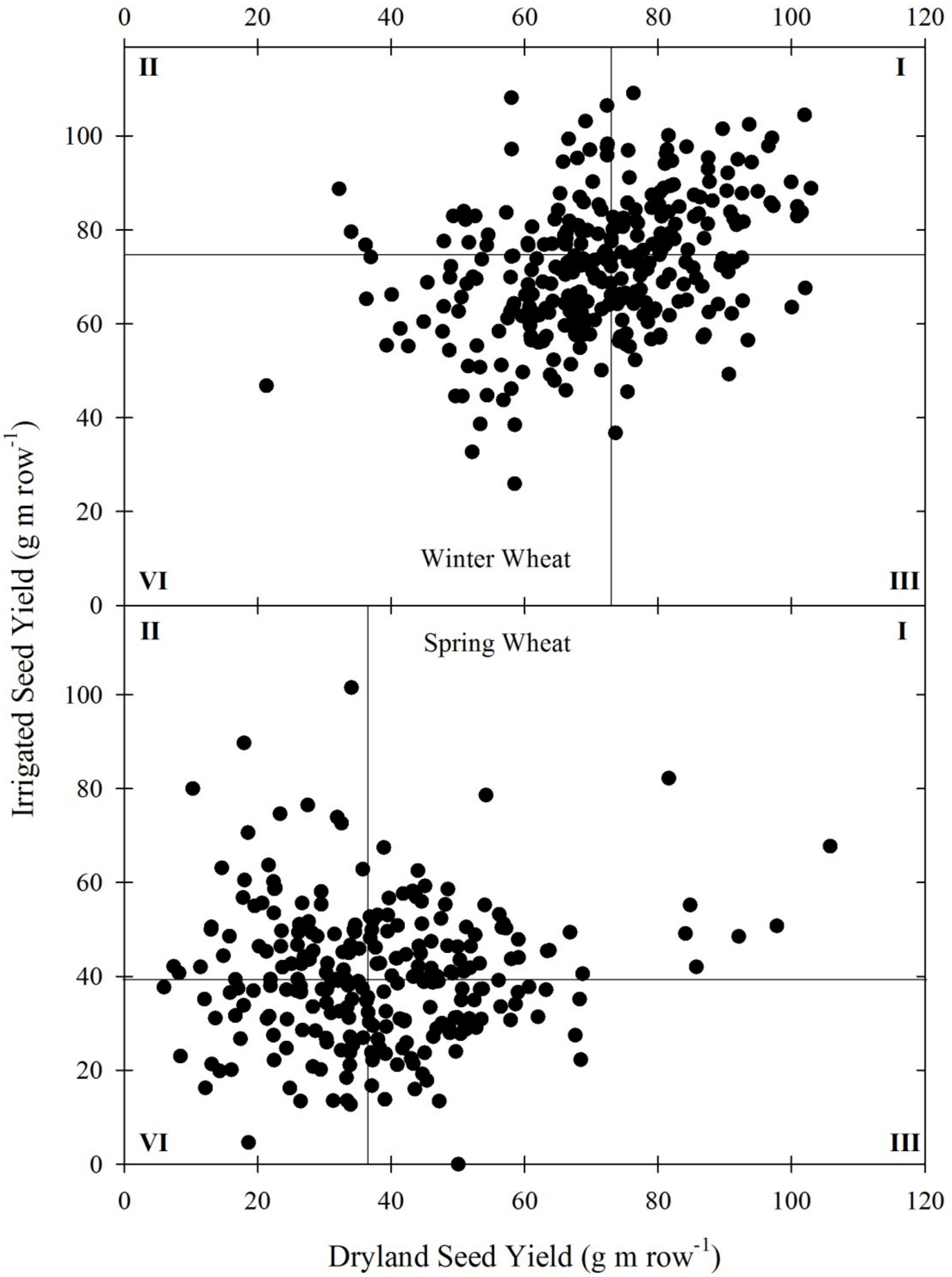

Figure 2-13. Quadrant plot of seed yield when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

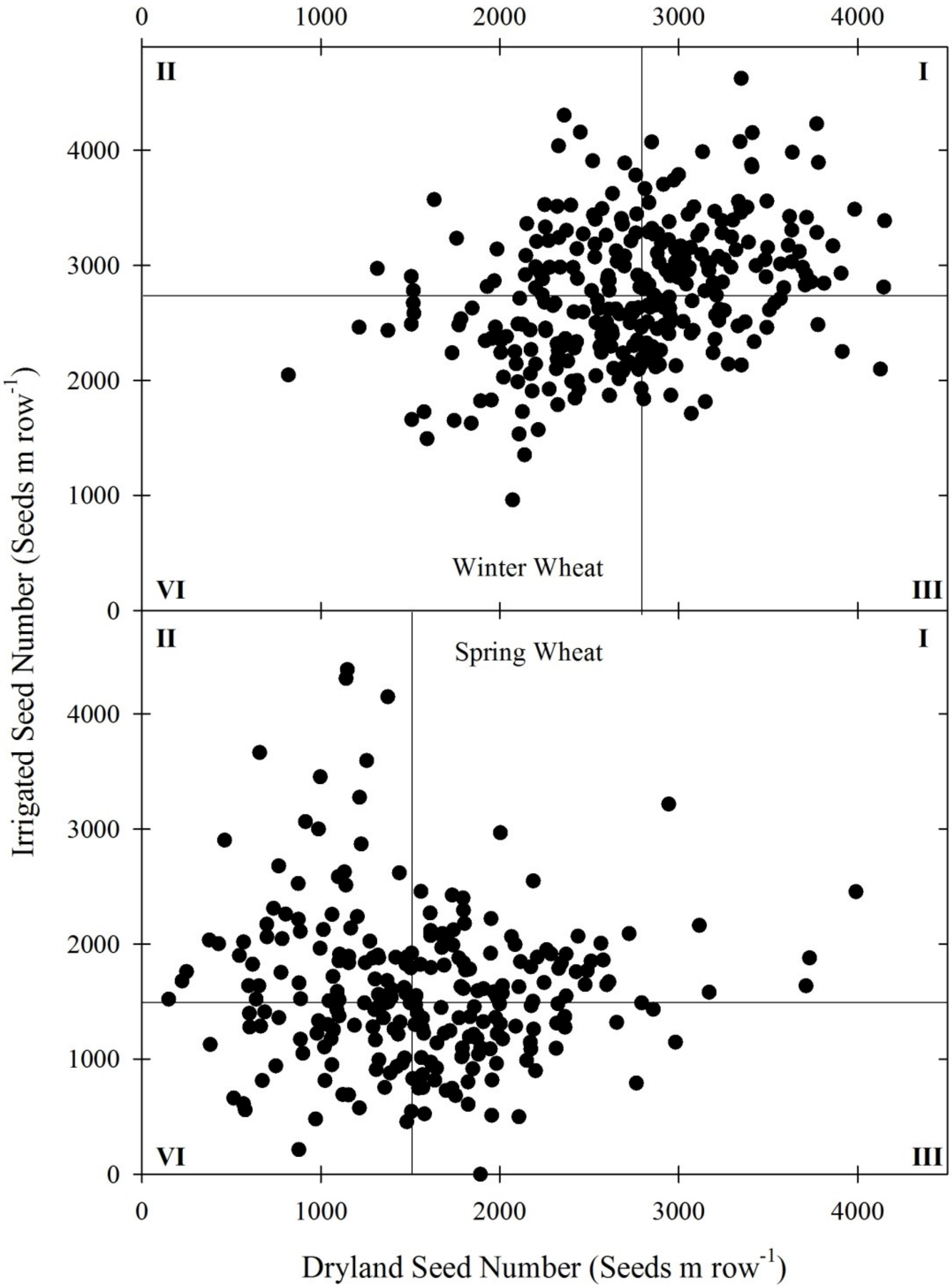

Figure 2-14. Quadrant plot of seed number when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

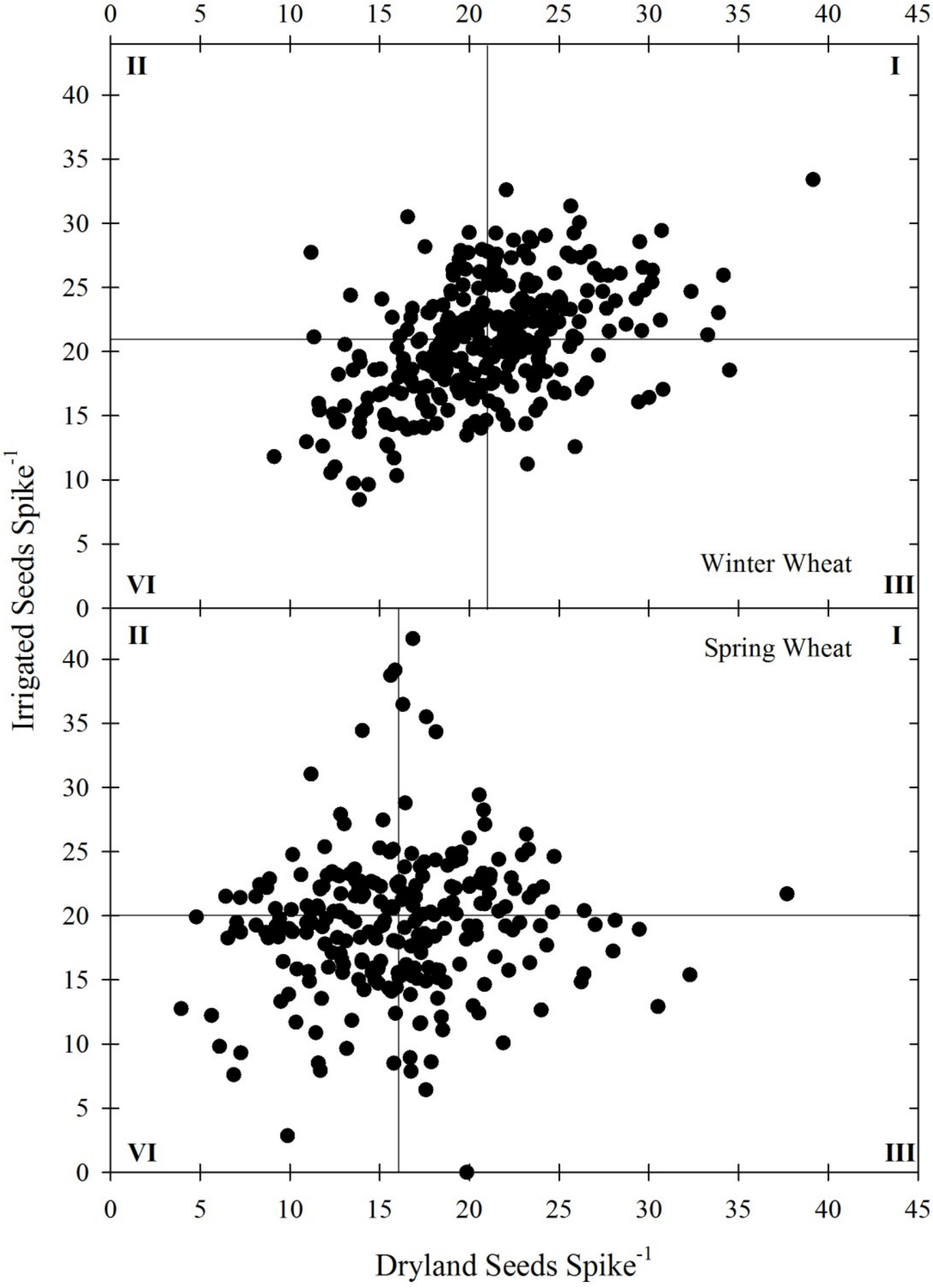

Figure 2-15. Quadrant plot of seeds per spike when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

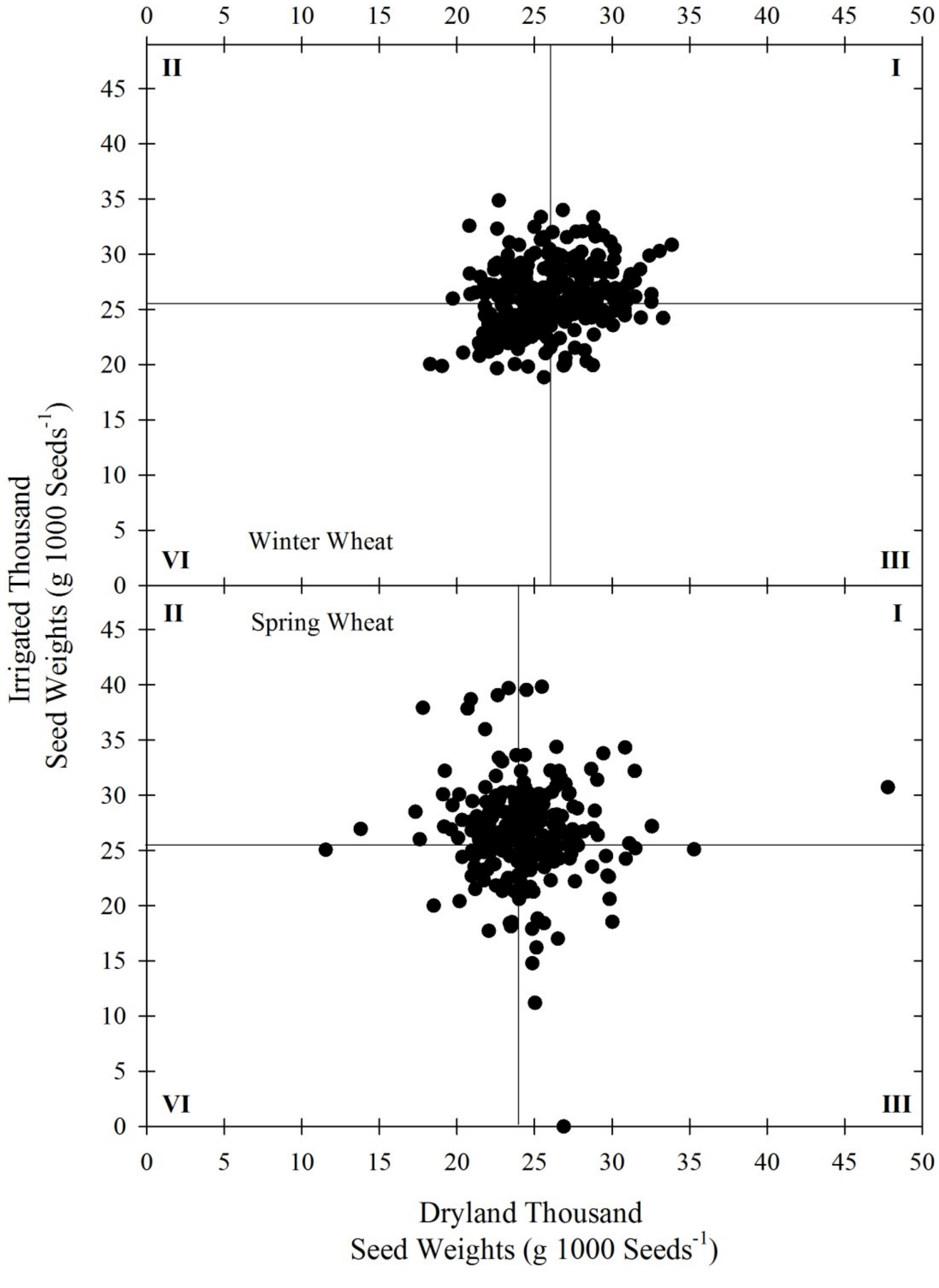

Figure 2-16. Quadrant plot of thousand seed weights when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

