

IMPACT OF NITROGEN AND WATER MANAGEMENT TO GRAIN YIELD,
YIELD COMPONENTS AND TRAITS, AND GRAIN QUALITY OF TWO
CONTRASTING WHEAT CLASSES

by

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DEDICATION

To my grandmother Aparecida Bicego Vieitez. A great person in my life who passed away during this journey. I could never say goodbye, but maybe it was not necessary since she will always be by my side.

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TABLE OF CONTENTS

1. LITERATURE REVIEW	1
Spring Wheat (<i>Triticum aestivum</i> L.)	1
Management.....	3
Nitrogen	3
Irrigation	4
Heat Stress	4
Wheat Quality	5
Yield Components	7
Research Objectives.....	8
References.....	10
2. DIFFERENTIAL NITROGEN AND WATER IMPACTS ON YIELD AND QUALITY OF WHEAT CLASSES.....	18
Contribution of Authors and Co-authors	18
Manuscript Information Page	19
Abstract.....	20
Introduction.....	21
Materials and Methods.....	25
Site Description.....	25
Nitrogen Main Plot	26
Cultivar Subplot.....	26
Planting and Pest Control.....	28
Environment.....	28
Data Collection	29
Statistical Analysis.....	30
Yearly Weather and Irrigation	30
Results.....	32
Correlation Between Yield and Quality Traits	32
Main Effects and Interactions	33
Grain Yield.....	33
Grain Protein Content	36
Falling Number	39
Grain Test Weight.....	40
Discussion	43
Grain Yield.....	43
Grain Quality	45

TABLE OF CONTENTS CONTINUED

Grain Protein Content	45
Falling Number	48
Grain Test Weight.....	48
Conclusion	49
Acknowledgments.....	50
References.....	51
3. NITROGEN AND WATER IMPACTS ON GRAIN YIELD AND YIELD COMPONENTS OF DIFFERENT WHEAT CLASSES.....	59
Contribution of Authors and Co-authors	59
Manuscript Information Page	60
Abstract	61
Introduction.....	62
Materials and Methods.....	65
Experimental Design.....	65
Data Collection	66
Statistical Analysis.....	67
Weather and Irrigation	67
Results.....	68
Correlation Analysis	68
Main Effects and Interactions	71
Discussion.....	79
Conclusion	84
Acknowledgments.....	85
References.....	86
4. CONCLUSION.....	91
CUMULATIVE REFERENCES	94

LIST OF TABLES

Table	Page
2.1. Selected semi-dwarf spring wheat cultivars.	27
2.2. Correlation coefficients between grain yield (GY), grain protein content (GPC), grain test weight (GTWT), and falling numbers (FN), for hard red (HRSW), soft white (SWSW) spring wheat, and the two market classes combined.....	32
2.3. Yearly analysis of variance showing probability values of the main and interactions effects in each market class.	34
2.4. Grain test weight and falling number responses of wheat cultivars under irrigated and rainfed environments in 2016/17. Same letter assignment indicates lack of significant differences between cultivars within market classes across irrigated and rainfed environments of each year ($\alpha = 0.05$).	42
3.1. Average monthly minimum (Tmin) and maximum (Tmax) ambient temperature and monthly precipitation from 2016, 2017, and the 29-yr average obtained at Creston, MT weather station (USBR, 2019). Total monthly irrigation and total water received are recorded in the table in mm.	68
3.2. Correlation coefficients between grain yield and its components and related traits across cultivars under irrigated environment in 2016.....	70
3.3. Correlation coefficients between grain yield and its components and related traits across cultivars under rainfed environment in 2016.....	70
3.4. Correlation coefficients between grain yield and its components and related traits across cultivars under irrigated environment in 2017.....	71
3.5. Correlation coefficients between grain yield and its components and related traits across cultivars under rainfed environment in 2017.....	71
3.6. Analysis of variance for the 2-yr split-plot experiment with five nitrogen levels as main plot and eight cultivars as subplots over two environments (irrigated and rainfed). Table shows the source of variation, numerator degrees of freedom (ndf), and probability values for the <i>F</i> -test of each main effect and interactions.....	72

LIST OF TABLES CONTINUED

3.7. Environment x year interaction means for aboveground biomass, thousand kernel weight, productive tiller number, and spikelets per head. Same letter assignment indicates the lack of significant differences across environment and year for each trait ($\alpha = 0.05$)76

LIST OF FIGURES

Figure	Page
2.1. Daily maximum (Tmax) and minimum (Tmin) ambient temperatures from planting to harvest in 2016 (A) and 2017 (B). The corresponding cumulative daily crop evapotranspiration (ETc), precipitation (Pr), and irrigation (Ir) are shown for 2016 (C) and 2017 (D). Downward arrows indicate each of the irrigation events. Vertical lines indicate average occurrences of growth and development and the dates of emergence and harvest. Horizontal dotted lines (in panels A and B) represent the wheat critical temperature (32°C; Reynolds et al., 2016).	31
2.2. Nitrogen (N) x environment (Ir, irrigated; Rf, rainfed) interaction means for grain yield response of hard red (HRSW) and soft white (SWSW) spring wheat in 2016 (A) and 2017 (B). N treatment check are 118 and 45 kg ha ⁻¹ for 2016 and 2017, respectively. The X0 represents the maximum grain yield response to N from both the mean separation of the analysis of variance and the non-linear upper plateau model. The ns assignment represent the non-significant linear regression coefficient to zero	35
2.3. Grain yield response of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat cultivars for 2016 and 2017. Error bars are the standard error of the difference among cultivars within each market class and year. Same letter assignment indicates the lack of significant differences between cultivars within a market class across irrigated and rainfed environments for each year ($\alpha = 0.05$).....	36
2.4. Grain protein content response of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat cultivars for 2016 and 2017. Error bars are the standard error of the difference among cultivars within each market class and year. Same letter assignment indicates the lack of significant differences between cultivars within a market class across irrigated and rainfed environments for each year ($\alpha = 0.05$).....	38
2.5. Nitrogen (N) x environment interaction means for grain protein content (GPC) of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat in 2016 and 2017. The X0i and X0r represent the maximum GPC response to N using a non-linear upper plateau model for irrigated and rainfed environments, respectively. The horizontal dotted lines represent the common market protein requirement for HRSW (i.e., > 140 g kg ⁻¹) and SWSW (i.e., < 105 g kg ⁻¹).	39

LIST OF FIGURES CONTINUED

- 3.1. Three-way interaction means of environment, nitrogen (N), and year for grain yield (A, B), kernels m^{-2} (C, D), physiological maturity (E, F), and grain fill duration (G, F). Error bars are the standard error of the differences across the three-factor interaction means. Same letter assignment indicates the lack of significant differences across the three factors interaction ($\alpha = 0.05$)73
- 3.2. Environment x cultivar x year interaction means for physiological maturity (A, B), and grain fill duration (C, D). Error bars are the standard error of the differences across the three factors interaction means. Same letter assignment indicates lack of significant differences across the three factors interaction ($\alpha = 0.05$)75
- 3.3. Cultivar x year interaction means for grain yield (A), aboveground biomass (B), thousand kernel weight (C), and spikelets per head (D). Error bars are the standard error of the differences across the two factors interaction means. Same letter assignment indicates the lack of significant differences across the two factors interaction ($\alpha = 0.05$)77
- 3.4. Environment x cultivar interaction means for grain yield (A), thousand kernel weight (B). Error bars are the standard error of the differences across the two factors interaction means. Same letter assignment indicates the lack of significant differences across the two factors interaction ($\alpha = 0.05$)78
- 3.5. Cultivar means for kernels m^{-2} (A), and productive tiller no. m^{-2} (B). Error bars are the standard error of the difference among cultivars. Same letter assignment indicates the lack of significant differences among cultivars ($\alpha = 0.05$)79

ABSTRACT

Wheat (*Triticum aestivum* L.) breeders and physiologists must consider not only grain yield but also its quality. Physiological selection may be an important tool to aid breeders achieve improvements more rapidly. However, different genotypes may have distinct responses to agronomic management and environments. The relationship between those traits also may vary according to wheat class. In the present study we characterized the grain yield, yield components and traits, and quality parameters response of four hard red and four soft white spring wheat cultivars subjected to various nitrogen (N) levels and moisture regimes (stressed vs non-stressed environment) over two years. About one-third grain yield reduction from 2016 to 2017 could be attributed to heat stress. Overall, soft whites had higher grain yield than hard reds, but a stronger negative grain yield-grain protein content relationship. Considering a given year, increments in grain yield also resulted in higher grain protein in hard reds except when N was very low. The cultivar with *Gpc-B1* gene for higher grain protein, had similar grain yield to its parent material and to other well adapted hard red cultivar. Vida, characterized by extended green leaf duration after heading (stay-green trait), was better adapted to water and heat stress than the rest of hard reds. Grain fill duration was an important trait especially under heat and drought stress for both wheat classes. We found that, across moisture regime environments and year, productive tiller number had consistently a direct relation with kernel number per area, which was strongly related to grain yield. During the heat and drought stressed year, kernel weight was an important yield component and had neutral relation with kernel number. Nitrogen fertilization had effect on grain yield only during the hot and dry year with irrigation, but no effect was observed under rainfed conditions for this year. Based on the lower grain protein requirement as well the lack of N effect on grain yield for the tested conditions, soft whites may be grown with lower N input than hard reds.

CHAPTER ONE

LITERATURE REVIEW

Spring Wheat (*Triticum aestivum* L.)

Wheat (*Triticum aestivum* L.) is the most widely grown staple crop worldwide (Hanson et al., 1982) and almost the entirety is for human consumption (Evans, 1993). Its adaptability to diverse environments, end use diversity, and high calorific and proteic value make it an important crop to fight against global food insecurity and hunger (Stone and Savin, 2000; Curtis, 2002). As estimated by the Food and Agriculture Organization (2018), about 65 kg of wheat and its products are consumed per person per year, representing 18% of the daily calorie intake.

Wheat is categorized according to its growth habit, yield, and quality. There are six wheat classes grown in the USA (hard red winter, hard red spring, soft red winter, soft white, hard white, and durum; US Wheat Associates, 2018). For each of these classes, yield and specific class-required quality are met and improved via breeding and agronomic management. Breeding program are sought to increase grain yield while maintaining adequate quality through trait selection, including resistances to biotic and abiotic stressors. Management is expected to vary according to each of the wheat market classes. A generic agronomic management is ineffective knowing that the quality requirement of each of the classes is very specific. The combined effort (breeding and

management) contributes to improved yield and quality (Frederick and Bauer 2000; Fischer, 2014; Graybosch, 2014). Fine-tuning management based on class or trait specificity (less on cultivar specificity) is imperative to increase productivity per unit farming input with little to no negative impacts on quality.