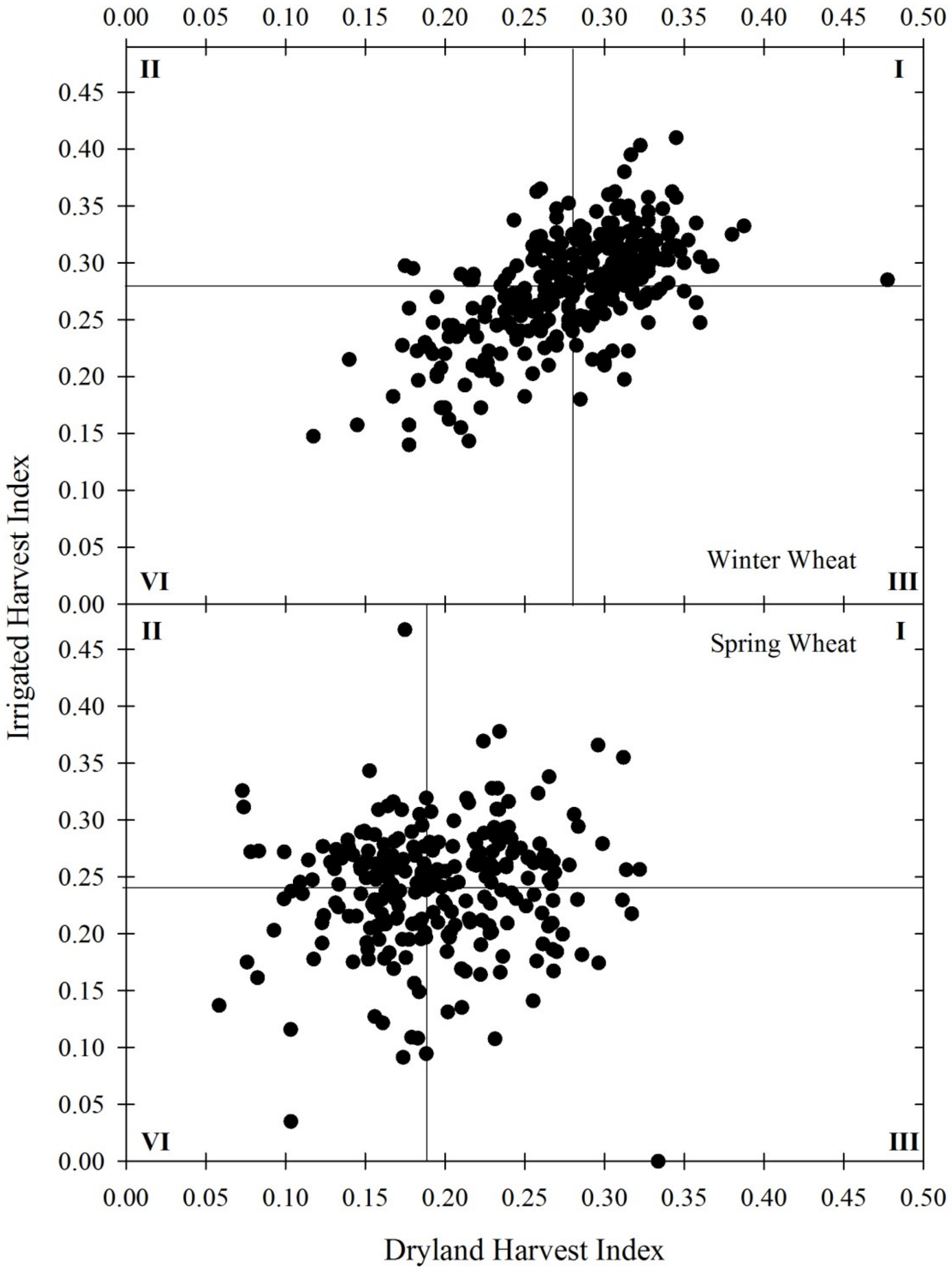

Figure 2-17. Quadrant plot of harvest index when compared by water regime for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

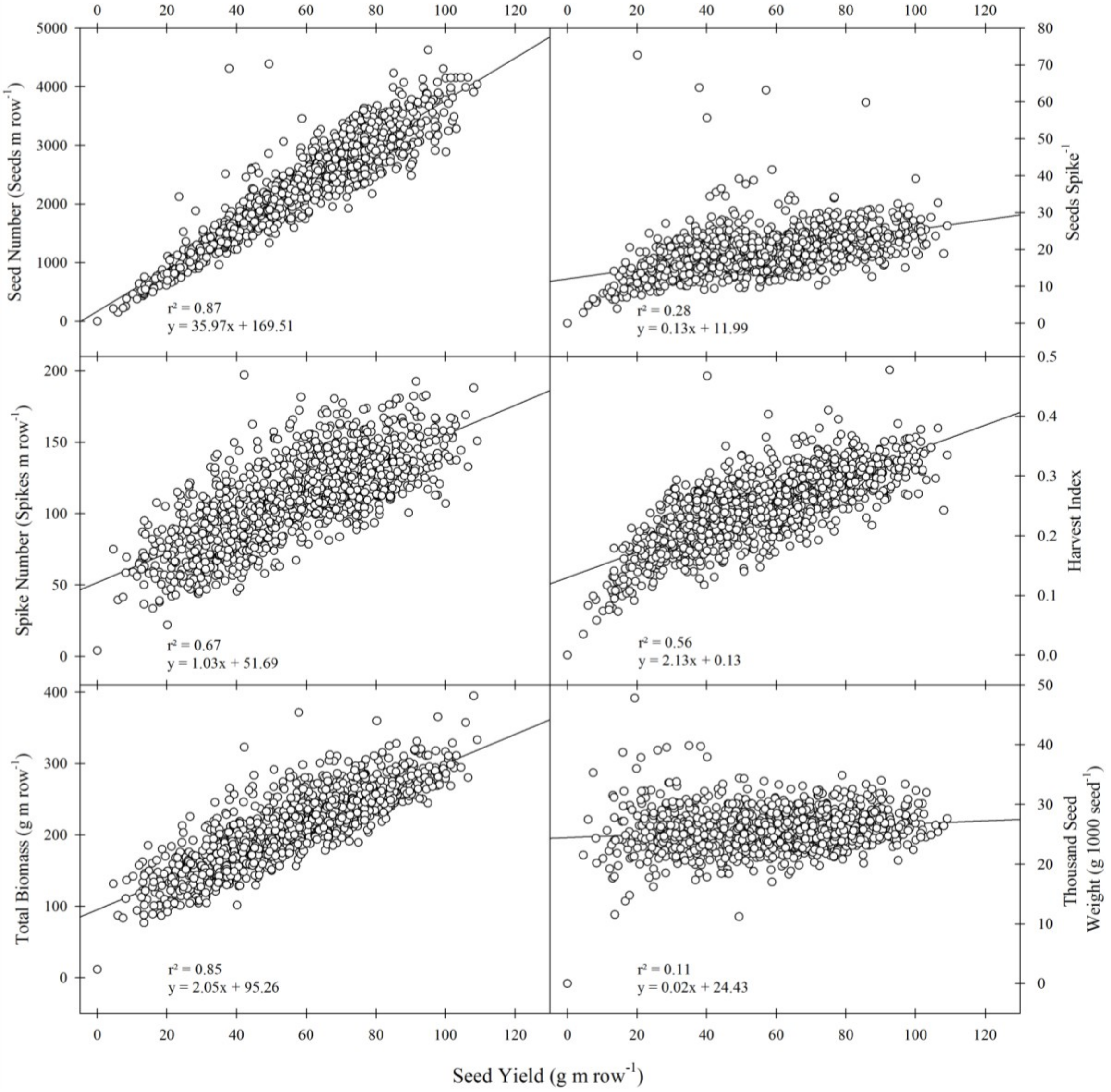

Figure 2-18. Regression of seed yield against seed number, spike number, total biomass, seeds per spike, harvest index, and thousand seed weights. for spring and hard winter wheat association mapping panels from the combined 2011-2012 and 2012-2013 growing seasons.

Table 2-1. Summary Table of average yield traits for spring and hard winter wheat association mapping panels by water regime.

Variable	Unit	Spring Wheat			Winter Wheat			Combined		
		Average	Dryland	Irrigated	Average	Dryland	Irrigated	Average	Dryland	Irrigated
Total Biomass	g m row^{-1}	172.67	184.61	160.63	247.43	246.00	248.85	226.59	228.65	224.51
Spike Number	spikes m row^{-1}	87.88	95.94	79.63	130.26	128.86	131.65	118.43	119.59	117.27
Seed Yield	g m row^{-1}	37.86	36.66	39.09	74.48	74.27	74.70	64.25	63.64	64.86
Seed Number	seeds m row^{-1}	1533	1521	1570	2829	2824	2833	2472	2456	2488
Seeds Spike^{-1}	seeds spike^{-1}	17.95	16.20	19.70	21.07	21.24	20.90	20.19	19.82	20.57
Thousand Seed Weights	g 1000 seeds^{-1}	26.10	24.33	26.23	26.18	26.16	26.21	25.93	25.64	26.22
Harvest Index	Unit-less	0.2141	0.1919	0.2363	0.2829	0.2832	0.2826	0.2636	0.2574	0.2698

Table 2-2. Variance Component Analysis for spring (SWAMP) and hard winter wheat association mapping panels (HWWAMP) by water regime, for the combined 2011-2012 and 2012-2013 growing seasons. Variance Component Estimates were created for Genotype (G), Environment (E), GxE interaction, Replication nested within E (Rep(E)) or Column and Row Blocking, and Residual Experimental Error, shown as percent of error.

SWAMP	Variable	G	E	GxE	Rep(E)	Error
		Variance Component Estimate (percent of error)				
Dryland	Total Biomass	10.29	0.49	*0.00*	*0.00*	3069.20
Irrigated	Total Biomass	5.17	21.35	11.79	41.03	1753.40
Dryland	Spike Number	*0.00*	18.49	5.81	9.47	964.28
Irrigated	Spike Number	9.97	61.22	7.20	39.96	620.51
Dryland	Seed Yield	13.23	21.77	10.06	*0.00*	330.38
Irrigated	Seed Yield	4.16	19.63	*0.00*	*0.00*	317.21
Dryland	Seed Number	5.70	2.57	*0.00*	*0.00*	682140.90
Irrigated	Seed Number	6.85	42.44	34.10	4.87	435969.20
Dryland	Seeds Spike^{-1}	*0.00*	18.26	13.05	*0.00*	70.85
Irrigated	Seeds Spike^{-1}	*0.00*	*0.00*	8.82	*0.00*	91.11
Dryland	Thousand Seed Weights	*0.00*	54.95	*0.00*	8.68	52.22
Irrigated	Thousand Seed Weights	*0.00*	55.54	383.84	20.71	50.26
Dryland	Harvest Index	8.18	41.78	*0.00*	*0.00*	0.0056
Irrigated	Harvest Index	9.50	4.67	*0.00*	*0.00*	0.0053

HWWAMP	Variable	G	E	GxE	Col	Row	Error
		Variance Component Estimate (percent of error)					
Dryland	Total Biomass	4.12	379.82	8.42	0.49	5.81	3483.50
Irrigated	Total Biomass	*0.00*	505.96	11.83	11.33	15.51	3488.50
Dryland	Spike Number	11.05	205.98	12.42	1.64	6.67	998.06
Irrigated	Spike Number	6.15	318.42	9.37	14.93	8.30	985.95
Dryland	Seed Yield	11.41	613.37	13.50	*0.00*	10.98	411.64
Irrigated	Seed Yield	6.83	645.33	18.19	6.51	18.40	424.61
Dryland	Seed Number	3.22	333.75	9.28	0.35	10.03	834328.80
Irrigated	Seed Number	6.88	387.29	6.92	6.52	20.04	786486.40
Dryland	Seeds Spike^{-1}	15.04	73.56	*0.00*	*0.00*	5.25	55.13
Irrigated	Seeds Spike^{-1}	13.97	43.30	12.78	*0.00*	10.71	53.16
Dryland	Thousand Seed Weights	9.46	38.98	*0.00*	0.15	8.55	22.36
Irrigated	Thousand Seed Weights	10.85	31.44	*0.00*	1.71	4.28	25.33
Dryland	Harvest Index	44.40	218.36	18.75	*0.00*	11.53	0.0026
Irrigated	Harvest Index	33.33	146.63	26.64	2.64	16.76	0.0028

Italic *0.00* denote a negative variance assumed to zero.

Table 2-3. Analysis of Variance for spring and hard winter wheat association mapping panels by genotype (G) nested within water regime (Trt) and water regime nested within environment (E), for the combined 2011-2012 and 2012-2013 growing seasons.

Analysis of Variance		Spring Wheat Association Mapping Panel			Hard Winter Wheat Association Mapping Panel		
Variable	Unit	Mean	G(Trt)	Trt(E)	Mean	G(Trt)	Trt(E)
			Pr > F			Pr > F	
Total Biomass	g m row^{-1}	226.59	0.0853	<.0001	247.43	0.0049	<.0001
Spike Number	spikes m row^{-1}	118.43	0.4217	<.0001	130.26	<.0001	0.0413
Seed Yield	g m row^{-1}	64.25	0.0637	<.0001	74.48	<.0001	0.0212
Seed Number	seeds m row^{-1}	2472	0.1338	<.0001	2829	<.0001	0.0038
Seeds Spike^{-1}	seeds spike^{-1}	20.19	0.7241	<.0001	21.07	<.0001	0.0061
Thousand Seed Weight	g 1000 seeds^{-1}	25.93	0.4897	<.0001	26.18	<.0001	0.2320
Harvest Index	Unit-less	0.2636	0.0304	<.0001	0.2829	<.0001	0.0726

Table 2-4. Pearson correlation coefficients for total biomass, spike number, seed yield, seed number, seeds per spike, thousand seed weights, and harvest index by water regime for combined spring and hard winter wheat association mapping panels.

	Total Biomass		Spike Number		Seed Yield		Seed Number		Seeds Spike^{-1}		Thousand Seed Weight		Harvest Index	
	Dryland	Irrigated	Dryland	Irrigated	Dryland	Irrigated	Dryland	Irrigated	Dryland	Irrigated	Dryland	Irrigated	Dryland	Irrigated
Total Biomass	1	1												
Spike Number	0.87	0.91	1	1										
Seed Yield	0.91	0.93	0.78	0.85	1	1								
Seed Number	0.87	0.89	0.78	0.84	0.93	0.93	1	1						
Seeds Spike^{-1}	0.46	0.31	0.20	0.13	0.62	0.44	0.70	0.54	1	1				
Thousand Seed Weight	0.26	0.23	0.12	0.12	0.37	0.29	0.08	*-0.01*	*0.04*	-0.12	1	1		
Harvest Index	0.54	0.47	0.46	0.43	0.80	0.71	0.75	0.67	0.71	0.59	0.38	0.27	1	1

Red Italic text is not significant at an alpha of 0.05

Table 2-5. Multiple linear regression table for seed yield, representing models of differing input variables, ranked by adjusted R^2 and root mean squared error. Models are the best predictors of seed yield with 6, 5, 4, 3, 2, and 1 input parameters. Input parameters are seed number, spike number, total biomass, seeds per spike, harvest index, and thousand seed weights.

Adjusted R^2	Root Mean Squared Error	Intercept	Seed Number	Spike Number	Total Biomass	Seeds $Spike^{-1}$	Harvest Index	Thousand Seed Weights
		Parameter Estimates						
0.978 ǂ	6.258	-50.74	0.0132	-0.0622	0.1813	-0.3139	105.4460	1.0508
0.977 ǂ	6.417	-56.62	0.0117	-0.0008	0.1676	.	92.8916	1.1456
0.977 ǂ	6.416	-56.65	0.0117	.	0.1673	.	92.8931	1.1463
0.968	7.451	-54.55	0.0200	.	0.0885	.	.	1.9043
0.965	7.785	-56.10	.	.	0.2924	.	182.8135	0.2283
0.965	7.871	-51.50	.	.	0.2938	-0.0388	189.4967	.
0.965	7.875	-51.55	.	.	0.2936	.	186.9167	.
0.959	8.442	-56.36	0.0252	.	.	.	.	2.2506
0.916	12.107	-13.21	0.0147	.	0.1815	.	.	.
0.870	15.116	1.28	0.0255	.	.	.	.	.
0.849	16.243	-19.97	.	.	0.3718	.	.	.
0.669	24.078	-15.64	.	0.6746	.	.	.	.
	g m row^{-1}		seeds m row^{-1}	spikes m row^{-1}	g m row^{-1}	seeds $spike^{-1}$		g 1000 $seeds^{-1}$

ǂModels with one or more parameter with a variance inflation factor above 10

Table 2-6. Top and bottom five genotypes selected from quadrate plots based on seed yield from spring and hard winter wheat association mapping panels. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

Hard Winter Wheat Association Mapping Panel					**Spring Wheat Association Mapping Panel**				
Average Irrigated Yield- 72.27 g m^{-1} row					Average Irrigated Yield- 40.24 g m^{-1} row				
Average Dryland Yield- 71.24 g m^{-1} row					Average Dryland Yield- 38.02 g m^{-1} row				
I. High Irrigated and Dryland					- Above average irrigated and above average dryland yield				
HWWAMP Genotypes	Rank	Irrigated	Dryland	Difference	SWAMP Genotypes	Rank	Irrigated	Dryland	Difference
INTRADA	1	102.45	93.65	8.80	Lassik	1	78.60	54.20	24.40
SETTLER_CL	2	99.56	97.08	2.48	SD4181	2	82.20	81.60	0.60
OK05830	3	104.45	101.98	2.48	IDO560	3	55.20	84.80	-29.60
GALLAGHER	4	97.88	96.53	1.34	MN02072-7	4	67.70	105.80	-38.10
KEOTA	5	90.20	99.95	-9.75	GP069	5	50.75	97.80	-47.05
II. High Irrigated, low Dryland					- Above average irrigated and below average dryland yield				
HWWAMP Genotypes	Rank	Irrigated	Dryland	Difference	SWAMP Genotypes	Rank	Irrigated	Dryland	Difference
TAM303	1	88.73	32.20	56.53	9254	1	89.70	17.95	71.75
GOODSTREAK	2	108.13	58.03	50.10	UC896 5+10 Lr34/Yr18 Yr5 Gpc	2	80.00	10.25	69.75
PROWERS	3	97.20	58.05	39.15	SD4165	3	101.50	34.05	67.45
THUNDERBOLT	4	82.95	49.30	33.65	MT0813	4	74.60	23.35	51.25
TX06A001132	5	83.97	50.90	33.07	TRAVERSE	5	76.50	27.50	49.00

*Irrigated, Dryland, and Difference of Yield (g m^{-1} row)

Table 2-7. Top and bottom five genotypes selected from quadrate plots based on seed yield from spring and hard winter wheat association mapping panels. The four quadrants are: I. above average irrigated and dryland, II. above average irrigated and below average dryland, III. below average irrigated and above average dryland, and VI. below average irrigated and dryland.

Hard Winter Wheat Association Mapping Panel					**Spring Wheat Association Mapping Panel**				
Average Irrigated Yield- 72.27 g m^{-1} row					Average Irrigated Yield- 40.24 g m^{-1} row				
Average Dryland Yield- 71.24 g m^{-1} row					Average Dryland Yield- 38.02 g m^{-1} row				
III. Low Irrigated, High Dryland					- Below average irrigated and above average dryland yield				
HWWAMP Genotypes	Rank	Irrigated	Dryland	Difference	SWAMP Genotypes	Rank	Irrigated	Dryland	Difference
WICHITA	1	64.90	92.68	-27.78	BRICK	1	37.15	63.20	-26.05
BOND_CL	2	67.60	102.05	-34.45	SD4178	2	31.35	62.00	-30.65
OK05723W	3	63.53	100.05	-36.52	AC Andrew	3	35.15	68.25	-33.10
LAKIN	4	56.48	93.47	-36.99	Snowstar	4	27.45	67.60	-40.15
CHISHOLM	5	49.23	90.60	-41.37	Choteau	5	22.25	68.40	-46.15
VI. Low Irrigated and Dryland					- Below average irrigated and below average dryland yield				
HWWAMP Genotypes	Rank	Irrigated	Dryland	Difference	SWAMP Genotypes	Rank	Irrigated	Dryland	Difference
W04-417	1	46.80	21.30	25.50	Neepawa	1	23.00	8.40	14.60
MT9513	2	55.40	39.31	16.09	9249	2	21.30	13.10	8.20
ARAPAHOE	3	55.23	42.58	12.65	SD4280	3	19.85	14.30	5.55
JERRY	4	44.60	49.65	-5.05	MTHW1069	4	16.25	12.15	4.10
NUSKY	5	44.58	50.65	-6.08	Marquis	5	4.60	18.60	-14.00

*Irrigated, Dryland, and Difference of Yield (g m^{-1} row)

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Chapter 3 - Source-Sink Interactions with Limited Moisture and Varying Levels of Defoliation in Post-Anthesis Wheat

The Food and Agriculture Organization stated in 2012 that wheat (*Triticum aestivum* L.) was the third most important crop worldwide. It was estimated that 670 million Mg of wheat were produced in 2012 with an average yield of 3.2 Mg ha^{-1} (FAO, 2012). With an ever increasing population and the increasing risk of food scarcity due to climate change, the need for improved production per unit of land is of necessity (IPCC, 2013). In the arid and semi-arid regions of the world food supply is already at risk, due to high temperatures and low rainfall. Climate change could make this worse (IPCC, 2013).

Wheat is one of the major crops grown in the arid and semi-arid regions of the world (FAO, 2012). The major environmental stresses of these regions are high temperature and drought (Nicolas et al., 1984; Shah and Paulsen, 2003). Of the two, drought stress may be the most important stress for most of these regions (Boyer, 1982; Curtis, 2002; Condon et al., 2004; Fischer et al., 2009; Mirbahar et al., 2009).

Wheat has adapted to withstand environmental stress, to a certain degree, but it is still susceptible during certain growth stages (Blum, 1996; Frederick and Bauer, 1999; Curtis, 2002). The most sensitive growth stages to drought stress, for wheat, are at the growth stages in which yield components are formed (Blum, 1996; Frederick and Bauer, 1999). These yield components are: plants per unit area (emergence), reproductive units per plant (tillering), seeds per reproductive unit (anthesis), and weight per seed (seed fill) (Giunta et al., 1993; Simane et al., 1993; Shah and Paulsen, 2003; Mirbahar et al., 2009). Seed fill is the period of time after anthesis and seed set, during which the plant is partitioning carbon and nutrients to the seed. Drought affects this stage in several ways; by reducing photosynthesis (Shah and Paulsen, 2003; Flexas et al., 2004), increasing respiration from oxidative damage (Reddy, 2004; Zhou et al., 2007), cellular death, and rapid leaf senescence (Siddique et al., 1989; Shah and Paulsen, 2003). This is by no means a complete list, but it covers the more important points. Drought stress at this stage is typically called terminal stress.

One of the ways in which wheat has adapted to stress is in the ability to use pre-anthesis carbon, stored in the stem and leaf sheaths, to fill seed when stress has reduced the ability to photosynthesize (Shah and Paulsen, 2003; Ji et al., 2010). This is not a perfect mechanism however; with increased respiration and rapid leaf senescence, the stored carbon is divided between two strong sinks, the seed and the rest of the plant, used to stay alive (Cook and Evans, 1978; Ahmadi and Baker, 2001). If the drought stress continues, this process is a race against the clock and there will be a reduction in the yield compared to what it could have been (Cook and Evans, 1978; Yang et al., 2001). Yield produced from reserves is not typically as high as when it is produced through photosynthesis (Kruk et al., 1997; Inoue et al., 2004). Because photosynthesis is so important for yield and there are numerous ways in which field plants can lose leaves, from drought stress caused leaf senescence to damage from foliar diseases, maintaining leaf area is important. Or at the very least, maintaining productive leaf area is important. So this begs the questions: How do the leaves and stem reserves interact under drought stress and how do they contribute to yield? Which leaves are the most productive? To answer these questions, a series of three experiments were preformed with the following objectives.

Objectives

1. Characterize the relationship in photosynthetic area and stored reserves during seed-filling to grain yield and yield components in irrigated and limited moisture environments.
2. Characterize contributions of leaves and stems to grain yield.

Materials and Methods

Research was conducted at the facilities of the Department of Agronomy at Kansas State University, Manhattan, KS, USA. A series of three identical experimental rounds were conducted under greenhouse-controlled environments to quantify the impact of limited water and leaf defoliation on the source-sink relationships of spring wheat during seed-fill. Experiments were conducted over a period of time starting in the spring of 2013 and the final experiment was in spring of 2015.

Plant Culture

The spring wheat cultivar, 'Seri 82' (CIMMYT, 1982) was planted in 32, 3.4-L, 15x15x15 cm (length x width x height, respectively) square pots containing 1.5 kg of Metro-mix 360 (Hummert International, Topeka, KS). Five seeds were sown at a 4-cm depth in each pot. Growing medium was fertilized with 4 g of Osmocote (controlled-release fertilizer, 14:14:14% N:P_2O_5:K_2O, respectively; Hummert International, Topeka, KS), applied at the time of sowing. A systemic insecticide, (Imidacloprid: 1–[(6-Chloro-3-pyridinyl)methyl]-N–nitro-2-imidazolidinimine) was applied at 1 g per pot after planting to control sucking insect pests. Pots were hand watered to insure moisture was not limiting to growth. To eliminate the potential of fungal disease, plants were sprayed 20 d after planting and again when flag leaves were fully emerged with a foliar fungicide (Propiconazole: 1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]Methyl]-1h-1,2,4-triazole) at the labeled rate. Plants were maintained under optimum temperature (24/14°C, daytime maximum/ nighttime minimum) conditions from planting to harvest at a photoperiod of 16 h.

Moisture and Defoliation Treatments

The two independent variables, or treatments, for this experiment were moisture and defoliation. After anthesis, the 32 pots were divided into 4 replications of two moisture treatments and four defoliation treatments. The two moisture treatments were: cessation of watering (limited water) and a well-watered control (irrigated). Moisture treatments were maintained for the remainder of the experiment. Within each moisture treatment, pots were divided randomly into 4 defoliation treatments: a control of no leaves removed; all leaves removed; all leaves except the flag leaf removed; and only the flag leaf removed. These defoliation treatments were the same for all experimental rounds.

Harvest

There were nine dependent variables examined in this experiment in relation to each treatment (moisture and defoliation). These dependent variables were: leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seeds per spike, and harvest index. The whole above-ground plant biomass was harvested for all experiments and replications. The biomass was weighed and separated into three components: leaves below the collar, spikes above the peduncle, and the remaining stems. All biomass components were weighed. Spikes from all pots were counted, hand threshed, and seeds were counted and weighed. Three more yield components were calculated from observed data: seed yield divided by number of seeds for single seed weight; seed yield divided by spike number for seed yield per spike; seed yield divided by total biomass for harvest index. All biomass and yield components were reported on a per pot basis (sum of 5 plants per pot).

Experimental Design and Analyses

The experiment was setup as a randomized complete block design with a spilt-plot treatment arrangement. The whole-plot treatment was water regime and the sub-plot treatment was defoliation. Data were analyzed with correlations, analysis of variance (ANOVA), Fisher's protected least significant difference (LSD), and multiple linear regression; using the CORR, MIXED, and REG procedures in SAS 9.2 (SAS Institute, Cary, NC). Experimental round, replication nested within round, and moisture x replication nested within round interaction were used as random effects. Fisher's protected LSDs were calculated using the SAS macro pdmix800 at an alpha of 0.05 and 0.1 (Saxton, 1998). Multiple linear regressions were fit, by water regime and defoliation, to the models that had the highest R^2, the lowest root mean square error (RMSE), and the lowest Mallow's C_p, using a stepwise model-selection method. From the ANOVA three dependent variables were selected, graphed, and analyzed to estimate the contribution of leaves and stem to seed yield, single seed weight, and seed yield per spike. Seed yield per spike was selected to help remove any compensation to seed yield from tillering. Stem contributions are the percent of final stem weight divided by the no leaf removed control treatment. Losses were calculated as reductions in yield or yield components, caused by removing leaves; either all the leaves except flag or only the flag leaf removed treatments, as compared to the control. The contribution of the flag leaf and all but the flag leaf treatments, are calculated as the difference between all leaves removed, divided by the no leaf removed control. All units are expressed as a percent of the no leaf removed control which is assumed to be 100%.