In Montana, there are a number of management information for hard red, yet lacking for soft white. In the US, hard red represent 92% of spring wheat production and it is the only spring wheat class produced in Montana (USDA-NASS, 2018). As to soft whites, no production of this class in the state is recorded. However, it is an important class for the rest of the Pacific Northwest, as Idaho, Oregon, and Washington had respective 24, 44, and 50% of their spring wheat production as soft whites in 2017 (USDA-NASS, 2018). Nevada increased the proportion of soft whites, among spring wheats, from 64% in 2016 to 90% in 2017. This market class can be economically attractive because of its relatively higher yield potential and lower grain protein requirement ($<105 \text{ g kg}^{-1}$; Bole and Dubetz 1986; Sowers et al., 1994) compared with hard reds ($>140 \text{ g kg}^{-1}$; Brown et al., 2005). Presumably, with soft whites grain protein content requirement much lower than hard reds, its nitrogen (N) input can be reduced. For producers to manage soft white, following its management in reference to hard reds can be economically risky knowing that these two classes have different end-use quality requirement. Mahler and Guy (2007) proposed a specific N fertilization for soft white in Northern Idaho - a much lower N requirement than the general recommendation for spring wheat by the fertilizer guidelines for Montana crops (Jacobsen et al., 2005). A better knowledge of N management on recent hard reds breeds such as high GPC trait

(*Gpc-B1* gene) and high-yielding (stay-green), and a better understanding on how they differ from the other hard reds and soft white cultivars, is necessary considering N is an expensive farm input.

Management

Nitrogen

Among all mineral nutrients, N is the one required in higher amounts. Nitrogen is essential for increased biomass production and healthy canopy that intercepts energy for photosynthesis (Barraclough et al., 2014). Nitrogen availability is related to canopy longevity (Sinclair and Jamieson, 2006). Nitrogen is the largest farming input in wheat production and it is usually over applied intending to ensure adequate levels for both yield and quality (Diacono et al., 2012). Often times the over application is to increase grain protein for higher market price, as observed for hard red spring wheat. In wheat, N is essential for the production of biomass and N storage which is further remobilized to the grains. It is estimated that up to 95% of the N remobilized to the grains is taken up prior to anthesis (Slafer et al., 1990; Palta and Fillery, 1995; Masoni et al., 2007; Waters et al. 2009; Bogard et al., 2010). Applying N as top-dress after anthesis may increase grain protein content. However, this strategy is risky when irrigation is not available due to unpredictability of precipitation. Although it has been reported that fertilizer application can improve the efficiency of crops to use the available water (Garg, 2013), it is also known that nitrogen availability and uptake are dependent on available soil moisture. Under ideal conditions grain yield is closely related to N availability and uptake

(Barraclough et al., 2010). When water is adequate, available N will first increase yield and if in excess will increase protein (Terman et al., 1969; Fowler et al., 1990). In some instances, such as with deficient moisture and high temperatures, grain yield response to applied N can be insignificant (Long et al., 2017).

Irrigation

Drought stress is one of the most yield limiting factors in wheat production (Morris et al., 1991; Fahaad et al., 2017) as to other crops. Plants under drought stress reduce efficiency in utilizing photosynthetic active radiation into new dry matter (Earl and Davis, 2003). Supplemental irrigation suppresses this problem as transpiration helps cooling down canopy temperature preventing stomata to close, thereby keeping the green tissues photosynthetically active much longer (Acevedo et al., 2002;). However, even in a non-water-limiting environment, high ambient temperatures can still affect grain yield (McDonald et al., 1984). Optimally using transpirable water resulting in a cooler canopy temperature (Pinto and Reynolds, 2015) mitigating the impact of heat stress. When drought was combined with heat stress, the grain development was even more compressed, which is described as a mechanism to maintain the ability to produce viable seeds (Altenbach, 2012).

Heat Stress

The exponential rising temperature predictions (IPCC, 2018), make it imperative to improve management and develop more adaptative crops. Increasing temperatures

globally is also affecting production even on high latitudes with mild temperatures that usually favor wheat production. Lanning et al. (2010) reported how high temperatures, especially when coincident with reproductive stages, affect wheat in Montana as also demonstrated in Torrion and Stougaard (2017). The heat stress is pointed as a major constraint in wheat production especially during reproductive phase (Barnabas et al., 2008; Farooq et al., 2011; Fahaad et al., 2017). Excessive temperature during anthesis can cause floret abortion (Wardlaw and Wrigley, 1994). This severely impacts the potential number of grains per area – an important yield component (Slafer et al., 2014). High temperatures during grain filling accelerates senescence including the seed maturation process, and consequently reduce grain size and weight (Wardlaw and Moncur, 1995). As reported by Farooq et al. (2011), heat stress speeds up growth rate that consequently reduces the time duration to accumulate photoassimilates. Traditional management practices such as N fertilization can do little to reduce the effects of heat stress (Altenbach et al., 2003; Elia et al., 2018), and irrigation could only mitigate the heat stress effects in wheat production (McDonald et al., 1984; Acevedo et al., 2002; Fahaad et al. 2017), if abortion of florets is avoided as discussed in Torrion and Stougaard (2017).

Wheat Quality

Grain quality such as grain test weight, grain protein content, and falling number are important end-use quality parameters in wheat. Low grain test weight can reduce wheat market price (CHS, 2018). Reduced test weight during stressed growing conditions

and management has been previously reported (Guttieri et al., 2001; Torrion and Stougaard, 2017). A relatively shorter grain fill duration due to temperature stress can result in lowered test weights (Hernandez-Espinosa et al., 2018; Yabwalo et al., 2018)

The grain protein content is a quick and cheap tool for grain quality that sets a standardized market pricing. In hard reds, its premium pricing for higher grain protein content and the concern with protein dilution oftentimes lead to excessive N fertilization. Protein dilution caused by increasing yields have been widely reported (Kibite and Evans, 1984; Slafer et al., 1990; Triboi and Triboi-Blondel, 2002; Barneix, 2007; Iqbal et al., 2016). Although, a recent review about the introduction of the *Gpc-B1* gene (upregulates grain protein accumulation) showed that cultivars carrying this gene tend not to follow this known protein penalty with increased yield or the other way around (Tabitta et al., 2017).

Lastly, the falling number (FN) test (Hagberg, 1960 and 1961) approved by the International Association of Cereal Science and Technology (ICC, 1968) is used to indicate amylase activity of the grains. The FN result can be inversely related to alpha-amylase activity independent of genetic background (Finney, 1985), meaning that high FN indicates low alpha-amylase activity. Alpha-amylase is responsible for breaking down the starch stored in the grains into sugar inferring a germination process. The FN number test can detect the alpha-amylase activity even in the absence of pre harvest sprouting. Some alpha-amylase activity is necessary to make some sugar available for a proper baking process. However, the excess of sugar in the flour (indicated by low FN), reduces the bread loaf volume or results to a mushy pasta. There is not a consensus yet as

to what triggers alpha-amylase activity. Many authors proposed different factors or a combination of them that could influence FN such as: seed coat color (Groos et al., 2002; McCrate et al., 1981), nitrogen application (Morris and Paulsen, 1984; Kettlewell, 1999; Kindred et al. 2005), grain drying rate (Kettlewell and Cashman, 1997), spikelet physical characteristics (King and Richards, 1984), temperature oscillation (Farrell and Kettlewell, 2008), and application of irrigation nearing soft dough stage (Torrión and Stougaard, 2017).

Yield Components

Identifying target traits is a first step to a successful breeding program (Trethowan et al., 2010). Detecting traits that are easily screened in early stages may aid breeders in selecting potential parent material (Talbert et al., 2001). Physiological selection is a complementary tool to breeding techniques and have potential to improve yield gains more rapidly (Reynolds, 2002). Although a given trait may be advantageous in one environment, but insignificant or detrimental in other, plastic traits may provide a genotype stability in diverse environments (Sadras et al., 2009). For example, high tillering was reported as an important trait related to phenological plasticity under drought (Blum et al., 1990; Baum et al., 2003). Naruoka et al. (2011) reported positive correlation between productive tiller number and grain yield in either irrigated or drought and heat stressed conditions. However, Nasseer et al. (2016) did not always find higher grain yield in high tillering wheat, because tillering negatively affected kernel weight and

the number of kernels per head. Nonetheless, productive tiller number remains a trait that can easily be determined in early stages.

Another trait that may be used in early screening is the grain-fill duration. An extended grain fill is reported to result in grain yield advantage especially under rainfed conditions not only in wheat (Chen et al., 2011; Naruoka et al., 2012; Semenov et al., 2014) but also in other crops (Banziger et. al, 1999; Borrell et al., 2000). Grain fill duration has been correlated with kernel weight (Blake et al., 2018). Kernel weight along with kernel number per area are the major determinants of final grain yield. Kernel number is reported a major limiting factor to achieve grain yield potential (Fischer, 2011). While kernel number is considered a coarse regulator of grain yield, grain weight is mostly responsible for the final adjustments (Slafer et al., 2014). Most of the grain yield gains during the twentieth century was obtained by increasing the kernel number and consequentially, the kernel weight has been reduced in modern cultivars (Calderini et al. 2000).

Research Objectives

The research analyzes the grain yield, grain quality, and yield components and traits of two spring wheat classes. Four hard reds and four soft white spring wheat were subjected to differential moisture regime environments and nitrogen fertilization over two years. Fortuitously, the second year's ambient temperature and precipitation highly deviated from the other and from the 29-yr average. This allowed assessment in yield yield components, and grain quality performance and resiliency to heat and drought

stress. Chapter two focuses on the aspects involving grain yield and grain quality analyzing the two wheat classes separately, whereas chapter three focuses on analyzing wheat classes to identify resilient cultivars and plastic traits.

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CHAPTER TWO

DIFFERENTIAL NITROGEN AND WATER IMPACTS ON YIELD AND QUALITY
OF WHEAT CLASSES

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DIFFERENTIAL NITROGEN AND WATER IMPACTS ON YIELD AND QUALITY
OF WHEAT CLASSES

The following chapter has been submitted to a peer-reviewed journal

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Abstract

Wheat (*Triticum aestivum* L.) breeders and physiologists must consider not only grain yield but also its quality. Wheat classes and genotypes may respond differently to agronomic management and environmental conditions. Our goal was to characterize the yield, protein, test weight, and falling number of four hard red and four soft white spring wheat cultivars subjected to various nitrogen (N) levels and moisture regimes (rainfed and irrigated environments). One-third yield reduction from 2016 to 2017 was attributed to heat stress. Irrigation increased both grain yield and test weight. However, falling number was generally higher under rainfed environment, but also cultivar dependent. Egan, McNeal, and Alpowa falling number values were more resilient to environmental differences than other cultivars. Overall, soft whites had higher yields than hard reds, but with a stronger negative yield to protein relationship. Achieving high yield in hard reds

via irrigation did not reduce grain protein in relation to rainfed, except at very low N (2017 control). The cultivar Egan, with *Gpc-B1* gene for higher grain protein, had similar yield to its parent material and to other hard red, though inferior to Vida (characterized by extended green leaf duration after heading) under heat and drought conditions. During the less limiting year (2016), the maximum protein was achieved with much less N under irrigated environment compared with rainfed. Soft whites, due to lower grain protein requirement and lack of yield response to N in our study, can be grown with lower N input than hard reds.

Introduction

Wheat (*Triticum aestivum* L.) is the most widely grown staple crop worldwide (Hanson et al., 1982), and is used mostly for human consumption (Evans, 1993). Its adaptability to diverse environments, end use diversity, and high calorie and protein values make wheat an important crop to reduce global food insecurity and hunger (Stone and Savin, 2000; Curtis, 2002). However, wheat production is greatly reduced by drought, which is one of the most yield-limiting abiotic stressor in crops (Morris et al., 1991; Fahaad et al., 2017). Plants under drought stress reduce photosynthetic efficiency (Earl and Davis, 2003). The impact of drought can be minimized with supplemental irrigation which attenuates the large year-to-year grain yield variation due to erratic rainfall events and amounts. Reliable water supply maintains transpiration, allowing plants to be photosynthetically active much longer (Acevedo et al., 2002). Despite the

availability of transpirable water under non-water-limiting conditions, the occurrence of above-optimal ambient temperature still reduces yield (McDonald et al., 1984).

Heat stress can significantly reduce grain yield, especially when occurring during reproductive development (Barnabas et al., 2008; Farooq et al., 2011; Fahaad et al., 2017). Specifically, temperature above optimal at anthesis can cause abortion of wheat florets (Wardlaw and Wrigley, 1994) which decreases the number of grains spike⁻¹ and area⁻¹ – important wheat yield components (Slafer et al., 2014). Moreover, the elevated temperature during the grain-filling phase accelerates senescence, resulting in reduced grain size and weight (Wardlaw and Moncur, 1995). As reviewed by Farooq et al. (2011), heat stress speeds up developmental rates reducing the duration of photoassimilate accumulation in the grains. Plants which can avoid accelerated development (i.e., the stay-green trait) can be resilient under heat stress (Reynolds, 2002; Kumari et al., 2007). The accelerating metabolism of plants under heat stress reduces grain yield even when the availability of water or nutrients is not limiting (Dias and Lidon, 2009).

Nutrient availability, particularly nitrogen (N), is crucial in producing yield and quality in wheat. Plants need N for healthy canopy growth to effectively intercept solar radiation for photosynthesis (Barraclough et al., 2014). In wheat, N is essential for the production of biomass; N stored in this biomass is later remobilized to the grain. It is estimated that up to 95% of the remobilized N is taken up prior to anthesis (Slafer et al., 1990; Palta and Fillery, 1995; Masoni et al., 2007; Waters et al. 2009; Bogard et al., 2010). In some instances, N is over-applied to achieve high grain yield without compromising quality (Diacono et al., 2012).

Optimal wheat quality is desired to prevent market price discounts. Abiotic factors such as water, temperature, and N affect grain quality. Grain quality parameters such as grain test weight, grain protein content, and falling number are important end-use quality indicators with marketing implications. The test weight, a traditional standard grain quality measurement, can be influenced by N levels and weather conditions during reproductive phase (Pushman and Bingham, 1975). The grain protein, is influenced by abiotic factors and can be diluted with increased yield - a common concern in wheat production (Kibite and Evans, 1984; Slafer et al., 1990; Barneix, 2007; Lollato and Edwards, 2015; Iqbal et al., 2016). However, wheat cultivars with the *Gpc-B1* gene, which upregulates protein concentration in the grain, were reported less likely to follow the known grain protein penalty with increasing yield (Tabitta et al., 2017).

Another important desirable quality in wheat is high falling number. The falling number (Hagberg, 1960 and 1961) values in wheat flour have an inverse relationship with alpha-amylase activity (Finney, 1985). Alpha-amylase breaks down grain starch into sugar reducing end-product quality (Chamberlain et al., 1981). Multiple factors interact impacting alpha-amylase activity, including seed coat color (McCrate et al., 1981; Groos et al., 2002), N application (Morris and Paulsen, 1984; Kettlewell, 1999; Kindred et al., 2005), grain drying rate (Kettlewell and Cashman, 1997), oscillating temperature near grain maturation (Farrell and Kettlewell, 2008), and applying irrigation near soft dough stage (Torrión and Stougaard, 2017).

The negative impacts of growing conditions on grain yield and quality, in part, can be reduced with management but are also influenced by genotype (Cooper et al.,

2001; Zheng et al., 2009; Hatfield and Walthall, 2015; Paderewski et al., 2016). Wheat classes have specific grain quality requirements based on their intended end use (Guttieri et al., 2005). Six classes of wheat are grown under diverse growing conditions in the United States (US Wheat Associates, 2018). Hard red spring wheat (HRSW) accounts for 92% of total spring wheat production in the United States (USDA-NASS, 2018). This wheat class is the only one with recent yearly survey records in the state of Montana - the third largest spring wheat producer in the country.

Another class is the soft white spring wheat (SWSW). Although SWSW represents only 6% of spring wheat production in the United States, it is an important market class in the Pacific Northwest. In 2017, SWSW represented 24, 44, and 50% of spring wheat production in Idaho, Oregon, and Washington, respectively (USDA-NASS, 2018). Because of the relatively high grain yield potential and low grain protein requirement of SWSW ($<105 \text{ g kg}^{-1}$; Bole and Dubetz 1986; Sowers et al., 1994) compared with HRSW ($>140 \text{ g kg}^{-1}$; Brown et al., 2005), the SWSW could be an alternative to HRSW for wheat growers in high-yielding regions of Montana, presumably allowing for a reduction in N input. Agronomic management should be tailored specifically for the class of wheat being grown. Currently, there are no specific N recommendations available for SWSW in Montana. Also, the recently available HRSW cultivars with the *Gpc-B1* which upregulates grain protein and the stay-green traits warrant similar investigation.

This study analyzes a relatively small yet diverse pool of HRSW and SWSW cultivars, subjected to different N fertilization and moisture regimes. Grain yield and

three quality parameters (grain protein, test weight, and falling number) were evaluated to characterize the response of HRSW and SWSW to N in either rainfed or irrigated environments. The specific objectives were to: 1) characterize grain yield and protein relationship in each market class, 2) assess grain yield and protein of various HRSW cultivars showing distinct genotypes (*Gpc-B1* gene, non-*Gpc-B1*, and stay-green cultivars); and 3) identify resilient cultivars in terms of yield and other quality parameters when inputs and growing conditions are limiting.

Materials and Methods

Site Description

The study was conducted in 2016 and 2017 at the Northwestern Agricultural Research Center in Creston, MT (48°11'24" N lat, 114°8'24" W long, 894 m elevation, 0% slope) on a Flathead fine sandy loam soil (coarse-loamy, mixed, superactive, frigid Pachic Haplustolls; USDA-NRCS, 2009) with 2.5% organic matter and pH 7.5-8.0. The experiment was a split-plot design with four replications over two environments (irrigated and rainfed). Five N treatments were the main plots and eight cultivars (four HRSW and four SWSW), were the subplots.

Previous crops were alfalfa (*Medicago sativa* L.) and barley (*Hordeum vulgare* L.) in 2016 and 2017, respectively. The soil was plowed during fall and disked during spring. Soil samples were taken during spring before planting at 0-15, 15-60, and 60-90-cm depths and submitted to a commercial laboratory (Agvise Labs., Northwood, ND).

Monoammonium phosphate (MAP, 11-52-0) and potassium chloride (0-0-62) fertilizers were applied according to local guidelines (Jacobsen et al., 2005).

Nitrogen Main Plot

Five total N rates were applied in both years differing on the control treatment. In 2016, the total N for the control treatment was 118 kg ha⁻¹ (76, 8.0, and 34 kg ha⁻¹ from residual NO₃-N plus estimated organic matter mineralization, MAP fertilization, and alfalfa previous crop credit, respectively). In 2017, the total N of the control treatment was 45 kg ha⁻¹ (37 and 8.0 kg ha⁻¹ from residual NO₃-N plus organic matter mineralization and N amounts from MAP fertilization, respectively). Urea (46-0-0) was applied as the N source using a 6-m fertilizer boom spreader calibrated for the amount of urea needed to a summed total N of: 155, 200, 244, and 289 kg ha⁻¹. Fertilizers were incorporated to minimize volatilization losses and seedbed packed for improved seed-to-soil contact.

Cultivar Subplot

The cultivar selection was based on historical data from local field trials addressing yield performance and quality variations. The four HRSW cultivars were ‘Egan’, ‘McNeal’, ‘Solano’, and ‘Vida’. Solano and McNeal have a respective low and high falling number values (Torrion and Stougaard, 2017). Egan has high grain protein due to an introgressed *Gpc-B1* gene (Blake et al., 2014). Vida is known for its relatively low grain protein and higher yields due to an inherited stay-green trait from the cultivar

Reeder (Lanning et al., 2006). The four SWSW cultivars were ‘Alturas’, ‘Alpowa’, ‘Penawawa’, and ‘UI Stone’. Alturas is a high yielding cultivar but with low falling number values. Alpowa yields lower than Alturas but has higher falling number values (Stougaard et al., 2015). Penawawa is an older SWSW cultivar released in late 1980s. UI Stone is a recently released cultivar with high grain yield and end-use quality (Chen et al., 2012). Details of the cultivar pedigrees and sources are shown in Table 2.1.

Table 2.1. Selected semi-dwarf spring wheat cultivars.