Results

Experimental conditions were similar for all three experimental rounds. This was made possible by using high pressure sodium, high intensity discharge, lamps for supplemental light and growing the experiments during the same season, early spring, each year to help avoid high temperatures. The average daytime maximum and nighttime minimum temperatures were 24°C and 18°C, respectively. Canopy level photosynthetic photon flux density was measured at noon three times during each experimental round (early growth, flowering, and late seed-fill) and averaged 1200 μmol m^{-2} s^{-1}. Of the three experimental rounds the first round had the highest yields, while the second had the lowest yields, and the third round resulted in seed yields between the first and second. These differences in seed yield for each experimental round resulted in higher variability for seed yield compared to the other dependent variables. The other dependent variables didn't have as much variability. In each experimental round there was a difference in complete senescence between the moisture limited and the irrigated (Data not shown). The range in time of senescence between moisture treatments was 13-19 d with the irrigated treatments maturing an average 16 d after the moisture-limited treatments senesced. The defoliation treatments did not cause any difference in maturity.

Analysis of Variance

Analysis of variance and mean separation (LSD) were used to quantify whether treatments and least square means were significantly different because of the treatment effects or random chance (Tables 3-1 and 3-2). Of the nine dependent variables (leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seed yield per spike, sand harvest index), only six were affected by one or both of the treatments (moisture and defoliation). These six affected variables were leaf weight, total biomass, seed yield, single seed weight, seed yield per spike, and harvest index.

Of these six affected variables, only two, seed yield and single seed weight, were significant in both treatments (moisture and defoliation) and their interactions at an $Pr<0.05$ (Tables 3-1 and 3-2). Leaf weight was only significant for the defoliation treatment, where the weight differences were caused by the treatment. Total biomass was significantly different in both the moisture and defoliation treatments. In the limited moisture regime, the total biomass was significantly lower than in the irrigated regime. Total biomass for all leaves removed and all leaves removed except the flag leaf treatments, were similar and significantly different from the control and only the flag leaf removed treatments, which were also similar. Seed yield was significantly different for both treatments (water and defoliation) and their interactions. Seed yield was higher in the irrigated treatments compared to the limited water treatments. Within the irrigated water treatments, there were no significant differences among defoliation treatments, except when all leaves were removed, which resulted in a significantly lower seed yield. A similar trend was noted within moisture regimes and defoliation interactions, with the irrigated defoliation treatments having higher seed yields than the limited moisture treatments. The ANOVA wasn't able to resolve the small numerical differences among defoliation treatment means for seed yield. Single seed weight was also significantly different in both water regimes and defoliation treatments and their interactions. Single seed weight had the same trend as seed yield with the irrigated treatment having almost twice the single seed weight (29.98 mg seed^{-1}) as the limited moisture treatment (15.06 mg seed^{-1}). The same trend continued with the defoliation and the moisture treatment x defoliation interaction, except the ANOVA seemed to be better able to resolve the mean differences. This can be seen in the defoliation treatments where the control treatment (no leaves removed and irrigated moisture regime) had the highest and a significantly different single seed weight (Tables 3-1 and 3-2). The high control treatment single seed weight was followed by the only the flag leaf removed and only the flag leaf remaining treatments, which were not significantly different from each other. The all leaves removed treatment had the lowest single seed weight and was significantly different from the other irrigated treatments. With the interaction of moisture regime and defoliation treatments, all irrigated regimes were significantly different and the defoliation treatments were ranked the same as the defoliation main effect. Seed yield per head was analyzed to differentiate the compensatory effect of the other tillers. It was significant in both the water and defoliation treatments which were similar with seed yield and single seed weights. Only if the alpha is raised from 0.05 to 0.1 does the water regime x defoliation interaction become significant. When significant, the water regime x defoliation interaction has all limited moisture defoliations to be the same (no significant difference). Within the water treatment x defoliation interaction the irrigated control was the highest. This is followed by only the flag leaf removed and the flag leaf remaining treatments, which were similar to each other (no significant differences), but flag leaf removed was significantly different from the control. Lastly, harvest index was only significantly different in the moisture regime main effect, with the irrigated treatment having a higher harvest index (0.36) compared to the limited moisture treatment (0.23).

Correlations of Physiological and Yield Traits

Correlations for all variables were created to observe underlying associations and relationships (Table 3-3). Underlying associations and relationships were of particular interest for the relationships the ANOVA could not resolve, due to the wide range of values across the three experiments and thus, high variability of the treatment means. In the combined correlations, the highest correlations were observed between total biomass by stem weight and total biomass by seed yield, both with an r value of 0.94. Seed yield per spike also had high correlations (0.90) with both seed yield and single seed weight. Stem weight, although not significant in the ANOVA, had high correlations (above r=0.80) with spike number, seed yield, and seed number. Six more correlations that had an r value above 0.8 were: total biomass by spike number and seed number; seed number by spike number; seed yield by seed number and single seed weight; and single seed weight by harvest index. Leaf weight also had six significant correlations, that ranged between r=0.40 (single seed weight) and r=0.76 (total biomass) with seed yield being in the middle with r=0.56.

Due to the observed correlations in Table 3-3, another correlation table was made (Table 3-4). This new table was created to focus only on seed yield and single seed weight across the water regime and defoliation main effects. Seed yield and single seed weight were correlated against all the other variables. There were two main observations from this table: the changes in correlation between irrigation and defoliation, and the relationship of leaf and stem weight to seed yield and single seed weight. When compared across moisture regime main effect, the differences of several correlation combinations stand out. They were: seed yield by stem weight (limited moisture – irrigated of r=0.22) and single seed weight (r=-0.18); and single seed weight by spike number (r=-0.19); and seed number (r=-0.38). Completing a similar analysis for defoliation, except examining the difference between the control and treatments with leaves removed, more correlation combinations were observed. For all leaves removed minus the control, the five correlation combinations that stood out were: seed yield by stem weight (r=0.14), spike number (r=0.23), and harvest index (r=0.14); and single seed weight by stem weight (r=0.18) and spike number (r=0.30). For only flag leaf left minus the control, the correlation differences of note were: seed yield by leaf weight (r=-0.22), stem weight (r=0.16), and spike number (r=0.19); and single seed weight by stem weight (r=0.16) and spike number (r=0.21). Examining the only flag leaf removed minus control treatment, only single seed weight demonstrated noteworthy correlation changes between treatments and they were: stem weight (r=0.14) and seed number (r=0.20).

There are some interesting relationships for the changes in correlations between seed yield and single seed weight by leaf and stem weight by moisture regime and defoliation treatment. First, with the moisture regime, correlations increased from limited moisture to irrigated regimes with seed yield correlations going from r=0.64 and r=0.71 to r=0.73 and r=0.94, for leaf and stem weights, respectively. The single seed weights also increased, but to a smaller extent. When looking at the relationship between seed yield, single seed weights, and stem weight, the highest correlations were found in the treatments with the least leaves. All leaves removed and the all leaves removed except flag left both had seed yield and stem weight correlations in the 0.90s, while single seed weights correlations were in the 0.60s. The correlation between seed yield, single seed weight, and stem weight decreased as more leaves were left on the plant with the control having the lowest at 0.77 and 0.44, for seed yield and single seed weight by stem weight, respectively. The correlations of seed yield and single seed weight to leaf weight seem to be inverse to the stem weight. With leaf weight, the highest correlations to seed yield and single seed weights were in the control and decreased as the leaves were removed.

Multiple Linear Regressions

Multiple linear regressions were performed to quantify if the relationships observed with the correlations had any causal effect on seed yield and single seed weight in this experiment (Table 3-5). Using the stepwise model selection method, parameters were fit to the best model for seed yield and single seed weight by moisture and defoliation treatments. The parameters used were leaf weight, stem weight, single seed weight (seed yield only), seed number, and harvest index. The other variables weren't included because of multicollinearity, tested by the variance inflation factor (VIF) and Mallow's C_p (Data not shown). The first model generated was for the overall experiment, where all data were combined. In this model, using seed yield as the dependent variable, stem weight, single seed weight, and seed number were chosen, with an R^2 of 0.94. Single seed weight had a different model with leaf weight, stem weight, seed number, and harvest index chosen and an R^2 of 0.89. For the seed yield and single seed weight models comparing water regimes, the models' fit were almost the exact same. The only differences were that in the seed yield model, harvest index was not included in the irrigated model. For the single seed weight model, the only difference was that seed number was added to the irrigation model. Both models have a high R^2 in both moisture regimes. For the defoliation models with seed yield, it was observed that stem weight was only selected in the model when the treatments modeled had the least amount of leaves (i.e. all leaves removed and only the flag leaf remaining). Oddly, leaf weight was only used in the model by the flag leaf remaining and flag leaf removed treatments. Single seed weight and seed number were used in all seed yield models. For single seed weight, stem weight was used in all the models but leaf weight was only used in models involving the control and the flag leaf remaining treatments. Seed number and harvest index were used in all single seed weight models. All the defoliation models had high R^2 values that ranged from 0.91 to 0.98.

Contribution of Leaves and Stem to Yield

The contribution of leaves or stems to yield is an estimate of the potential translocation of carbon from leaves and stem based on the differences in weight at maturity (Figure 3-1 and Table 3-6). The no leaves removed and all leaves removed treatments were used as the maximum and minimum potential yield, respectively. The all leaves removed is used as the estimate for stem contribution to yield. In the moisture limited treatment, the potential contribution to seed yield, single seed weight, and seed yield per head were reduced in all defoliation treatments to the same level as the all leaves removed treatment. In the moisture limited treatment, the stem contributed 95-98% to the final yield. In the irrigated treatment the contribution from the stem was smaller at 65% for seed yield and single seed weight, and 69% for seed yield per spike. The yield potential lost, the difference between the control and leaf removal, in the irrigated treatment, ranged from 9-16% when all leaves except the flag leaf were left and 5-12% lost when only the flag leaf was removed. The flag leaf contributions (the difference from the stem contribution) in the moisture limited treatment, for seed yield, single seed weight, and seed yield per spike, were 4%, 1%, and 11%, respectively. In the irrigated treatment the flag leaf contributed 25%, 19%, and 15% for seed yield, single seed weight, and seed yield per spike, respectively. When the flag leaf was removed the remaining leaves contributed 4% of seed yield, 13% of single seed weight, and 9% of seed yield per spike, for the moisture limited and 24%, 23%, and 26% to seed yield, single seed weight, and seed yield per spike, respectively for the irrigated treatment.

Discussion

Almost all irrigated treatments had higher values for the dependent variables than the moisture limited treatments. Six of the nine dependent variables were affected by one or both of the treatments. Some, like leaf weight, were only significant because of the defoliation treatment of removing leaves. Three dependent variables were significant in both treatments (moisture and defoliation) and their interactions. They were seed yield, single seed weight, and seed yield per spike (interaction was significant at an alpha of 0.10).

Leaf and stem weight did not seem to be affected by any of the treatments. This is interesting because they were highly correlated and highly selected in the regression models. This leads to the idea they are important to both seed yield and single seed weight. Total biomass was affected by the water treatment. The total biomass difference seems to mostly be due to the difference in seed yield with these variables having one of the highest correlations (r=0.93). Others have found total biomass to be highly correlated with seed yield (Frederick and Bauer, 1999), but not necessarily in drought conditions. Seed yield was higher in the irrigated water treatments compared to the limited water treatments. The seed yield difference was caused primarily by the single seed weight, which was almost twice the weight in the irrigated treatment as it was in the moisture limited treatment (Wardlaw and Willenbrink, 2000; Ahmadi and Baker, 2001). All other yield components were not as affected by the imposed stresses. This response was to be expected because all other yield components are formed before seed set (time of water cessation) and the only remaining yield component to be developed was single seed weight (Ahmadi and Baker, 2001; Ji et al., 2010). With the water and defoliation interaction, most of the yield and yield components had very small differences. Only a few of the moisture limited x defoliation treatments were significantly different from the all leaves removed treatment. It would seem the moisture stress was a greater limitation to yield and yield components than any damage to the source size. Possibly the biggest reason for this was the faster maturity observed in the moisture limited treatment (Siddique et al., 1989; Yang et al., 2001; Shah and Paulsen, 2003). The moisture limited treatment caused plants to fully senesce an average of 16 d before the irrigation treatment. That is potentially a loss of 16-d of seed filling. This can be observed in the aforementioned single seed weights. Looking at seed yield in the irrigated x defoliation treatment interaction, all the defoliations were virtually the same, except when all the leaves were removed. There are two possible reasons for the three irrigated x defoliation treatments having the same seed yield. One reason is that they are different, but the ANOVA and mean separation could not differentiate them due to the variability of the combined experiments. The more likely reason, however could be due to the ability of wheat to compensate through other means, such as, increased photosynthesis (awns or glumes) or some sort of compensation of the other tillers (Evans and Wardlaw, 1996). Photosynthesis was not measured, so it is not known if it increased or if awns/glumes contributed, but it is a possibility. To try to control for the affect of tillers (although it was not significantly different), seed yield per spike was used. This seemed to work as intended and the irrigation x defoliation treatment means separated a little more.

When comparing correlations across variables and water regime, it was observed that some variables had higher correlations in irrigated and vice versa. Leaf weight, stem weight, total biomass, and spike number had correlations with seed yield that all increased from the moisture limited to the irrigated treatments. Stem weight had the highest increase in correlation with seed yield, from moisture limited to the irrigated treatments. This would lead one to think stem weight was important for seed yield; but, in this case, it appeared to be more important in the irrigated treatment. The correlations of seed yield by seed number, single seed weight, and harvest index all did the opposite and decreased from the moisture limited treatment to the irrigated treatment. The same trend was observed for single seed weights, where seed number had the largest observed decrease in correlation going from the moisture limited treatment to the irrigated treatment. Seed number's correlations to single seed weight were nearly cut in half. This could mean these yield components are what maintained seed yield and single seed weight at their final maturity levels in the moisture limited treatment. When the stress was not present, the seed yield and single seed weight were increased by other yield components.

Another interesting relationship was observed within the correlations. This relationship was the changes in correlations of seed yield and single seed weight to leaf weight and stem weight when compared across the defoliation treatments. The correlation between seed yield and stem weight decreased as the number of leaves increased. The opposite relationship was observed with leaf weights. As the total leaf weight increased, so did the correlations with seed yield. The response of single seed weight was the same, but to a lower magnitude. Both of these responses make sense. This is because the lower the leaf weight (fewer leaves), the more the developing seed will need stored reserves from the stem for energy and resources. As the number of leaves increase along with the increase in the leaf weight, the plant may be able to rely more on photosynthesis than the stored reserves (Wardlaw, 1990; Evans and Wardlaw, 1996). Others have found that photosynthesis during seed-fill will result in higher yields than stem remobilization (Cook and Evans, 1978; Yang et al., 2001; Shah and Paulsen, 2003). If this is true, it would explain the change in source preference.

Multiple linear regressions were performed to quantify if the relationships observed with the correlations have any causal effect on seed yield and single seed weight in this experiment (Table 3-5). Overall, seed number was the most selected parameter. Seed number was selected in all but one of the six models produced by stepwise selection. This is interesting, because like stem and leaf weight, seed number was not affected by the imposed treatments, according to the ANOVA. However, it was still very important when modeling both seed yield and single seed weights. Seed number was most likely what gave the baseline yield and the other yield components just added to it. Stem weight was the next most selected parameter. It was selected in the overall model, both the irrigation models, and two of the four defoliation models. The only defoliation treatments it was not selected in were the two treatments with the most leaves remaining. Single seed weight was also important as it was selected in every seed yield model. After seed number, single seed weight was what increased seed yield (Shah and Paulsen, 2003; Ji et al., 2010; Madani, 2010).

Based off the estimations of leaf and stem contributions to yield, the stem supplied 95-98% of the yield potential in the moisture limited treatment and 65-69% of the yield in irrigated (Table 3-6 and Figure 3-1). Others have found stem contributions to be similar (Evans et al., 1975; Yang et al., 2001; Madani, 2010) or lower (Cook and Evans, 1978; Papakosta and Gagianas, 1991) than this, but very few sources found stem contributions in non-stressed conditions to be as high. It was not believed that the irrigated treatments were stressed. Seri 82 is thought to be drought tolerant and this may have some influence as drought tolerant genotypes may favor remobilizing stem reserves.

Although not conclusive, in all irrigated treatments the spike was the first organ to mature followed by the leaves. The contribution of the flag leaf and all the leaves except the flag leaf was not as high as others have found (Cook and Evans, 1978; Madani, 2010). Also of interest was that the flag leaf alone could contribute to seed yield as much as all other leaves combined (when only the flag leaf was removed). Whether this is due to proximity to the sink or due to an increased productivity of the flag leaf is not known.

Conclusions

The cessation of water after seed-set significantly reduced total biomass, seed yield, single seed weight, seed yield per spike, and harvest index. Because the stress was imposed after seed set, seed number and spike number were unaffected. Defoliation affected the source-sink relationship by reducing the source strength of the leaves. This caused the stem to contribute more to overall yield. The defoliation also caused the remaining leaves to compensate for the removed leaves. It was found that with the spring wheat genotype Seri 82, the stored reserves in the stem contributed to yield the most in severe stress and also contributed a substantial amount when no stress was present. In addition to the stem contributions, when the flag leaf was all that remains it contributes as much to seed yield as all other leaves on the plant when the flag leaf is the only leaf removed. So the flag leaf contributes as much to seed yield as all the other leaves on the plant. But even at that level, in this experiment, the flag leaf only contributed about 25% percent of the total seed yield in ideal conditions.

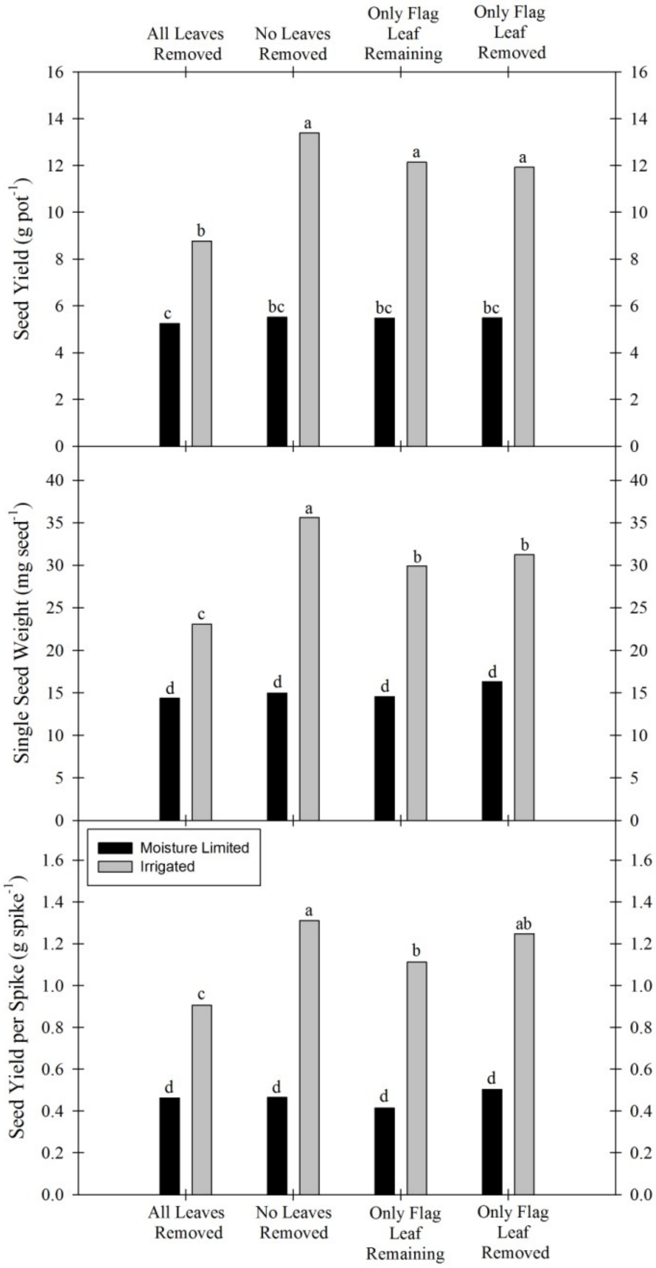

Figure 3-1. Changes in the weight of seed yield, single seed weight, and seed yield per spike, for the interaction of water and defoliation treatments. The water treatment was two levels, cessation of watering and irrigated. The defoliation treatment was four levels, all leaves removed, a no leaf removed control, all leaves removed except the flag leaf, and only the flag leaf removed. Letters denote the rank of means separated by LSD at an alpha of 0.05 for seed yield and single seed weight and 0.1 for seed yield per spike.

Table 3-1. Analysis of variance and mean separation (Fisher's protected LSDs), for leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seeds per head, and harvest index, for water regime, defoliation, and water regime x defoliation interaction.

Analysis of Variance and Treatment LSMeans	Leaf Weight (g pot^{-1})	Stem Weight (g pot^{-1})	Total Biomass (g pot^{-1})	Spike Number (spikes pot^{-1})	Seed Yield (g pot^{-1})	Seed Number (seeds pot^{-1})	Single Seed Weight (mg seed^{-1})	Seed Yield Spike^{-1}	Harvest Index
ANOVA					**Pr > F**				
Water Regime	0.2250	0.1222	0.0013	0.8840	0.0003	0.6528	<.0001	0.020	0.0010
Defoliation	<.0001	0.8566	<.0001	0.4575	0.0141	0.9035	0.0002	0.047	0.2681
Water Regime x Defoliation	0.6174	0.8682	0.8383	0.5720	0.0371	0.8029	0.0016	0.099	0.3761
Water Regime					**LSMean**				
No Water	4.21	6.94	21.64 b	9	5.43 b	216	15.06 b	0.46 b	0.231 b
Irrigated	3.46	8.07	28.57 a	9	11.56 a	230	29.96 a	1.14 a	0.359 a
LSD	***-***	***-***	***3.833***	***-***	***2.861***	***-***	***5.501***	***0.416***	***0.069***
Defoliation					**LSMean**				
All Leaves Removed	0.00 c	7.31	19.41 c	9	7.01 b	218	18.72 c	0.68 b	0.305
No Leaves Removed	6.49 a	7.69	29.28 a	9	9.45 a	242	25.29 a	0.89 a	0.284
Flag Leaf Left	3.21 b	7.45	24.51 b	9	8.81 a	211	22.25 b	0.76 ab	0.308
Flag Leaf Removed	5.82 a	7.57	27.23 ab	9	8.71 a	222	23.79 ab	0.88 a	0.282
LSD	***1.720***	***-***	***3.107***	***-***	***1.508***	***-***	***1.508***	***0.164***	***-***

All LSD are significant at an alpha of 0.05, except * LSD significant at an alpha of 0.1, - non-significant F-test

Table 3-2. Analysis of variance and mean separation, for leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seeds per head, and harvest index, for water regime, defoliation, and water regime x defoliation interaction.

Treatment LSMeans Cont.	Leaf Weight (g pot^{-1})	Stem Weight (g pot^{-1})	Total Biomass (g pot^{-1})	Spike Number (spikes pot^{-1})	Seed Yield (g pot^{-1})	Seed Number (seeds pot^{-1})	Single Seed Weight (mg seed^{-1})	Seed Yield Spike^{-1}	Harvest Index
No Water					**LSMean**				
All Leaves Removed	0.00	6.95	16.71	8	5.25 c	193	14.36 d	0.46 d	0.258
No Leaves Removed	6.70	7.12	24.99	9	5.51 bc	237	14.98 d	0.47 d	0.208
Flag Leaf Left	4.28	6.85	21.72	10	5.48 bc	228	14.57 d	0.41 d	0.240
Flag Leaf Removed	6.03	6.83	23.15	9	5.49 bc	206	16.31 d	0.50 d	0.215
Irrigated									
All Leaves Removed	0.00	7.67	22.10	9	8.77 b	242	23.08 c	0.91 c	0.353
No Leaves Removed	6.27	8.26	33.57	9	13.39 a	248	35.59 a	1.31 a	0.360
Flag Leaf Left	2.15	8.05	27.30	9	12.14 a	193	29.92 b	1.11 b	0.376
Flag Leaf Removed	5.61	8.31	31.32	9	11.93 a	237	31.24 b	1.25 ab	0.349
LSD	**-**	**-**	**-**	**-**	***2.795***	**-**	***5.348***	***0.213****	**-**

All LSD are significant at an alpha of 0.05, except * LSD significant at an alpha of 0.1, - non-significant F-test

Table 3-3. Pearson Correlation Coefficients of leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seeds per spike, and harvest index; of water regime and defoliation combined.

Correlations	**Leaf Weight**	**Stem Weight**	**Total Biomass**	**Spike Number**	**Seed Yield**	**Seed Number**	**Single Seed Weight**	**Seed Yield Spike^{-1}**	**Harvest Index**
Leaf Weight	1								
Stem Weight	0.62	1							
Total Biomass	0.76	0.94	1						
Spike Number	0.62	0.86	0.84	1					
Seed Yield	0.56	0.85	0.94	0.72	1				
Seed Number	0.55	0.86	0.88	0.84	0.85	1			
Single Seed Weight	0.40	0.54	0.68	0.41	0.81	0.49	1		
Seed Yield Spike^{-1}	0.45	0.64	0.79	0.45	0.91	0.69	0.90	1	
Harvest Index	*0.08*	0.34	0.47	0.30	0.67	0.50	0.83	0.82	1

All correlations significant at an alpha of 0.05, except red italic, denotes non-significant correlations

Table 3-4. Pearson Correlation Coefficients of seed yield and single seed weight versus leaf weight, stem weight, total biomass, spike number, seed yield, seed number, single seed weight, seeds per spike, and harvest index by water regime and defoliation.

Correlations	**Leaf Weight**	**Stem Weight**	**Total Biomass**	**Spike Number**	**Seed Yield**	**Seed Number**	**Single Seed Weight**	**Seed Yield Spike^{-1}**	**Harvest Index**
Moisture Limited									
Seed Yield	0.64	0.71	0.90	0.79	1	0.94	0.94	0.91	0.68
Single Seed Weight	0.56	0.54	0.78	0.66	0.94	0.81	1	0.90	0.79
Irrigated									
Seed Yield	0.73	0.94	0.98	0.83	1	0.86	0.76	0.91	0.62
Single Seed Weight	0.60	0.60	0.71	0.46	0.76	0.43	1	0.94	0.76
All Leaves Removed									
Seed Yield	0.00	0.91	0.99	0.83	1	0.87	0.75	0.95	0.82
Single Seed Weight	0.00	0.62	0.72	0.58	0.75	0.41	1	0.80	0.83
No Leaves Removed									
Seed Yield	0.73	0.77	0.92	0.61	1	0.83	0.82	0.94	0.68
Single Seed Weight	0.39	0.44	0.63	*0.27*	0.82	0.47	1	0.89	0.86
Flag Leaf Left									
Seed Yield	0.50	0.93	0.94	0.80	1	0.91	0.78	0.92	0.66
Single Seed Weight	*0.24*	0.60	0.64	0.49	0.78	0.55	1	0.89	0.89
Flag Leaf Removed									
Seed Yield	0.73	0.82	0.93	0.65	1	0.91	0.87	0.88	0.64
Single Seed Weight	0.50	0.58	0.73	0.38	0.87	0.66	1	0.95	0.87

Correlation significant at an alpha of 0.05; except Green (p-value >0.05<0.1) and *Red Italics* which are not significant

Table 3-5. Fit statistics and parameter estimates for multiple linear regression of seed yield and single seed weights; by leaf weight, stem weight, single seed weight (seed yield only), seed number, and harvest index; for overall experiment, water regime, and defoliation; using stepwise model selection.

Treatment	Variable	R^2	Mallow's C_p	Intercept	Leaf Weight	Stem Weight	Single Seed Weight	Seed Number	Harvest Index
				Parameter Estimate					
Overall	Seed Yield	0.937	4.0	-7.937	-	0.427	0.331	0.018	-
	Single Seed Weight	0.894	5.0	-9.903	0.825	1.624	-	-0.040	102.4
Limited Moisture	Seed Yield	0.990	6.0	-3.168	-0.149	-0.339	0.566	0.026	-20.6
	Single Seed Weight	0.895	3.2	-1.489	0.554	0.209	-	-	57.1
Irrigated	Seed Yield	0.967	5.2	-8.428	0.235	0.706	0.259	0.017	-
	Single Seed Weight	0.878	5.0	-7.882	1.092	1.578	-	-0.038	95.9
All Leaves Removed	Seed Yield	0.977	3.0	-6.244	-	0.507	0.275	0.014	-
	Single Seed Weight	0.910	4.0	-8.888	-	1.448	-	-0.030	88.8
No Leaves Removed	Seed Yield	0.929	1.1	-9.882	-	-	0.361	0.031	-
	Single Seed Weight	0.912	5.0	-10.100	2.121	2.611	-	-0.107	128.4
Flag Leaf Left	Seed Yield	0.978	4.0	-8.052	-0.537	0.948	0.212	0.021	-
	Single Seed Weight	0.932	5.0	-9.376	0.463	2.649	-	-0.055	92.0
Flag Leaf Removed	Seed Yield	0.980	6.0	-5.078	-0.538	-	0.560	0.041	-31.2
	Single Seed Weight	0.937	3.1	-10.588	-	1.881	-	-0.025	98.6

Table 3-6. Contribution of the stem and contribution and losses of the flag leaf and all leaves except the flag leaf in limited moisture and fully irrigated treatments. Stem contributions are the percent of final stem weight divided by the no leaf removed control. Losses are, loss- leaves except flag and loss-flag removed; the losses caused by removing all leaves except the flag leaf and only the flag leaf, respectively. Contribution of the flag and all but flag are the difference from all leaves removed divided by the no leaf removed control. All units are expressed as percent of the no leaf removed control.