Cultivar	Pedigree	PI	Year of Release	Reference
-----Hard Reds-----				
Egan	CAP19/Choteau // McNeal*7/Glupro	671855	2014	Blake et al., 2014
McNeal	RS 6880 / Glenman	574642	1995	Lanning et al., 1995
Solano	DA993-191/Express	644067	2005	AOSCA-NSGVRB, 2006
Vida	Scholar/Reeder	642366	2006	Lanning et al., 2006
-----Soft Whites-----				
Alpowa	Fielder/Potam 70 // Walladay/3/walladay/Potam 70	566596	1994	Washington Agric. Res. Cent. et al, 1998
Alturas	Whitebird / Centennial	620631	2002	Souza et al., 2004
Penawawa	Poram 70 / Fielder	495916	1985	Washington Agric. Res. Cent. et al, 1990
UI Stone	Pomerelle*2/Tui	660550	2013	Chen et al., 2012

*PI = Plant identification

Planting and Pest Control

The experiment was planted on 21 Apr. 2016 and 01 May 2017 using a 7-row planter with 15.2 cm inter-row spacing and 5-cm sowing depth. Target seeding was 270 seeds m^{-2} , adjusted based on thousand-kernel weight, on a 5.5-m long by 1.2-m wide seedbed. Seeds were treated with fungicide (a.i. sedaxane, difenoconazole and mefenoxam) and insecticide (a.i. thiamethoxam). Herbicide (a.i. pyrasulfotole, bromoxynil octanoate, bromoxynil heptanoate and pinoxaden) was applied at 2-tiller stage. Hand weeding was done to remove any surviving weeds. Because the cultivars have different resistance to biotic pressures, fungicides (a.i. prothioconazole and tebuconazole in 2016 and a.i. propiconazole in 2017) were applied at the flag leaf stage. Insecticide (a.i. lambda-cyhalothrin) application was only necessary in 2016.

Environment

Two environments were set; one relied only on rainfall (rainfed) and the other was provided supplemental water through sprinkler irrigation. The irrigated environment plots were supplied with water during the growing season based on the soil water balance and daily crop evapotranspiration (ET_c). The soil water holding capacity was 47 mm 30-cm⁻¹ soil depth. Plant available water was estimated to the active root zone depth (0.45 m from emergence to boot stage and 0.9 m thereafter). To simulate a non-water-stressed environment, irrigation was applied when 35% of plant available moisture was depleted in reference to field capacity. Water depletion was calculated daily by subtracting the ET_c from the current day plant available water. The ET_c was calculated by multiplying

the daily reference grass-based evapotranspiration, retrieved from the Creston weather station (USBR, 2018) ~1000 meters from the plots, by the wheat crop coefficient (Allen et al., 1998). Daily crop coefficient values were linearly interpolated according to the phenological stage: 0.3 from emergence to four-leaf stage; 0.3 to 1.1 from four-leaf to first awn; 1.1 from first awn to medium-milk stage; and 1.1 to 0.2 from medium-milk to physiological maturity (Torrión and Stougaard, 2017).

Data Collection

Growth and reproductive stages were recorded weekly on 10 contiguous plants (early in the season) or 10 contiguous heads (later in the season) using Zadoks et al. (1974) scale. Heading date was recorded when 50% of the heads completely emerged. Physiological maturity occurrence was recorded when 50% of the spikes in the plot had lost green color. Maturation was calculated as the number of days from emergence to maturity. Grain-fill duration was calculated as the number of days from heading to maturity.

Experimental plots were harvested on 25 Aug 2016 and 17 Aug 2017. Grain weight was adjusted to 13% grain moisture. Moisture was determined using near-infrared technology (InfratecTM 1241 Grain Analyzer, Hilleroed, Denmark) which was also used to determine grain protein and grain test weight. The falling number values were obtained using a FN 1700 (PertenTM, Hagersten, Sweden). Falling number, in seconds, is a viscosity measurement obtained by recording the time it takes a stir rod to reach the

bottom of a flour and water suspension, and is a measure of alpha-amylase activity (Finney, 1985).

Statistical Analysis

Data were first analyzed for normality using PROC univariate in SAS 9.4 (SAS Institute, 2014, Cary, NC) following the Shapiro-Wilk test of normality hypothesis. PROC GLIMMIX was used for its efficiency in computing complete analysis for split-plot experiments (Littell, 2006). Year 2017 deviated from the 30-year average and from 2016 (USBR, 2018), thus each year was analyzed separately. Environment, N treatment, and cultivar were set as fixed effects. The option DDFM=KR was used to estimate the denominator degrees of freedom. Replication was set as random effect. SLICE option in SAS was used to analyze any two-way interactions when three-way interaction was insignificant. LINES option for LSMEANS comparisons was used. CONTRAST analysis was performed between the two market classes and the consistent significant difference in grain yield, protein, and falling number between wheat classes led to reanalyzing the data separately for each market class. When the response was insignificant or minimal, regression analyses were carried out to examine trends of LSMEANS using GraphPad Prism 7 (La Jolla, CA).

Yearly Weather and Irrigation

Increase in day time temperatures (maximum) and night time temperatures (minimum) had slow progressions in 2016, but rose rapidly in 2017 (Fig. 2.1A;B). Precipitation received from emergence to harvest was 183 mm in 2016, but only 76 mm

in 2017. Water applied through irrigation was 142 and 167 mm for 2016 and 2017, respectively (Fig. 2.1C;D).

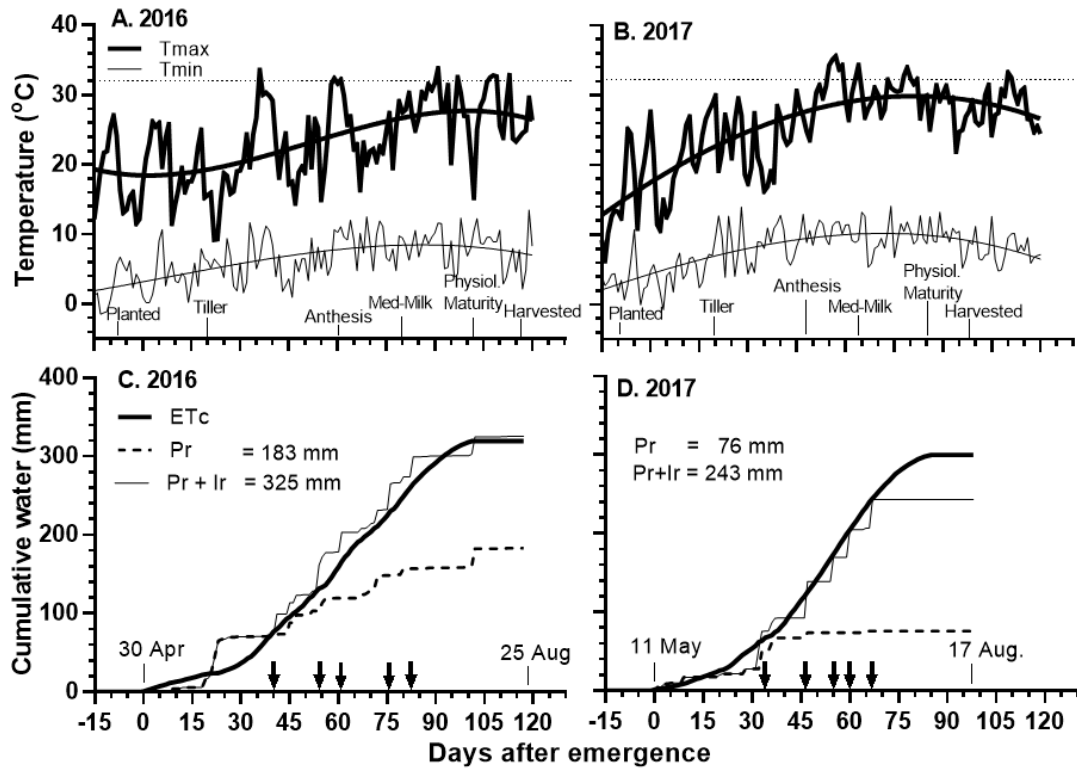


Figure 2.1. Daily maximum (Tmax) and minimum (Tmin) ambient temperatures from planting to harvest in 2016 (A) and 2017 (B). The corresponding cumulative daily crop evapotranspiration (ETc), precipitation (Pr), and irrigation (Ir) are shown for 2016 (C) and 2017 (D). Downward arrows indicate each of the irrigation events. Vertical lines indicate average occurrences of growth and development and the dates of emergence and harvest. Horizontal dotted lines (in panels A and B) represent the wheat critical temperature (32°C; Reynolds et al., 2016).

Results

Correlations Between Yield and Quality Traits

Table 2.2 shows the correlation coefficients between yield and quality traits for HRSW, SWSW, and the two market classes combined. Each of the market classes and the combined data had the same positive or negative correlations, but varying association strengths (coefficients). The exception is that yield and falling number of HRSW had no significant association. A significant ($P < 0.01$) inverse relation between grain yield and protein was observed. However, this negative correlation was smaller in HRSW, than in SWSW.

The HRSW had higher falling number than SWSW. For SWSW, its falling number was inversely correlated ($P < 0.01$) with yield. However, this specific association was not observed in HRSW ($P > 0.05$). The grain protein and falling number were positively related ($P < 0.01$) for both classes although the association in HRSW was not as strong as in SWSW. For each classes and the combined data, grain yield and test weight were positively correlated ($P < 0.01$).

Table 2.2. Correlation coefficients between grain yield (GY), grain protein content (GPC), grain test weight (GTWT), and falling numbers (FN), for hard red (HRSW), soft white (SWSW) spring wheat, and the two market classes combined.

Traits	Class			HRSW			SWSW			All		
	Grain yield (GY)	Grain protein content (GPC)		Grain test weight (GTWT)			Falling number (FN)					
GY	1	-0.26**	-0.64**	-0.36**	0.83**	0.77**	0.80**	-0.08	0.33**	-0.25**		
GPC		1	1	1	-0.34**	-0.44**	-0.38**	0.15**	0.30**	0.65**		
GTWT					1	1	1	-0.24**	-0.22**	-0.32**		
FN								1	1	1		

** indicates significance at $P < 0.01$

Main Effects and Interactions

Grain Yield. For HRSW, yield response to N was observed only under irrigated condition (significant E x N, Table 2.3). The influence of N (statistically) to grain yield in 2016 irrigated environment was due to the depressed grain yield of the 200 kg N ha⁻¹ N level in relation with the higher N level applications, but similar to the control (Fig. 2.2A). However, no yield trends were identified in either environment in 2016. In 2017, yield regression analysis coefficients were insignificant from slope 0 ($P > 0.05$) for the rainfed environment even with the low level of N control (45 kg N ha⁻¹). Under irrigated environment, yield response to N was observed at 155 kg N level and no yield gain was obtained with N application that exceeded this N level, also referred here as the ‘response breakpoint’ (X0; Fig. 2.2B) using an upper-plateau model.

The 2016 growing season (Fig. 2.1) resulted in at least 7-d longer mean grain filling duration (44 d) than the warmer and drier 2017 (37 d). In 2016, irrigation increased ($P = 0.03$) yield of HRSW but only 14% in relation to the rainfed. In 2017, irrigation increased ($P < 0.01$) yield by 35% - at least twice the irrigation impact in 2016. Overall, yield reduction from a near-average to a drought year was 38% (Fig. 2.3A,C).