Contributions and Losses From Stem and Leaves	Seed Yield (g pot^{-1})	Single Seed Weight (mg seed^{-1})	Seed Yield Spike^{-1}
Moisture Limited		Percent	
Stem Contribution	95.28	95.86	97.87
Loss -Leaves Except Flag	0.54	2.74	12.77
Loss- Flag Removed	0.36	-8.88	-6.38
Flag Leaf Contribution	4.17	1.40	10.64
All but Flag Contribution	4.36	13.02	8.51
Irrigated			
Stem Contribution	65.50	64.85	69.47
Loss -Leaves Except Flag	9.34	15.93	15.27
Loss- Flag Leaf Removed	10.90	12.22	4.58
Flag Leaf Contribution	25.17	19.22	15.27
All but Flag Contribution	23.60	22.93	25.95

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Chapter 4 - The Effect of High Temperature Stress on the Seed-filling Rate and Duration of Three Winter Wheat (*Triticum aestivum* L.) Cultivars [Armour, Jagger, and Karl 92].

In a future of unpredictable climate and an increase in human population, stable production of food is paramount. In arid and semi-arid regions of the world food supply is already at risk, due to high temperatures and low rainfall. A changing or more variable climate may also cause an increased risk of food security (IPCC, 2013; FAO, 2012).

The Food and Agriculture Organization stated in 2012 that wheat (*Triticum aestivum* L.) was the third most important crop worldwide behind maize (*Zea mays* L.) and rice (*Oryza sativa* L.). It was estimated that 670 million Mg of wheat were produced in 2012 with an average yield of 3.2 Mg ha^{-1} (FAO, 2012). Wheat is one of the major crops grown in the arid and semi-arid regions of the world (FAO, 2012) and increasing temperature may cause large losses in wheat yield potential. Temperature increase and/or timing of high temperature stress is problematic for wheat production (Al-Khatib and Paulsen, 1990; Ortiz et al., 2008; Semenov and Shewry, 2011).

Air temperatures above 32ºC can affect wheat yield in different ways depending upon timing and magnitude of the high temperature stress in relation to the plants' growth stage (Stone and Nicolas, 1994; Gibson and Paulsen, 1999; Al-Khatib and Paulsen, 1984). Wheat has four sensitive growth stages to high temperature stress, each is linked to the formation of a different yield component. These times are in early seedling development or right after planting (emergence), just prior to stem elongation (panicle initiation), boot through anthesis, and the seed-filling period after seed set. High temperature stress at these times affects yield by reducing plant population (plants ha^{-1}), panicle size (potential seeds ha^{-1}) , seed number (seeds ha^{-1}), and individual seed weight (weight seed^{-1}), respectively (Saini and Aspinall, 1982; Stone and Nicolas, 1995; Gibson and Paulsen, 1999; Kansas Wheat Production Handbook, 1997). Each of these timings is more or less important depending on the wheat growing region. For example, in the North American Great Plains region high temperature stress at anthesis and during seed fill are the two largest causes of yield loss. In some areas and years this loss is similar, if not greater than losses due to water stress (Gibson and Paulsen, 1999; Shah and Paulsen, 2003). Although high temperature stress at anthesis can be very damaging to yield due to reduction in seeds ha^{-1}, post-anthesis high temperature stress is just as important in many of the world's regions (Paulsen, 1994; Wardlaw and Moncur, 1995).

Post-anthesis high temperature stress is often overlooked, as it is not dramatic, because there is an increase in the senescence rate or perceived senescence, during this period, which often compounds symptoms of high temperature stress (Al-Khatib and Paulsen, 1984; Ristic et al., 2007; Farooq et al., 2011). Major yield damage of post-anthesis high temperature stress is caused by a decline in the seed-filling period. Plants can partially overcome the shorter duration by increasing the rate at which photosynthates and stored carbon are translocated to the seed (Stone and Nicolas, 1994; Shah and Paulsen, 2003).

Little research has looked into post-anthesis high temperature stress in winter wheat (Al-Khatib and Paulsen, 1990; Stone and Nicolas, 1994; Gibson and Paulsen, 1999; Ristic et al., 2007). A vast majority of the research is on spring wheat and durum, which is understandable since they are the major forms of wheat grown world wide

(Nicolas et al., 1984; Tashiro and Wardlaw, 1990; Schapendonk et al., 2007). In most of the research temperature treatments tended to be at or below 32°C and/or episodic in nature (i.e. a 3-10 d high temperature stress) (Nicolas et al., 1984; Wardlaw and Moncur, 1995; Stone and Nicolas, 1998; Dias and Lidon, 2009). While lower temperatures and the episodic nature of treatments work well for many regions, the North American Great Plains suffer from terminal post-anthesis high temperature stress at greater than 35°C (Harding et al., 1990; Al-Khatib and Paulsen, 1984; Ristic et al., 2007). Another missing component in past research is harvest intervals on a finer timescale (10-15 times), where the majority of research has been on a coarser interval (4-8 times) (Blum et al., 1994; Fokar et al., 1998; Stone and Nicolas, 1998; Shah and Paulsen, 2003). This may have the potential to capture smaller changes and be more accurate in determining seed-filling rates and durations. The final gap is that many studies removed sub-tillers or only used main tillers, in order to utilize the largest spike (Nicolas et al., 1984; Stone and Nicolas, 1995; Prasad et al., 2008). This does not completely replicate field conditions where all tillers would be subjected to high temperature stress and the average seed weight of all tillers would be the source of total yield. A more holistic approach should at least be attempted. In order to fill some of these research gaps this experiment was designed to satisfy the following objectives:

Objectives

1. Quantify the effects of terminal post-anthesis, high temperature stress on yield and yield components of three cultivars.

2. Quantify and observe any varietal differences in seed-filling rate and duration due to high temperature stress on a finer time interval in winter wheat cultivars.

Materials and Methods

Experimental Design and Treatment Structure

The study was conducted in controlled environments during 2012 at the Department of Agronomy, Kansas State University, Manhattan, KS. The experiment was a randomized complete block design with a split-split-plot treatment arrangement. The whole plot treatment was two temperature treatments, one per growth chamber. The sub-plot was three winter wheat cultivars. The sub-sub-plot was 13 harvest times during seed fill. Harvest time intervals were replicated 3 times for each cultivar. Due to the large number of pots and potential spatial variations within the growth chambers replications were blocked perpendicular to the length of the chamber. The average of two pots was considered one experimental unit to insure adequate amounts of seed and to help further reduce potential spatial variability within the growth chambers.

Plant Culture

Winter wheat cultivars, 'Armour' (WestBred, Bozeman, MT) , 'Jagger', and 'Karl 92' (Kansas Agricultural Experiment Station, Manhattan, KS) were planted in 2.7-L, 11x11x22 cm (length x width x height, respectively) rectangular pots containing 1 kg of Metro-mix 360 (Hummert International, Topeka, KS). Five seeds were planted in each pot and thinned to 3 plants after vernalization. Pots were hand watered to insure moisture was not limiting to growth. Plants were fertilized with 4 g of Osmocote (controlled-release fertilizer, 14:14:14% N:P_2O_5:K_2O, respectively; Hummert International, Topeka, KS), applied at the time of sowing. To eliminate the potential of fungal disease, plants were sprayed after flag leaves were fully emerged with a foliar fungicide (Propiconazole: 1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]Methyl]-1h-1,2,4-triazole) at the labeled rate.

Growth Chambers

The four growth chambers (Conviron Model CMP 3244, Winnipeq, MB) were randomized to the two temperature treatments, an optimal temperature (OT) or a high temperature (HT). Inside each growth chamber pairs of pots were randomized to one of three varieties, and then one of 13 harvest times. After sowing, all four growth chambers were set to a vernalization temperature of 8.5°C with a 12-h photoperiod, relative humidity (RH) of 80%, and canopy level photosynthetic photon flux density (400-700 nm; PPFD) of 800 μmol m^{-2} s^{-1} provided by cool white fluorescent lamps (Phillips Lighting Co., Somerset, NJ, USA). After a period of 45-d the temperature in all four growth chambers was raised to 22/15°C (daytime maximum/nighttime minimum) with a 12-h photoperiod, RH of 80%, and PPFD was increased to 800 μmol m^{-2} s^{-1}. After 30-d of plant tillering and growth, flowering was initiated by increasing the photoperiod to 16-h and increasing the temperature to 25/18°C. Relative humidity and PPFD were maintained at 80% and 800 μmol m^{-2} s^{-1}, respectively.

Temperature Treatments

With the conclusion of anthesis and seed set (~80% of spikes) growth chambers were assigned one of two high temperature treatments; OT maintained at 25/18°C or HT increased to 35/28°C imposed as a high temperature stress. Photoperiod, RH, and PPFD were maintained at previously stated levels for the remainder of the experiment. All temperature regimes followed a diurnal plateau of 4 hours for daytime maximum, nighttime minimum, and the transition between. Air temperature and RH were continuously monitored at 10-min intervals in all growth chambers throughout the experiment using data loggers (HOBO, Model U14-001; Onset Computer Corporation, Bourne, MA).

Physiological Measurements

In order to quantify stress, two physiological measurements were taken every harvest on the pots reserved for the final harvest; chlorophyll content (chlorophyll index in SPAD units) and dark-adapted chlorophyll a fluorescence. Chlorophyll content was measured using a self-calibrating chlorophyll meter (Soil Plant Analytical Device, SPAD Model 502, Spectrum Technologies, Plainfield, IL). Three SPAD readings were taken on the flag leaf of one plant per pot and averaged. Chlorophyll a fluorescence was measured using a modulated fluorometer (OS30p, Opti-Sciences, Hudson, NH) on the flag leaf of one plant per pot. Instrument outputs of minimal fluorescence (Fo), maximum fluorescence (Fm), and photochemical efficiency of Photosystem II (Fv/Fm; ratio of variable to maximum fluorescence after dark adaptation, which represents maximum quantum yield of Photosystem II) were measured after a 30-min dark-adaptation of the leaves. For both SPAD and Fv/Fm the same leaves were marked and used for all measurements till final harvest.

Harvest

The whole plant biomass of all pots was harvested for all replications of the three cultivars at 0, 3, 5, 7, 9, 11, 15, 19, 23, 27, 31, 35, and 40-d (physiological maturity) intervals after imposed temperature treatments (days after treatment, DAT) for a total of 13 harvests. Each harvest and associated stress measurements were taken the same time of day. Total above ground biomass (total biomass) was dried at 40°C for 10-15 d until constant weight. Spikes from all three plants (and their tillers) per pot were counted, hand threshed, and seeds were counted and weighed. Harvest index (HI) was calculated from the ratio of seed yield to the weight of total biomass. Total number of seeds were divided by seed yield for average single seed weight. Total biomass, seed yield, and seed number were reported on a per plant basis (average of 3 plants per pot).

Data Analyses

Data were analyzed with ANOVA, Fisher's protected least significant difference (LSD), least-squares regression, and correlations using MIXED, REG, NLIN, and CORR procedures in SAS 9.1.3 (SAS Institute, Cary, NC). Total biomass, seed yield, HI, and seed weight of the final two harvests (35 and 40 DAT) were used in a separate analysis to estimate the effects of temperature (T), cultivar (C), and temperature cultivar interaction (T x C) on biomass, yield and yield components. Replication and temperature x replication were used as random effects. Fisher's protected LSDs were calculated using the SAS macro pdmix800 (Saxton, 1998). All regression responses were tested with linear, quadratic, and linear plateau models and were fit to the model that had the lowest RMSE, highest R^2, and best fit the bias for the response. Slope and infliction point of the plateau (as DAT) were further analyzed with ANOVA and LSMeans, to compare the rate (the slope, b) and duration (infliction point of plateau, x0). Replication and temperature x replication were used as random effects. Combined Pearson's Correlation Coefficients were computed for T, C, Fv/Fm, SPAD, total seed yield, average single seed weight, total biomass, and HI using the last two harvest, and the rate and duration Fv/Fm, SPAD, and seed-filling using all harvest.

Results

Temperature Control

Average day/night temperatures during vernalization for the OT treatments (growth chambers 1 and 3) were 8.5 ± 0.6 and 8.5 ± 0.7°C, for tillering were 22 ± 0.8/15 ± 0.6 and 22 ± 0.8/15 ± 0.6°C, and for maturation were 25 ± 0.7/18 ± 0.6 and 25 ± 0.7/18 ± 0.7°C. For the HT treatments (growth chambers 2 and 4) the average temperatures during vernalization were 8.5 ± 0.5 and 8.5 ± 0.6°C, for tillering were 22 ± 0.7/15 ± 0.7 and 22 ± 0.7/15 ± 0.6°C, and for maturity were 35 ± 0.8/28 ± 0.7 and 35 ± 0.8/28 ± 0.6°C. Relative humidity was similar for all day/night temperature regimes at 80 ± 15%. The growing conditions and uniformity within the growth chambers were all previously analyzed by Pradhan et al. (2012) and found to be consistent and uniform in all areas tested.

Yield Traits Analysis of Variance

Table 4-1 represents the results of the ANOVA for T, C, and T x C effects on total biomass, seed yield, seed number, HI, and seed weight for the final harvests. All traits were significantly affected by high temperature, except seed number. Cultivar had a significant effect on seed yield, seed number, HI, and seed weight, but not total biomass. None of the yield traits measured were significantly affected by the T x C interaction.

Maximum Quantum Efficiency and Chlorophyll Content

Maximum quantum efficiency of Photosystem II and chlorophyll content had rapid decreases in high temperatures (Figure 4-1). With the decline in Fv/Fm and SPAD both the rate and the duration until the start of decline where both only affected by T (Table 4-2). The rate of SPAD decrease being affected by T and the T x C interaction. Jagger had the slowest decline and Armour had the fastest, with 3.4 and 4.1 SPAD d^{-1}, respectively in the HT. Although the plateau models for HT and OT are different, the rates are similar with an average difference of only 0.34 SPAD d^{-1}. The biggest difference comes from the duration (plateau) before the decline which is longer in the OT and nonexistent in the HT. The changes in Fv/Fm and SPAD mirrored the plateau of seed yield and seed weight in both the high and optimum temperatures.

Seed Yield and Yield Components

Final seed yield was significantly affected by both T and C (Table 4-1). Seed yield under HT weighed less than the OT with 0.288 and 0.726 g $plant^{-1}$, respectively. Jagger had the highest seed yield $plant^{-1}$ with 0.666 g, followed by Armour with 0.540 g and Karl 92 with 0.308 g. Final seed numbers were only affected by C, with Jagger and Armour being the same with an average of 38.1 seeds plant^{-1} and almost twice that of Karl 92.