The cultivar main effect for HRSW in 2016 did not interact with other factors (Table 2.3). During this near-average year, Egan (with the *Gpc-B1* gene) yielded similarly to Solano and McNeal regardless of environment (Fig. 2.3A). Vida, a cultivar with the stay-green trait, was the highest yielding cultivar among HRSW regardless of environment. The E x C interaction ($P < 0.01$) of HRSW in 2017 is shown in Fig. 2.3B.

From this simple interaction (no criss-cross), Vida outperformed the rest of HRSW in both environments.

Table 2.3. Yearly analysis of variance showing probability values of the main and interactions effects in each market class.

Source of variation	-----2016-----				-----2017-----				
	df	GY	GPC	GTWT	FN	GY	GPC	GTWT	FN
-----hard red-----									
Environment (E)	1	0.035	0.005	0.004	<.0001	0.005	0.621	<.0001	0.824
Nitrogen (N)	4	0.313	0.001	0.079	0.309	0.958	<.0001	0.032	0.424
E x N	4	0.032	0.164	0.662	0.937	0.039	0.009	0.143	0.556
Cultivar (C)	3	0.002	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
E x C	3	0.341	0.026	<.0001	0.001	0.026	0.002	0.001	0.001
N x C	12	0.727	0.683	0.491	0.425	0.982	0.115	0.412	0.045
E x N x C	12	0.254	0.457	0.134	0.846	0.381	0.142	0.336	0.692
-----soft white-----									
E	1	0.007	0.228	0.006	0.001	0.002	0.003	<.0001	0.232
N	4	0.527	0.007	0.667	0.242	0.711	<.0001	0.261	0.214
E x N	4	0.845	0.332	0.163	0.069	0.11	0.009	0.734	0.445
C	3	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
E x C	3	0.74	<.0001	<.0001	0.001	0.001	<.0001	0.331	<.0001
N x C	12	0.245	0.781	0.426	0.844	0.967	0.026	0.117	0.087
E x N x C	12	0.923	0.347	0.382	0.469	0.838	0.051	0.443	0.37

df, degrees of freedom; GY, grain yield; GPC, grain protein content; GTWT, grain test weight; FN, falling number

For SWSW, two-way or three-way associations of main effects did not exist in 2016 (Table 2.3), but E and C effects were significant ($P < 0.01$) for yield. Irrigation increased yield but only a 16% advantage in relation to rainfed which was similar to the irrigation yield response of HRSW in 2016. Among SWSW cultivars, Alturas and UI Stone had the highest yield and Penawawa was the lowest. The rainfed yield for Alturas and UI Stone matched the irrigated yield for Alpowa and Penawawa (Fig. 2.3C).

The E x C interaction ($P = 0.001$) for 2017 SWSW yield was due to the similarity of all SWSW cultivars yield performance under rainfed environment, but Alturas and UI Stone had significantly greater yield under irrigation (Fig. 2.3D) than Alpowa and

Penawawa. Moreover, Alturas and UI Stone consistently performed better in both the near-average and the dry and hot year. Overall, the irrigation increased yield by 48% more compared with the rainfed, an approximately three-fold increase relative with 2016. The overall reduction in yield from 2016 to 2017 was 36%, which was similar to yield reduction for HRSW.

No significant N response was observed in either year or environment for SWSW. A linear-upper plateau or segmented linear model to evaluate yield trends was unjustifiable. Thus treatments means were fitted linearly in which the coefficient was insignificant from slope 0 (Fig. 2.2B).

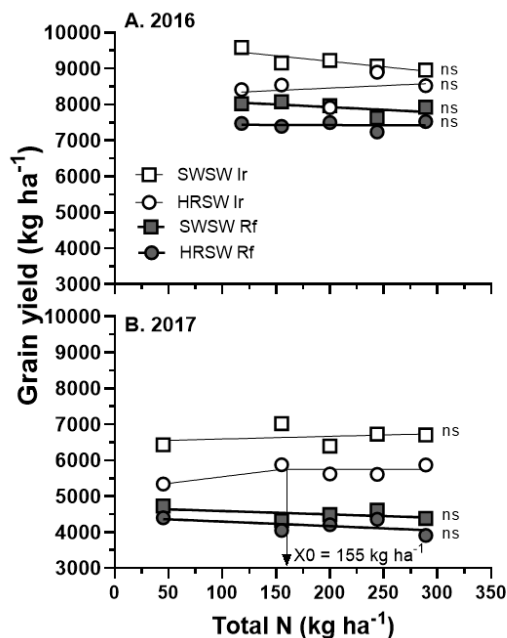


Figure 2.2. Nitrogen (N) x environment (Ir, irrigated; Rf, rainfed) interaction means for grain yield response of hard red (HRSW) and soft white (SWSW) spring wheat in 2016 (A) and 2017 (B). N treatment check are 118 and 45 kg ha⁻¹ for 2016 and 2017, respectively. The X0 represents the maximum grain yield response to N from both the mean separation of the analysis of variance and the non-linear upper plateau model. The ns assignment represent the non-significant linear regression coefficient to zero.

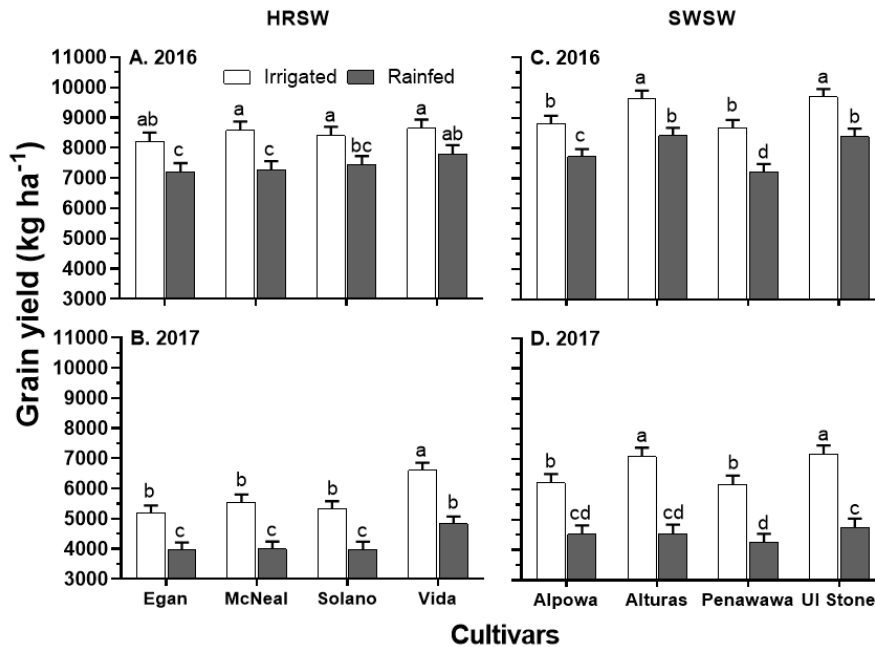


Figure 2.3. Grain yield response of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat cultivars for 2016 and 2017. Error bars are the standard error of the difference among cultivars within each market class and year. Same letter assignment indicates the lack of significant differences between cultivars within a market class across irrigated and rainfed environments for each year ($\alpha = 0.05$).

Grain Protein Content. There was an E x C interaction ($P < 0.05$) for grain protein for either of the market classes and years (Table 2.3). In 2016, the non-*Gpc-B1* cultivars (i.e., Solano, McNeal, and Vida), had 8.0-10 g kg⁻¹ higher grain protein in the irrigated environment, whereas the increase for the *Gpc-B1* gene cultivar (Egan) was only 5.0 g kg⁻¹ (Fig. 2.4A). During 2017, grain protein was similar in both environments for HRSW (Fig. 2.4B). Among SWSW cultivars, Alpowa had higher grain protein with irrigation over rainfed in 2016 (Fig. 2.4C). Other SWSW had similar grain protein across environments in 2016. In 2017, all SWSW cultivars but Penawawa had greater grain protein in the rainfed environment as opposed to the irrigated treatment (Fig. 2.4D).

In 2016, increased N levels improved ($P < 0.01$) grain protein of HRSW and SWSW without any interaction with the other main effects. Regression analysis shows the maximum grain protein-N response at a higher N level under rainfed compared with the irrigated environment for either class (Fig 2.5A;C). In 2017, the E x N interaction was significant ($P < 0.05$) for both HRSW and SWSW. The grain protein-N response of HRSW rainfed was significantly higher than the irrigated only when N level was low (i.e., 45 kg N ha⁻¹; Fig. 2.5B) but as N increased, the grain protein was numerically higher in irrigated than rainfed, although not significantly different. This scenario was not observed in 2016 for this class because grain protein was consistently higher in the irrigated environment compared with rainfed (Fig. 2.5A). The SWSW grain protein was consistently higher in the rainfed environment across N treatments in 2017 (Fig 2.5D), but no significant difference was observed between environments in 2016 (Fig. 2.5C).

The year 2016, with typical weather for the region, resulted in low grain protein-N response, and grain protein was relatively closer to the critical market protein requirement for the respective classes (Fig. 2.5A;C). During the dry year of 2017, grain protein-N response in SWSW resulted in grain protein that exceeded the market requirement except for the control N level (Fig. 2.5B;D).

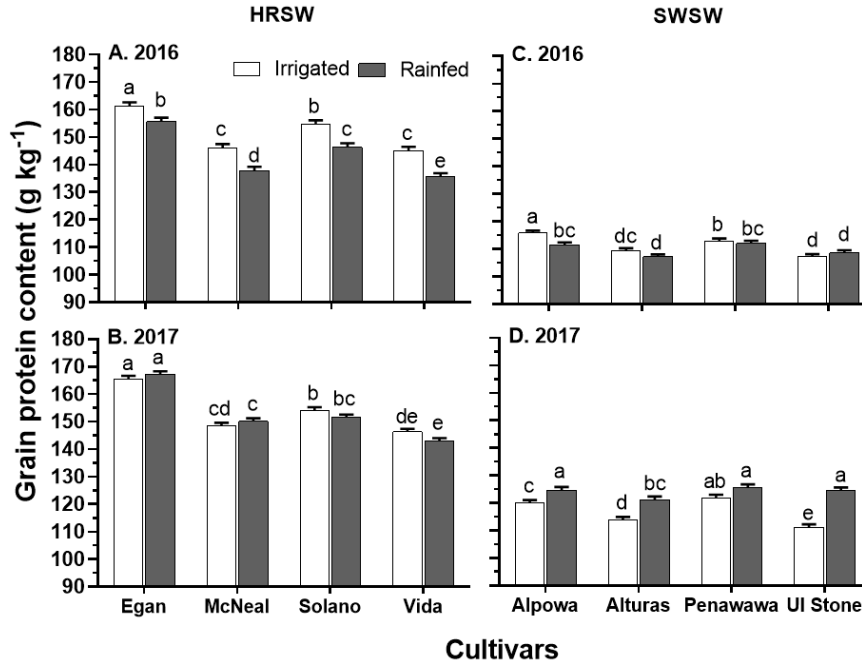


Figure 2.4. Grain protein content response of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat cultivars for 2016 and 2017. Error bars are the standard error of the difference among cultivars within each market class and year. Same letter assignment indicates the lack of significant differences between cultivars within a market class across irrigated and rainfed environments for each year ($\alpha = 0.05$).

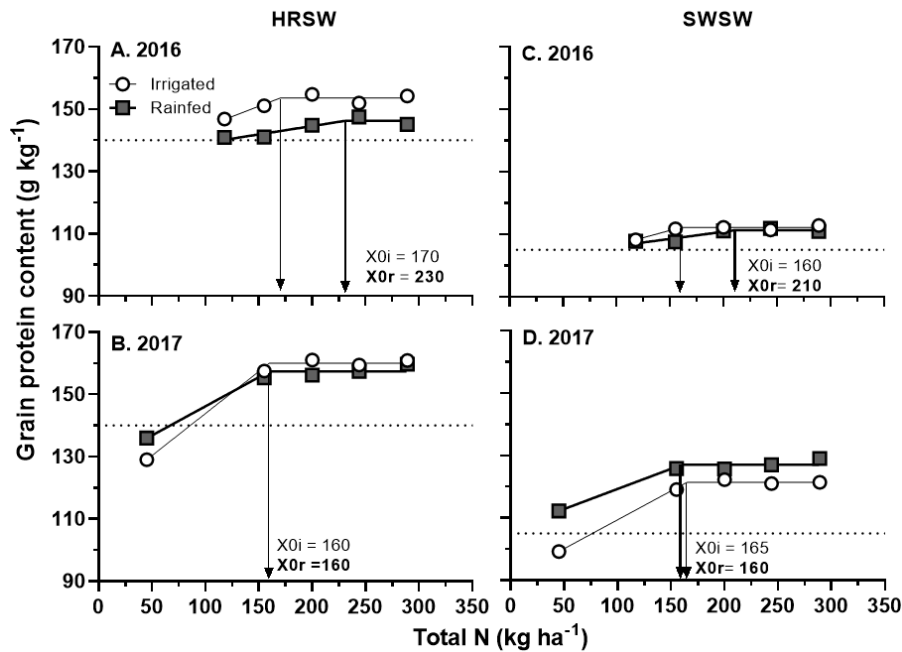


Figure 2.5. Nitrogen (N) x environment interaction means for grain protein content (GPC) of hard red (HRSW; A,B) and soft white (SWSW; C,D) spring wheat in 2016 and 2017. The X0i and X0r represent the maximum GPC response to N using a non-linear upper plateau model for irrigated and rainfed environments, respectively. The horizontal dotted lines represent the common market protein requirement for HRSW (i.e., > 140 g kg⁻¹) and SWSW (i.e., < 105 g kg⁻¹).

Falling Number. Falling number of each of the market class was consistently influenced by E x C association ($P < 0.01$) in both years. The reduction of falling number with irrigation for Egan and McNeal HRSW, as well as Alturas and Penewawa SWSW were more subtle than the rest of the cultivars in 2016. The observed lowering of falling number with irrigation in 2016 was not observed in 2017, except for UI-Stone SWSW. The E x C falling number interaction in HRSW in 2017 can be attributed to the numerically higher value of falling number of irrigated McNeal, though insignificant (Table 2.4). Despite the E x C interaction, McNeal and Egan HRSW had the highest falling number among cultivars across water regime environments and years. In general,

SWSW showed lower falling number than HRSW. Specifically, Alpowa showed higher falling number than the rest of the SWSW cultivars which was consistent across water regimes and years (Table 2.4).

In 2017, HRSW falling number also was influenced by N x C interaction (Table 2.3). Closely, this was because among cultivars, McNeal showed increased falling number (data not shown) at 155 kg N ha⁻¹ in 2017.

Grain Test Weight. The grain test weight was numerically higher under irrigated than rainfed, and also higher in 2016 than in 2017 (Table 2.4). The test weight difference between irrigated and rainfed conditions was higher in 2017. The test weight for HRSW had an E x C interaction in both years (Table 2.3). All cultivars, except Vida, increased test weight with irrigation in 2016. Solano and Vida had the highest test weight among HRSW across environments in 2017 (Table 2.4). The E x C interaction was attributed to the insignificant test weight response of Vida and UI Stone in 2016 with moisture regime environments, as well as the varying degree of test weight response (numerically) of Vida to irrigation in 2017 (Table 2.4). For SWSW, irrigation increased test weight at similar degree for all cultivars in 2017. During this year UI Stone and Alpowa had the highest test weights. However, during 2016 environment and cultivar interaction occurred because all SWSW but UI Stone responded to irrigation.

The N effect for grain test weight was significant only for HRSW during the 2017 season. The highest grain test weight was obtained with the control N (45 kg N ha⁻¹).

Increasing N applications resulted in significantly lower grain test weight compared with the control treatment.

Table 2.4. Grain test weight and falling number responses of wheat cultivars under irrigated and rainfed environments in 2016/17. Same letter assignment indicates lack of significant differences between cultivars within market classes across irrigated and rainfed environments of each year.

Classes/ Cultivars	Falling number		Grain test weight	
	2016	2017	2016	2017
	-----seconds-----		-----kg m ⁻³ -----	
HRSW	-----Irrigated-----			
Egan	479.0 c	482.2 bc	802.4 e	770.7 c
McNeal	477.8 c	512.5 a	814.8 b	778.5 b
Solano	396.4 f	398.9 de	818.1 a	795.8 a
Vida	347.9 g	358.7 f	809.1 cd	792.7 a
Mean	425.3 ± 4.5†	438.1 ± 7.5†	811.1 ± 1.7†	784.4 ± 2.3†
	-----Rainfed-----			
Egan	502.5 b	479.9 c	787.2 f	745.9 d
McNeal	525.8 a	495.2 ab	802.9 e	746.3 d
Solano	449.4 d	407.8 d	810.4 bc	769.8 c
Vida	409.4 e	377.8 ef	804.7 de	773.2 bc
Mean	471.8 ± 4.5†	440.2 ± 7.5†	801.3 ± 1.7†	758.8 ± 2.3†
SWSW	-----Irrigated-----			
Alpowa	355.9 b	399.5 ab	825.7 a	805.3 ab
Alturas	283.4 d	305.3 g	814.3 b	804.9 ab
Penawawa	318.7 c	356.3 cd	814.3 b	801.0 b
UI Stone	293.5 d	338.8 ef	809.9 bc	806.8 a
Mean	312.9 ± 6.4†	350.0 ± 8.0†	816.1 ± 2.6†	804.5 ± 2.5†
	-----Rainfed-----			
Alpowa	412.3 a	408.3 a	807.7 bc	774.3 c
Alturas	315.0 c	322.5 fg	800.8 d	769.2 d
Penawawa	348.7 b	347.6 de	795.2 e	766.1 d
UI Stone	345.8 b	376.3 bc	801.9 cd	775.7 c
Mean	355.5 ± 6.4†	363.7 ± 8.0†	801.4 ± 2.6†	771.3 ± 2.5†

† corresponds to the standard error within a market class across irrigated and rainfed environments of each year.

Discussion

Grain Yield

The overall grain yield reduction of 37% from a near-average year to a drought year across cultivars was attributed to the rising temperature that began at tillering and rose further to over 30°C between flowering and harvest (Fig. 2.1B). Wheat yield is typically reduced under these temperatures (Reynolds et al., 2016; Fahad et al., 2017; Torrion and Stougaard, 2017). The abrupt rise of temperature with low precipitation in 2017 resulted in faster physiological maturity, 16 d shorter in 2017 versus 2016, and was accompanied by abrupt cessation of crop water demand (Fig. 2.1C;D). This was due to an earlier occurrence of anthesis and a shorter grain filling duration in 2017 than in 2016. This rapid developmental progression and high water demand per unit time resulted in more frequent irrigation events and consequently more water applied in 2017 than during the near-average year of 2016 (Fig.2.1). The water applied to the irrigated environment in 2017 guaranteed no water stress. Thus, the observed grain yield reduction between years was associated with the elevated temperature.

The different yearly growing conditions, adding a contrasting water regime, favored evaluating cultivars with distinct genetic characteristics for resiliency. Given this variability, the SWSW yields were generally more resilient than HRSW (Fig. 2.3). Within HRSW, Vida (stay-green trait) was a resilient cultivar with the highest grain yield in both years. This advantage can be mainly attributed to an extended period of grain fill (Chen et al., 2011; Naruoka et al., 2012; Semenov et al., 2014) also observed in crops

other than wheat (Banziger et al., 1999; Borrell et al., 2000). Naruoka et al. (2012) related the longer green tissue activity of Vida's parent material (Reeder) to a more vigorous root system, especially under hot and dry conditions. A well-developed root system can reduce the negative impact of water stress (Manschadi et al., 2006) by optimally using transpirable water (deeper in the soil profile) resulting in a cooler canopy temperature (Pinto and Reynolds, 2015) mitigating the impact of heat stress.

The impacts of weather growing condition and water management on grain yield were greater than the impact of N levels (considering that in the first year of study, the control N had high N level). The less yield-limiting growing conditions of 2016 (and high N level for the control) contributed to the lack of effect of N on yield, regardless of wheat class. Even with the lower N level of the control in 2017, its effect on yield remained minimal for irrigated SWSW and both classes under rainfed conditions. The limited effect of N on yield, despite the low levels of N for the control in 2017, could be due to the effect of high temperatures depressing yield, even under irrigated conditions (McDonald et al., 1984). Still, the lack of effect of N levels on SWSW yield suggests a lower N requirement for this class than HRSW (Fig. 2.2B). High N application is frequently focused on grain protein increase (Corassa et al., 2018) rather than grain yield gains. Grain yield is more critical than protein for SWSW, leading to lower N requirement of this class.

Although, Egan usually has lower grain yield than other non-*Gpc-B1* cultivars (Heo et al., 2018), the *Gpc-B1* gene introgression (in Egan) was documented in our study not detrimental to grain yield when compared with the yield potential of McNeal (one of

Egan's parent material) regardless of irrigation treatment or N level (Fig. 2.3A;B). Egan's grain yield in 2016 with irrigation was similar to the rest of the HRSW including the highest yielding and resilient cultivar, Vida. However, Egan's yield during the 2017 dry year was significantly lower than Vida, yet remained similar to McNeal and Solano regardless of water regime environments or N levels.