Seed weight was affected by both T and C. The high temperatures effect on seed weight was the same as all other traits but at a greater magnitude. The seed weight of the HT was less than half that of the OT with 9.5 and 21.8 mg, respectively. The effect of C on seed weight was similar to the effect of temperature on seed weight, with Jagger still having the highest seed weight of 18.3 mg, but with Armour and Karl 92 being the same but lower.

Seed Filling Rate and Duration

The rate of increase for seed weight was only affected by C with Jagger and Armour being greater than Karl 92 (Figure 4-2 and Table 4-2). Average seed weight was affected by C, T, and the C x T interaction. High temperature stress reduced the duration of seed-filling (duration until plateau) by 11-15 d compared to the OT with Karl 92 having the slowest rate but longest duration. Jagger and Armour had similar seed-filling rates but different durations (4 d difference) with Jagger being longer.

Total Biomass and Harvest Index

Total biomass was negatively affected by HT with a weight of 14.2 g opposed to 16.6 g for the OT (Table 4-1). Cultivar had no effect on total biomass as all C were similar in maturity and height. The rate of increasing total biomass remained constant, with maybe a slight downward trend (not significant), throughout the harvest timings in the high temperature but increased in the optimum (Figure 4-3). Total biomass of the cultivars responded to the HT in a similar fashion. Harvest Index was affected by both T and C. Harvest Index was highest in the OT with 0.19 vs. 0.10 for the HT. Jagger had the highest HI of 0.19 followed by Armour at 0.15 and Karl 92 had the lowest HI with 0.09.

Correlation Analyses

Temperature had a large negative correlation with both Fv/FM and SPAD, with r=-0.97 and r=-0.95, respectively, whereas C had no correlation (Table 4-4). Total seed yield, seed weight, and HI also had high correlations to the temperature treatment. Cultivar had strong to moderate correlations with seed yield (r=-0.73), seed weight (r=-0.59), total biomass (r=-0.49), and HI (r=-0.74), while C had very weak to moderate correlations with the rate and duration of Fv/FM, SPAD, and seed-filling. With the rate of seed-filling having the highest correlation of r=-0.57 followed by r=-0.35 for the duration of seed-filling. Maximum quantum efficiency of Photosystem II and SPAD were highly correlated to each other, but also to the seed-filling rate (negatively correlated) and duration with SPAD having the highest correlation of r=0.88 with seed-filling duration. Total seed yield was moderately and positively correlated with the rate of Fv/Fm and the duration of SPAD, with r=0.65 and r=0.69, respectively. Average single seed weight had high to moderate correlations to total biomass, HI, and rate and duration of Fv/Fm and SPAD. Also, duration of Fv/Fm and SPAD had moderately high correlations to average single seed weight. Both total seed yield and seed weight had low to moderate correlations to seed-filling rate and duration with the combination of seed weight and seed-filling duration having the highest correlation of r=0.51.

Discussion

High temperature stress decreased Fv/Fm and increased the rate of SPAD decline in all three winter wheat cultivars. High temperature stress induced faster senescence. Studies have shown damage to the photosynthetic apparatus leads to higher respiration and altered source sink relationships (Al-Khatib and Paulsen, 1984; Blum et al., 1994). Senescence itself seems to be more caused by plant wide damage and competition for carbon (Al-Khatib and Paulsen, 1984; Blum, 1986; Paulsen, 1994; Shah and Paulsen, 2003). Although not conclusive, all OT plants had mature seed and still had green leaves before the final harvest. When comparing the duration of seed-filling, SPAD, and Fv/Fm the average point of decline (downward slope) is 21, 18, and 21 d, respectively. So, it is possible that in optimum environments leaf senescence is caused by mature seed, whereas in stressed environments, the stress itself causes senescence which stops seed-fill (Al-Khatib and Paulsen, 1984; Wardlaw and Moncur, 1995; Ristic et al., 2007).

All yield components were negatively affected by higher temperature during seed filling except seed number, which should be constant because seed set had already taken place (Gibson and Paulsen, 1999). Interestingly, cultivar difference of average seed weight seems to be the only cause of yield differences during high temperature stress with these three cultivars. The decrease in seed yield and yield components is very similar to the research done with spring and durum wheat (Nicolas et al., 1984; Tashiro and Wardlaw, 1990; Stone and Nicolas, 1998; Shah and Paulsen, 2003; Schapendonk et al., 2007). Maybe because of the more whole plant approach the overall yield reductions were not as large as in other studies (Fokar et al.,1998; Tashiro and Wardlaw, 1990).

Also, because all tillers were harvested and averaged together the seed weights tended to be lower than other studies. Although, they are still within the 'normal' range for winter wheat in the Great Plains region and the state of Kansas (i.e. 15-30 mg seed^{-1}).

The seed-filling duration was reduced quite dramatically from the OT to HT, by an average of 13-d. The seed-filling rate increased an average of 1.4 mg d^{-1} when under HT. Both Fv/Fm and SPAD were highly correlated to rate and duration of seed-filling for all three cultivars. Possibly due to the temperature and cultivar influence, rate and duration of seed-filling had moderate to low correlations to total seed yield and average single seed weight, though duration had a higher correlation (0.51). Also of interest is the T x C interaction for both rate and duration. If one can control for the T or environmental effects there may be some potential for breeding.

Total biomass in the HT was constant while the OT increased at the same time as seed yield. Although neither respiration nor photosynthesis were directly measured, the changes (or lack thereof) in total biomass while at the same time an increase in seed weight are a clue as to what is happening. This may signify the remobilization of stored carbon from the stem and leaves to be used in seed development. In several studies stem reserves (and even ear photosynthesis) were found to be a major source of seed yield in stressed conditions (Blum, 1896; Tahir and Nakata, 2005; Fokar et al., 1998). For the OT the increase in total weight and seed yield can presumably be because photosynthesis was maintained. These conclusions would follow suit with several other researchers (Shah and Paulsen, 2003; Al-Khatib and Paulsen, 1999) and if assumed, help clarify the slow decline of SPAD and Fv/Fm in the OT and the fast decline in the HT.

In slight conflict to studies supporting the importance of stem reserves for yield, some have found flag leaf 'stay green' to be a large influence in maintaining photosynthesis and higher yields (Shah and Paulsen, 2003; Al-Khatib and Paulsen, 1984; Blum et al., 1994). This study would tend to lend support to both ideas. In extreme stress, when chlorophyll is damaged rapidly, stem carbohydrate reserves may be a very important source to maintain yield. In this case it may be best to move as much stored carbon to seed quickly, similar to Jagger. In moderate stress 'stay green' and the maintenance of chlorophyll and thus photosynthesis may lead to higher yields. From this research, maintaining photosynthesis may lead to higher yields than stem reserves alone, but above certain high temperatures (as in this study) the plants cellular structure will degrade and continued photosynthesis may not be possible. Both from observations in this experiment and from the work of other researchers (Ristic et al., 2007; Maxwell and Johnson, 2000), when Fv/Fm and SPAD go much below 0.60 and 40, respectively, wheat is dying and remobilized or photosynthesized carbon is quickly declining.

In Kansas, all three cultivars are good yielding, but Jagger has always been popular and, until recently, was one of the most planted cultivars (USDA NASS 2005; 2013). Its widespread usage was obviously for a good reason. Armour also tends to be a better performer in the field. Karl 92 tends to be a high-yielder too, but this seems to be more from its tendencies to produce more tillers (data not shown). Based on the longer duration of seed fill, Karl 92 may also have some form of true biological temperature tolerance (though not expressed in total seed yield). In other field experiments (USDA TCAP T3 database) Karl 92 was able to maintain moderate and very similar yields to Jagger in both dryland and irrigated plots.

Similar to Ristic et al. (2007), correlations from this study found Fv/Fm and SPAD values to be highly correlated with each other and may be useful in future studies as a surrogate to the other.

Conclusions

High temperature stress decreased maximum quantum efficiency of PSII and increased the rate of chlorophyll loss in all three winter wheat cultivars. High temperature stress decreased seed yield of winter wheat by decreasing the seed-filling duration. The seed-filling rate is cultivar specific with Jagger and Armour being faster than Karl 92. At high temperatures the increased seed-filling rate did not compensate for the seed yield loss caused by decreased seed-filling duration.

Higher yields in the winter wheat growing regions, susceptible to post-anthesis high temperature stress, may be possible through selection of cultivars with faster seed-filling rates and/or duration of seed filling.

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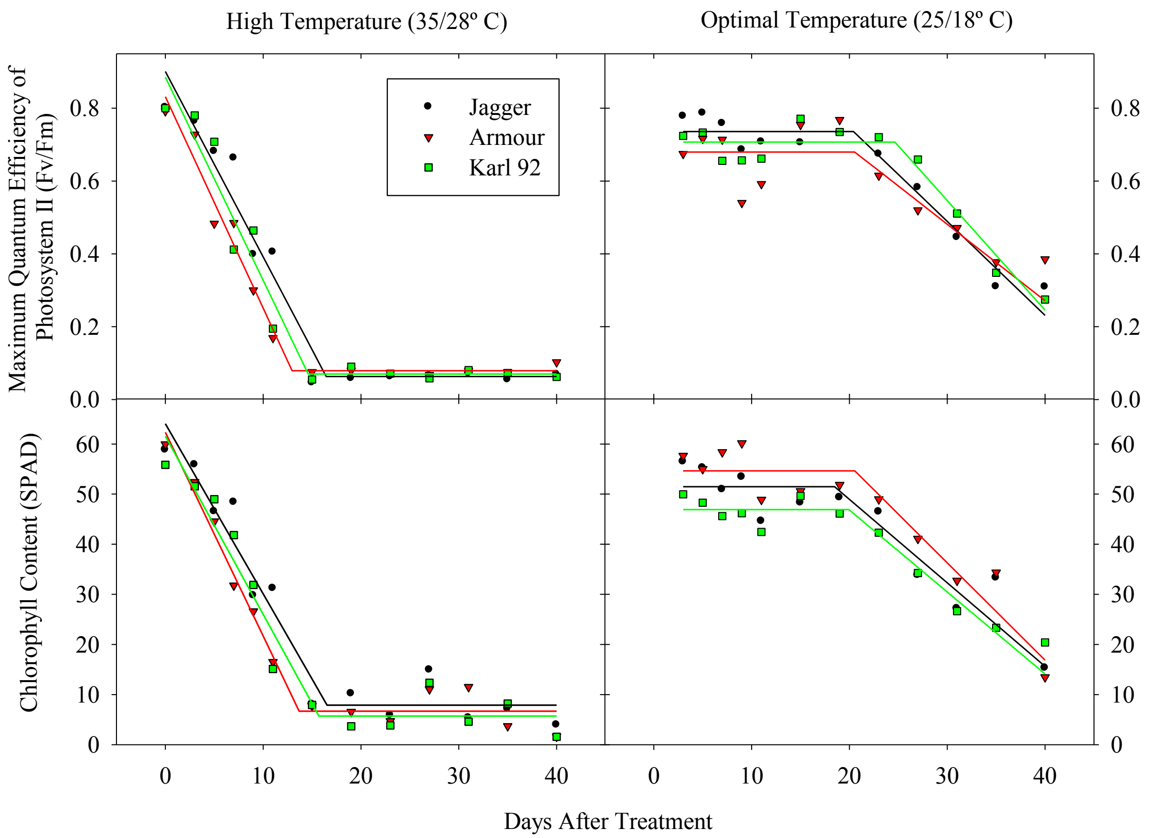

Figure 4-1. Linear plateau response models of maximum quantum efficiency of Photosystem II and leaf chlorophyll content of Jagger, Armour, and Karl 92 to high and optimum temperatures during seed-filling.

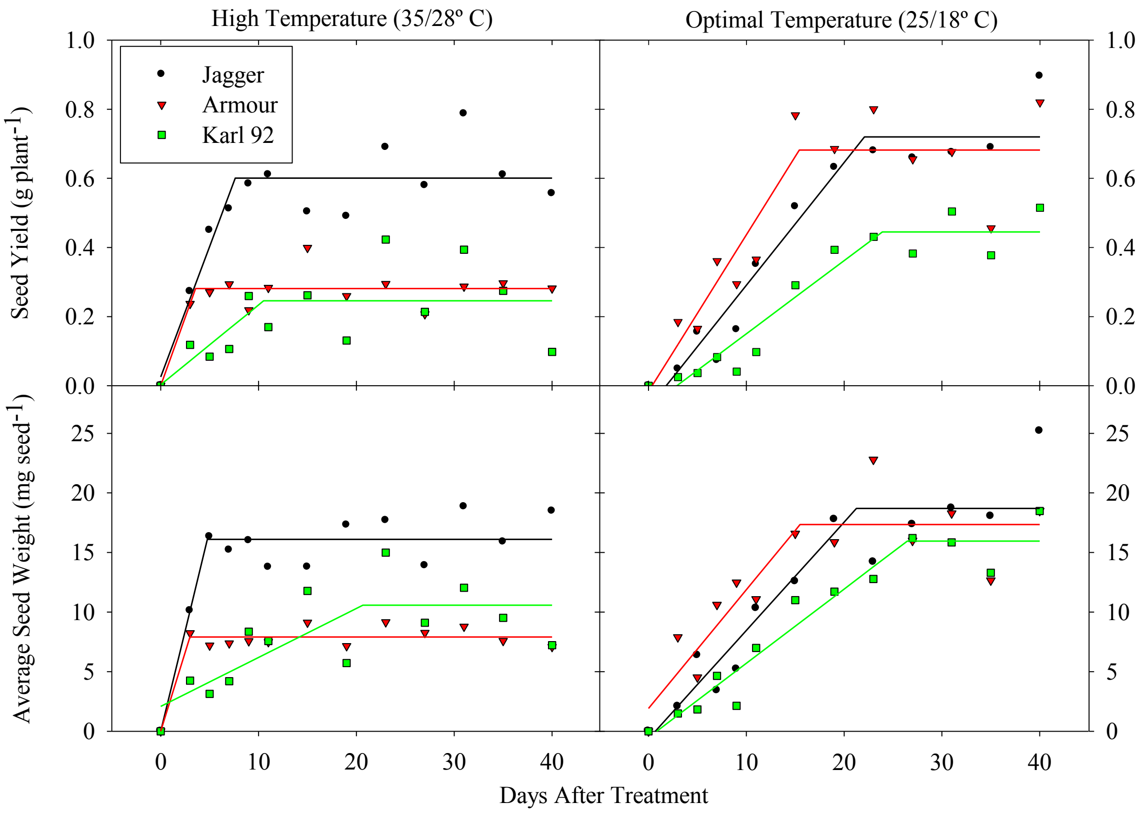

Figure 4-2. Linear plateau response models of total seed yield and average seed weight of Jagger, Armour, and Karl 92 to high and optimum temperatures during seed-filling.