Generally, increased grain yield was negatively correlated with grain quality specifically grain protein and falling number (Table 2.2). The inverse relationship of grain yield with protein is commonly reported (Kibite and Evans, 1984; Slafer et al., 1990; Barneix, 2007; Lollato and Edwards, 2015; Iqbal et al., 2016). However, the main effects and interactions had significant impact on protein and other quality parameters. Thus in the next subsection, the various effects were evaluated to examine this relationship.

Grain Quality

Grain Protein Content. Based on our results, protein dilution showed in Table 2.2 (negative correlation with yield) is not straightforward particularly when analyzing different classes and environments. For example, during the less-limiting growing year (2016), the grain protein of irrigated environment was consistently higher than the rainfed for HRSW (Fig. 2.4A). A similar response was observed for Alpowa (Fig. 2.4B) whereas the other SWSW had statistically similar protein content in both environments. As expected, irrigation resulted in a higher yield. But our data suggest no indication of grain protein reduction as a result of higher yield when irrigated for either wheat class in an

average year (2016). However, in 2017, the HRSW grain protein between water regime environments did not differ whereas the SWSW increased under rainfed conditions. This explains the sharper negative grain yield-protein association in SWSW.

For SWSW, protein dilution would be advantageous given its low grain protein requirement ($< 105 \text{ g kg}^{-1}$). Therefore, managing irrigation to maximize yield potential for SWSW is appealing to growers because the supplemental water likely leads to increased yield without negatively impacting grain protein threshold. However, the observed rise in temperature in the region (Lanning et al., 2010) may become an important issue for this wheat class. The 2017 results suggest that yield suppression in a year with high temperature may lead to an undesirable increase in protein, especially with increased N levels (Fig. 2.5D).

Nitrogen application consistently increased grain protein across classes, environments, and years. In 2017, there appeared to be protein dilution in irrigated SWSW – which is a desirable aspect of this class (Fig. 2.5D). This was evident from the negative yield-protein correlation which was stronger in SWSW than HRSW. For HRSW, grain protein dilution with irrigation (via increased yield) was only critical when N level was low (N control treatment of 2017; Fig. 2.5B). In fact, in HRSW the irrigated treatment during the near-average year of 2016 had significantly higher grain protein content than the rainfed across N levels (Fig. 2.5A). Long et al. (2017) reported similar findings with the present study where low grain protein was observed when low N was combined with more favorable growing conditions, but when N was sufficient and yield increased, protein increased as well.

Although the critical N level for yield remained unclear in this experiment, the critical level for grain protein is provided in Fig. 2.5. We define protein critical-N here as the X0 breakpoint (maximum protein response with the lowest N level). The SWSW protein maximum response advances beyond the ideal protein threshold for this class (<105 g kg⁻¹). For HRSW, the maximum protein response is much more straightforward given the higher protein demand for this class (>140 g kg⁻¹). In some years, though, when premium for grain protein is nonexistent or low, the maximum protein-based response (X0; Fig. 2.5) is less meaningful. Historically, avoiding protein discounts has been more profitable than targeting a premium for higher protein (Baker et al., 2004).

Apprehension exists about adopting a leading cultivar for high yield due to protein dilution. Vida for instance, outyielded the rest of HRSW cultivars especially under severe drought and did have the lowest protein among HRSW in this study. However, its protein content only fell below the market threshold under rainfed conditions in 2016, which is not so unprecedented. In this region of Montana, irrigation tends to have no negative impact on grain protein content compared to rainfed during average years (Torrión and Stougaard, 2017). The protein-based market discount is not a concern when planting Egan (with the *Gpc-B1* gene) even with the overall negative yield-protein correlation within the HRSW pool (Table 2.2). Egan's relative yield stability compared with the other HRSW (except Vida; Fig. 2.3A;B), and its inherently superior quality (GPC > 150 g kg⁻¹) regardless of management or growing year, suggest a lack of yield-protein tradeoff with this *Gpc-B1* cultivar, as was also reported by Tabitta et al. (2017) in a meta-analysis of *Gpc-B1* gene.

Falling Number. Decreased falling number is a concern for wheat producers in northwestern Montana. Our study confirmed that there is a higher probability of lowered FN under irrigated environments regardless of market class. Torrion and Stougaard (2017) suggested that lowered FN is further triggered by irrigation later in the season. Lowered falling number is evident during times of extreme fluctuations in day and night temperatures during grain maturation (Farrel and Kettlewell, 2008) as in the case of this study's 2017 season. Growers may also choose cultivars such as McNeal or Egan, to obtain higher falling number (Table 2.3) under unpredictable growing conditions.

Light seed coat color of SWSW has been associated with low falling number (McCrate et al., 1981; Groos et al., 2002). On average, the HRSW (inherently darker seeds) indeed showed higher FN compared with SWSW (inherently lighter seeds). However, in some cases some SWSW cultivars had similar or higher falling number than some HRSW in this study. This suggests that even a lighter seed color in the case of SWSW may not lead to low FN in this region. However, this warrants more investigations as late-season triggers (rainfall, fluctuating air temperature) for lowered falling number vary from year-to-year.

Grain Test Weight. Low grain test weight can also reduce wheat market price (CHS, 2018). Regardless of cultivars, test weight was positively correlated with grain yield for HRSW (Tables 2.2 and 2.4). This was also true for SWSW except in the rainfed environment during the hot year of 2017. The lower test weight during stressed growing

conditions and management has been previously reported (Guttieri et al., 2001; Torrion and Stougaard, 2017). The lower test weight in 2017 than in 2016 can be attributed to the relatively shorter grain fill duration due to temperature stress (Hernandez-Espinoza et al., 2018; Yabwalo et al., 2018) that caused the accelerated maturation. Specifically, the impact of N on test weight was only observed for HRSW during the dry year (2017). Low N resulted in higher test weight than the higher N applications. This is contradictory to what is reported in the literature (Pushman et al., 1975), however this uncommon impact to test weight can be due to the compounded impact of abiotic factors (N and temperature). During a dry and hot year, wheat reduces number of kernels per head or unit area (Farooq et al., 2011; Fahad et al., 2017; Torrion and Stougaard, 2017) due to floret abortion. In our study, no floret abortion was expected at anthesis because the reach to a destructive level (Fig. 2.1). It could be that the low-level N in 2017 influenced the reduction of the potential seed number. As a consequence, the reduced seed number (carbon sink) leads to greater grain test weights on low N during dry and hot years compared with the high N levels.

Conclusion

The inverse relationship between the grain yield and protein was not exclusively due to high yields but was also greatly influenced by growing conditions that varied between years. The SWSW cultivars were more prone to lowering grain protein with increased yield, which is desirable for this class, than HRSW. The grain protein-N

response was maximized at lower N levels for irrigated versus rainfed environments for both HRSW and SWSW during the more favorable growing conditions (2016). This was not the case during the year in which yield was limited with temperature (2017), where the maximum grain protein-N response was similar between moisture regime environments for either of the market class. The yield of *Gpc-B1* cultivar (Egan) was comparable to the rest of the HRSW pool, except for Vida during the dry and hot year. Moreover, Egan remained to have high protein which suggests a lack of grain yield-protein tradeoff of this cultivar. In terms of cultivar selection for adaptation to temperature variation between years, Vida is resilient in terms of yield, but less resilient in terms of grain protein compared with Egan. For the SWSW class, Alturas and UI Stone were superior in terms of grain yield and quality. Our two years of data suggest that SWSW can be grown with lower N input than HRSW. This assessment is based on its lower grain protein requirement as well as the lack of yield response to N.

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CHAPTER THREE

NITROGEN AND WATER IMPACTS ON GRAIN YIELD AND COMPONENTS OF
DIFFERENT WHEAT CLASSES

Contribution of Authors and Co-Authors

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Author: Breno Bicego

Contributions: Collected and processed experimental data, analyzed and interpreted results, and wrote manuscript for journal submission.

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Contributions: Conceived and designed experiment, collected and processed experimental data, collaborated with interpretation of results, and manuscript preparation.

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NITROGEN AND WATER IMPACTS ON GRAIN YIELD AND COMPONENTS OF
DIFFERENT WHEAT CLASSES

The following chapter has been prepared for submission to a peer-reviewed journal

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Abstract

The changing climate demands identifying traits that are more plastic to heat and drought stresses. Physiological selection may be an important tool to aid breeders achieve improvements more rapidly. However, a genotype may respond differently to agronomic management and environmental variations. Ideally, the plant should perform well in both unfavorable and ideal conditions. The main objective of our study was to analyze the impacts of differential moisture regimes and nitrogen fertilization on grain yield, and its components and traits on a set of eight cultivars from two important spring wheat classes in the Pacific Northwest over two years. Specifically, our goal was to identify resilient cultivars and plastic yield components and traits related to heat and drought. Soft white had overall higher grain yield than hard red spring wheats. We found that, across moisture regime environments and year, productive tiller number had consistently a direct relation with kernel number per area, which was strongly related to grain yield.

Grain-fill duration was an important trait especially under heat and drought stress. During the heat and drought stressed year, kernel weight was an important yield component and had neutral relation with kernel number. Nitrogen fertilization had effect on grain yield only during the hot and dry year with irrigation, but no effect was observed under rainfed conditions for this year.

Introduction

Wheat (*Triticum aestivum* L.) is the staple crop covering a large share of the agricultural land and is the most important food source for humans worldwide (Curtis, 2002). As estimated by the FAO (2018), wheat and its products represent 18% of the daily calorie intake. The exponential increase in global population coupled with the rising temperature predictions (IPCC, 2018), make it imperative to adapt and increase food production. Heat stress is a major constraint in wheat production globally (Barnabas et al., 2008; Farooq et al., 2011; Fahaad et al., 2017). Lanning et al. (2010) reported how high temperatures, especially when coincident with reproductive stages, may affect wheat in Montana.

The Pacific Northwest is an important spring wheat producer region in the USA. Soft white spring wheats are mostly grown in the western states such as Washington, Oregon, and Idaho whereas hard reds are the main spring wheat produced in Montana (USDA-NASS, 2018). Hard red wheat has overall lower yield potential than soft white wheat (Stougaard et al., 2015), mostly because hard red wheat needs to obtain a higher grain protein content, which is usually inversely correlated with grain yield (Kibite and

Evans, 1984; Slafer et al., 1990; Barneix, 2007; Lollato and Edwards, 2015). However, recent cultivars that extend green leaf period after heading and consequently have longer grain-fill duration have shown grain yield advantage, specially under stressed conditions (Chen et al., 2011; Naruoka et al., 2012; Heo et al., 2016). The grain-fill duration is crucial for grain yield because up to 95% of the carbohydrate reallocated to grains is produced after anthesis (Evans, 1975). Longer grain-fill duration is reported to be directly related to kernel weight (Naruoka et al., 2012; Blake et al., 2018).