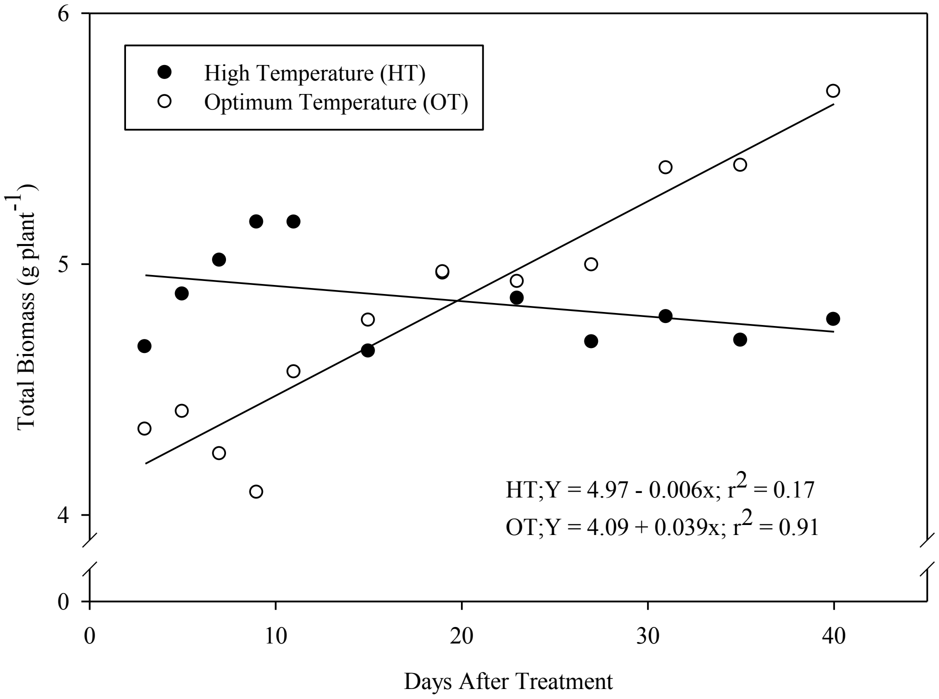

Figure 4-3. Effect of high (35/28°C) and optimum temperature (25/18°C) on the combined total biomass of Jagger, Armour, and Karl 92 during seed-filling.

Table 4-1. Analysis of Variance and LSMeans of the effects of temperature and cultivar on total biomass, seed yield, seed number, harvest index, and average seed weight.

Effect	Total Biomass (g $plant^{-1}$)	Seed Yield (g $plant^{-1}$)	Seed Number ($plant^{-1}$)	Harvest Index (Unit less)	Seed Weight (mg $seed^{-1}$)
			Pr > F		
Temperature	0.0006	0.0004	0.5697	0.0004	<.0001
Cultivar	0.6408	<.0001	<.0001	<.0001	0.0007
T x C	0.6017	0.4699	0.1582	0.9006	0.4660
Temperature			LSMean		
HT	4.736 b	0.288 b	30.639 ns	0.098 b	9.537 b
OT	5.539 a	0.726 a	32.676 ns	0.191 a	21.804 a
LSD	0.264	0.137	-	0.029	1.644
Cultivar			LSMean		
Jagger	5.071 ns	0.666 a	37.230 a	0.192 a	18.338 a
Armour	5.110 ns	0.540 b	38.980 a	0.154 b	13.597 b
Karl 92	5.233 ns	0.308 c	18.764 b	0.087 c	15.075 b
LSD	-	0.123	6.915	0.0291	2.45

LSD are Fisher's protected least significant difference at an alpha of 0.05

Table 4-2. F-test of the Analysis of Variance on the effect of Temperature (T), Cultivar (C), and T x C interaction on the Rate (b), and Duration (x0) of maximum quantum efficiency of Photosystem II, chlorophyll content, total seed yield, and average seed weight.

	Rate (b)			Duration (x0)		
Traits	Temperature	Cultivar	T x C	Temperature	Cultivar	T x C
		Pr > F			Pr > F	
Maximum Quantum Efficiency of Photosystem II (Fv/Fm)	<.0001	0.0847	0.0545	<.0001	0.7667	0.6759
Chlorophyll Content (SPAD units)	<.0001	0.0793	0.0334	<.0001	0.4759	0.9604
Seed Yield (g plant^{-1})	0.2228	0.0014	0.1891	0.0032	0.6185	0.1985
Average Seed Weight (mg seed^{-1})	0.0262	0.0197	0.0089	<.0000	0.0169	0.0169

Table 4-3. Line formula for figure 1 and 2 of the form Y=a+bx when x<x0 for Maximum quantum efficiency of Photosystem II and leaf chlorophyll content for the optimum temperature, and total seed yield and average seed weight in both high temperature and optimum temperature. Of the form Y=a+bx when x>x0 for Maximum quantum efficiency of Photosystem II and Chlorophyll content in high temperature.

	High Temperature (35/28°C)					Optimum Temperature (25/18°C)				
	a	b	x0	RMSE	R^2	a	b	x0	RMSE	R^2
Maximum Quantum Efficiency of Photosystem II (Fv/Fm)										
Jagger	0.901	-0.051	16.441	0.063	0.966	1.199	-0.048	19.635	0.041	0.952
Armour	0.832	-0.058	12.957	0.039	0.983	0.982	-0.034	19.000	0.069	0.772
Karl 92	0.885	-0.056	14.611	0.065	0.961	1.455	-0.049	24.697	0.041	0.945
Chlorophyll Content (SPAD)										
Jagger	64.054	-3.397	16.532	4.883	0.955	77.958	-3.398	17.661	4.583	0.890
Armour	62.343	-4.066	13.685	3.257	0.978	86.686	-3.665	18.563	4.369	0.925
Karl 92	61.571	-3.558	15.703	4.715	0.958	70.793	-2.950	17.952	2.508	0.950
Seed Yield (g plant^{-1})										
Jagger	0.025	0.076	7.621	0.255	0.843	-0.064	0.036	22.072	0.251	0.938
Armour	0.000	0.079	3.561	0.148	0.974	-0.017	0.045	15.399	0.345	0.859
Karl 92	0.000	0.023	10.518	0.308	0.929	-0.061	0.021	23.893	0.186	0.957
Average Seed Weight (mg seed^{-1})										
Jagger	0.000	3.370	4.777	1.837	0.884	-0.625	0.908	21.265	2.904	0.883
Armour	0.000	2.648	2.988	0.806	0.991	1.912	0.996	15.497	2.916	0.823
Karl 92	0.556	0.691	13.744	2.594	0.918	-0.522	0.623	26.465	1.735	0.948

Table 4-4. Pearson Correlation Coefficients of Temperature, Variety, Quantum Efficiency of Photosystem II (Fv/Fm), Chlorophyll Content (SPAD), Total Seed Yield, Average Single Seed Weight, Total Biomass, Harvest Index, Rate of decrease of Fv/Fm, Duration until plateau for Fv/Fm, Rate of decrease of SPAD, Duration until plateau for SPAD, Rate of Seed-fill, Duration of Seed-fill, for Jagger, Armour, and Karl 92 under High and Optimum temperatures during seed-fill.

Correlations	Temperature Treatment	Cultivar	Fv/Fm	SPAD	Total Seed Yield	Average Single Seed Weight	Total Biomass	Harvest Index	Rate of Fv/Fm	Duration of Fv/Fm	Rate of SPAD	Duration of SPAD	Seed-Filling Rate	Seed-Filling Duration
Temperature Treatment	1.00													
Cultivar	0.00	1.00												
Fv/Fm	-0.97	0.00	1.00											
SPAD	-0.95	0.04	0.87	1.00										
Total Seed Yield	-0.66	-0.73	0.62	0.65	1.00									
Average Single Seed Weight	-0.67	-0.59	0.56	0.74	0.94	1.00								
Total Biomass	-0.23	-0.49	0.11	0.46	0.64	0.77	1.00							
Harvest Index	-0.67	-0.74	0.65	0.63	0.99	0.91	0.56	1.00						
Rate of Fv/Fm	-0.73	-0.16	0.81	0.72	0.65	0.54	0.38	0.64	1.00					
Duration of Fv/Fm	-0.84	0.17	0.72	0.93	0.47	0.65	0.47	0.45	0.50	1.00				
Rate of SPAD	-0.50	0.17	0.30	0.72	0.30	0.60	0.65	0.24	0.19	0.85	1.00			
Duration of SPAD	-0.84	-0.07	0.78	0.94	0.69	0.77	0.62	0.65	0.83	0.82	0.68	1.00		
Seed-Filling Rate	0.65	-0.57	-0.61	-0.64	-0.02	-0.13	0.21	-0.03	-0.34	-0.54	-0.41	-0.53	1.00	
Seed-Filling Duration	-0.83	0.35	0.71	0.88	0.32	0.51	0.18	0.31	0.39	0.88	0.76	0.74	-0.86	1.00

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Chapter 5 - Conclusions and Future Direction

Conclusions

Drought and high temperature are major detriments to global wheat production. Wheat varies in its susceptibility to drought and high temperature stress. Three experiments were performed to address the challenges of drought and high temperature stress in wheat. The first experiment consisted of 256 genotypes of spring wheat and 301 genotypes of winter wheat, field screened for yield traits related to drought tolerance in irrigated and dryland conditions. At Ashland Bottoms Research Farm, in 2011-2013, two studies were conducted based on the following objectives: (i) characterize phenotypic variability of yield traits in genetic mapping populations; (ii) compare the variability and correlations of yield traits in different water regimes; and (iii) identify high yielding genotypes in irrigated and dryland. In the first experiment, characterizing spring and hard winter wheat association mapping panels for yield traits in differing water regimes, winter wheat had higher seed yield in Kansas than spring wheat. Kansas growers produce very little spring wheat. Spring wheat and winter wheat both had lower values for measured yield traits in dryland compared to irrigated environments. Both wheat types also demonstrated a large amount of variability within genotypes. This variability provides good potential for future scientific endeavors. Overall, spring and winter wheat responded similarly to the water regimes. No clear cut compensation to differing water treatments was observed other than the increase in correlation between seeds per spike and the other yield traits. Seed number, spike number, and total biomass were found to have the greatest relationship with seed yield, regardless of water regime. Using multiple linear regressions, seed number, total biomass, and thousand seed weights were the best three parameter model for predicting seed yield, regardless of water regime. Finally, using quadrate plots, where seed yield was graphed by water regime, 20 genotypes were identified, five from each quadrant, for future research or breeding purposes. Five genotypes had above average yields in both dryland and irrigated environments, five were above average in irrigated but below average in dryland environments, five were below average in irrigated and above average in dryland environments, and five were below average in both irrigated and dryland environments.

The second experiment was performed in greenhouse facilities to observe the source-sink relationship of spring wheat genotype, Seri 82, under two moisture regimes and four defoliation treatments. A series of three experiments were performed with the following objectives: (i) characterize the relationship in photosynthetic area and stored reserves during seed-filling to yield and yield components in irrigated and limited moisture environments; and (ii) characterize contributions of leaves and stems to yield. In the second experiment, source-sink interactions with limited moisture and varying levels of defoliation in post-anthesis wheat, the cessation of water after seed-set significantly reduced total biomass, seed yield, single seed weight, seed yield per spike, and harvest index. Because the stress was imposed after seed set, seed number and spike number were unaffected. Defoliation affected the source-sink relationship by reducing the source strength of the leaves. This caused the stem to contribute more to overall yield. Defoliation also caused the remaining leaves to compensate for the removed leaves. It was found that with the spring wheat genotype, Seri 82, the stored reserves in the stem contributed to yield the most in severe stress and also contributed a substantial amount when no stress was present. In addition to the stem contributions, the flag leaf was found to contribute as much to seed yield as all other leaves except the flag leaf. But even at that level, the flag leaf only contributed about 25% percent of the total seed yield in ideal conditions.

The final experiment looked at changes in seed-filling rate and duration of three winter wheat genotypes during high temperature stress. In the KSU controlled environment facilities, growth chambers, an experiment was performed with the following objectives: (i) quantify the effects of terminal post-anthesis, high temperature stress on yield and yield components of three cultivars; and (ii) quantify and observe any cultivar differences in seed-filling rate and duration due to high temperature stress on a finer time interval in winter wheat cultivars. In the third and last experiment, the effect of high temperature stress on the seed-filling rate and duration of three winter wheat cultivars, high temperature stress decreased maximum quantum efficiency of PSII and increased the rate of chlorophyll loss in all three winter wheat cultivars. High temperature stress decreased winter wheat seed yield by decreasing the seed-filling duration. The seed-filling rate is cultivar specific with Jagger and Armour being faster than Karl 92. At high temperatures the increased seed-filling rate did not compensate for the seed yield loss caused by decreased seed-filling duration. Higher yields in the winter wheat growing regions, susceptible to post-anthesis high temperature stress, may be possible through selection of cultivars with faster seed-filling rates and/or duration of seed filling.

Future Direction

As is typical in the quest for understanding and knowledge, "The more I learn, the more I realize how much I don't know" (Albert Einstein). The same is true for this study. There are areas of this research that could have been done differently and also areas in which more research is needed to fully understand what is happening. Suggestions and ideas for future research are described below.

A starting point for future directions in this field would be to screen populations for the effects of maturity along with yield and yield components in differing water treatments. In that same line of thought, looking at the variability of physiological traits (SPAD or chlorophyll index, canopy temperature depression, light/dark adapted chlorophyll fluorescence, and spectral reflectance) may also be of use. Future research would benefit from the development of tools (reflectance, SPAD, photosynthesis, etc) or protocols for screening large populations for yield or other traits of interest. These tools would be pivotal in overcoming the phenotyping bottleneck. Future research would also benefit from the development of experimental designs made specifically to screen large populations that maintain statistical power but also don't demand too much land area, such as what would be needed for true replication of all experimental units. Researchers might use a sub-set of this population, in more controlled environments, to look more in depth at the changes to maturity, physiology, and yield, with the goal of isolating mechanisms of tolerance or susceptibility (or better screening tools). Looking further into source-sink relationships, it would be useful to do a similar experiment with restricted water but add high temperature stress. This is because water and high temperature stress usually happen together. Also defoliation is useful for isolating sources, but I think adding a dark (no light) treatment, would remove spike, awn, and stem photosynthesis, as well as show the systemic damage caused by the act of defoliation. Changes in system wide and/or single leaf photosynthesis (looking for photosynthetic compensation of remaining laves) after defoliation and during stress, would be another interesting experiment or addition to these research results. Researchers could test if seed produced under stress effects the germination, growth, and vigor of the offspring. They might also further examine the interaction of water and high temperature stress on the seed filling rate and duration or screen genotypes for faster seed-filling rate and/or longer duration for breeding material.