Kernel weight along with kernel number per area are the major determinants of final grain yield. While kernel number is considered a coarse regulator of grain yield, grain weight is mostly responsible for the final adjustments (Slafer et al., 2014). Most of the grain yield gains during the twentieth century was obtained by increasing the kernel number and in fact, the kernel weight has been reduced in modern cultivars (Calderini et al. 2000). Therefore, identifying traits related to kernel number is crucial for grain yield increases.

Kernel number is highly influenced by productive tiller number (Golba et al., 2018). High tillering was reported as an important trait related to phenological plasticity under drought (Blum et al., 1990; Baum et al., 2003). Naruoka et al. (2011) reported positive correlation between productive tiller number and grain yield in either irrigated or drought and heat stressed conditions. However, Nasseer et al. (2016) did not always find higher grain yield in high tillering wheat, because tillering negatively affected kernel weight and the number of kernels per head. The number of spikelets per head might be a determinant of the potential number of kernels each head can produce. Borojevic (1986)

suggested that larger spikes would contribute to photosynthetic activity and increased storage capacity.

Identifying target traits is a first step to a successful breeding program (Trethowan et al., 2010). Detecting traits that are easily screened in early stages may aid breeders' selection of potential parents as limited seed supply preclude multi environmental trials (Talbert et al., 2001), and grain yield estimations are more reliable in further steps with higher number of individuals. Physiological selection is a complementary tool to breeding techniques and have potential to improve yield gains more rapidly (Reynolds, 2002). Although a given trait may be advantageous in one environment, but insignificant or detrimental in other, plastic traits may provide a genotype stability in diverse environments (Sadras et al. 2009).

In addition to genetic improvements, agronomic management is a key factor to increase wheat grain yield (Frederick and Bauer 2000; Fischer, 2014; Graybosch, 2014). Irrigation and nitrogen fertilization are major agronomic inputs in modern wheat production. Supplemental water prevents stomatal closure, insuring that the green tissues remain photosynthetically active (Acevedo et al., 2002). Stomata closure implies reduced efficiency in absorbing and converting photosynthetic active radiation into new dry matter (Earl and Davis, 2003). Although it has been reported that fertilizer application can improve the efficiency of crop use of available water, it is also known that nitrogen absorption is highly dependent on soil moisture availability (Garg, 2013). Nitrogen is essential for biomass production and healthy canopy to intercept energy for

photosynthesis. Under ideal conditions grain yield is closely related to N availability and uptake (Barraclough et al., 2010)

The main objective of the experiment was to analyze the impact of major management practices (N fertilization and water regime environments) on grain yield, maturity traits, and yield components of eight spring wheat cultivars from two important classes in the Pacific Northwest over two growing seasons. The specific objectives were to: 1) identify resilient cultivars based on yield component variation across environments and years; and 2) assess important key traits and yield components, which are more resilient to changing climate.

Materials and Methods

Experimental Design

The experiment was conducted at the Northwestern Agricultural Research Center in Creston MT, on a Flathead fine sandy loam soil in 2016 and 2017. The study had a split-plot design with four replications over two water regime environments (irrigated and rainfed). The main plot was level of nitrogen. Five levels of N were applied both years differing only on the control - 118 kg ha⁻¹ and 45 kg ha⁻¹ in 2016 and 2017 respectively. In both years, urea (46-0-0) was applied and incorporated to the soil to a summed total N of 155, 200, 244, and 289 kg ha⁻¹. The subplots were the eight spring wheat cultivars. Four hard red ('Egan', 'McNeal', 'Solano', and 'Vida') and four soft white cultivars ('Alturas', 'Alpowa', 'Penawawa', and 'UI Stone') were selected based on diversity in grain yield potential and phenological traits according to historical data from field trials.

Two water regime environments were set in each year –rainfed and irrigated. Irrigation was provided based on soil water balance and daily crop evapotranspiration. Each of the irrigation events was applied when the plant available water was depleted by 35%. Details about the experimental design, soil sampling and fertilization, cultivars, environment, planting, and pest control are available in materials and methods section of Chapter II.

Data Collection

Phenological development was recorded on a weekly basis on 10 contiguous plants using Zadoks et al. (1974). Heading date was recorded when 50% of the heads completely emerged. Physiological maturity date was recorded as days from emergence to when 50% of the spikes in the plot had lost green color. Grain-fill duration is the number of days from heading to maturity.

Aboveground biomass samples were collected from two random inner plot rows at 1-m length each (0.30 m^{-2}) at maturity and dried for at least 48h or until the dry weight was stable. Before drying, the productive tiller number per area was determined and 10 heads were randomly collected to determine the average number of spikelets per head.

Plots were harvested on 25 Aug. 2016 and 17 Aug. 2017. Yield was adjusted to 13% grain moisture as determined using near-infrared technology (InfratecTM 1241 Grain Analyzer, Hilleroed, Denmark). Thousand kernel weight was determined by weighing two sets of 500 kernels counted using vibratory seed counter (Seedburo 801 Count-A-

Pak, Chicago, IL). The harvested plot weight and the thousand kernel weight were used to estimate the kernel number per area.

Statistical Analysis

PROC GLIMMIX in SAS 9.4 (SAS Institute, 2014, Cary, NC) was chosen because of the lack of normality of the data after running PROC UNIVARIATE for each variable response. The GLIMMIX procedure is also efficient in computing complete analysis for split-plot experiments (Littell, 2006). Environment, N treatment, and cultivar were set as fixed effects whereas year and replication were set as random effect. SLICE option in SAS was used to analyze any interactions. LINES option for LSMEANS comparisons was used. Correlations among traits were computed using PROC CORR in SAS 9.4.

Weather and Irrigation

The 2017 growing season was characterized with severe heat and drought stress. Several days had temperatures above 32°C, and the total precipitation from Jul through Aug was only 7 mm. The Jul average maximum temperature (Tmax) in 2017 was 5.2 and 3.8 degrees higher than in 2016 and 29-yr average (1989-2017), respectively. Precipitation in 2017 was less than half (76 mm) of that received in 2016 (183 mm). Precipitation and ambient temperatures in 2016 were close to the 29-yr average (Table 3.1).

Table 3.1. Average monthly minimum (Tmin) and maximum (Tmax) ambient temperature and monthly precipitation from 2016, 2017, and the 29-yr average obtained at Creston, MT weather station (USBR, 2019). Total monthly irrigation and total water received are recorded in the table in mm.

Year	Month	Tmin	Tmax	Precipitation	Irrigation	Total
		-----°C-----		-----mm-----		
2016	May	4.6	18.7	71	-	71
	Jun	6.7	24.2	49	84	133
	Jul	8.9	25.9	39	58	97
	Aug	7.6	27.5	26	-	26
	<i>Season</i>	<i>5.9</i>	<i>22.7</i>	<i>185</i>	<i>142</i>	<i>327</i>
2017	May	4.4	20.2	35	-	35
	Jun	8.9	23.5	57	65	122
	Jul	10.1	31.1	3	102	105
	Aug	9.0	28.5	4	-	4
	<i>Season</i>	<i>6.8</i>	<i>22.9</i>	<i>99</i>	<i>167</i>	<i>266</i>
1989-2017	May	4.6	17.9	52	-	-
	Jun	7.8	21.4	79	-	-
	Jul	10.0	27.3	29	-	-
	Aug	8.9	27.0	24	-	-
	<i>Season</i>	<i>6.4</i>	<i>21.3</i>	<i>184</i>	-	-

Results

Correlation Analysis

Grain yield was largely driven by the kernel number, as these traits had the highest positive correlation across environments and years (Tables 3.2-5). The correlation between grain yield and kernel weight was negative in 2016, but positive in 2017, and in both years was higher under the rainfed than irrigated environment. Both grain-fill duration and maturity were positively correlated with grain yield for the 2016 irrigated and 2017 rainfed environments, but no significant correlation was observed for the 2016 rainfed or 2017 irrigated environments. Grain yield was positively correlated with

aboveground biomass and productive tiller number for both environments in 2017, but only on the irrigated environment in 2016. Spikelets per head had no significant correlation with grain yield across environments and years.

Kernel number and kernel weight were negatively correlated in 2016, but not correlated in 2017. Kernel number was positively associated with maturity only under irrigation in 2016. Kernel number and grain-fill duration were positively correlated in opposing moisture environments between years; 2016 irrigated and 2017 rainfed. Productive tiller number and kernel number had a consistent positive correlation, whereas kernel number and spikelets per head consistently had no association with each other. Aboveground biomass had a positive correlation with kernel number, except in 2016 rainfed environment. The aboveground biomass and productive tiller number had a consistent positive association.

Correlations of kernel weight and maturity varied with environment and year; positive under rainfed for both years, negative in 2017 irrigated, and not significant in 2016 irrigated. The kernel weight was negatively correlated with grain-fill duration under irrigated environment in both years, but was positively correlated in the 2017 rainfed environment. During 2016, kernel weight was negatively correlated with productive tiller number.

Table 3.2. Correlation coefficients between grain yield and its components and related traits across cultivars under irrigated environment in 2016.

Irrigated 2016								
	GY	AGB	KN	TKW	PM	GF	PTN	SPH
GY	1	0.38**	0.93**	-0.18*	0.22**	0.32**	0.36**	NS
AGB		1	0.41**	-0.28**	0.2**	0.29**	0.79**	0.2**
KN			1	-0.52**	0.21**	0.36**	0.46**	NS
TKW				1	NS	-0.21**	-0.43**	NS
PM					1	0.86**	0.2**	NS
GF						1	0.35**	NS
PTN							1	NS
SPH								1

GY, grain yield; AGB, aboveground biomass; KN, kernels number; TKW, thousand kernel weigh; PM, physiological maturity days after emergence; GF, grain-fill duration; PTN, productive tiller number; and SPH, spikelets per head. NS, not significant at $\alpha = 0.05$; *significant at $\alpha < 0.05$; and ** significant at $\alpha < 0.01$.

Table 3.3. Correlation coefficients between grain yield and its components and related traits across cultivars under rainfed environment in 2016.

Rainfed 2016								
	GY	AGB	KN	TKW	PM	GF	PTN	SPH
GY	1	NS	0.93**	-0.41**	NS	NS	NS	NS
AGB		1	NS	-0.17*	NS	NS	0.61**	NS
KN			1	-0.71**	NS	NS	0.22**	NS
TKW				1	0.24**	NS	-0.3**	NS
PM					1	0.64**	-0.17*	-0.25**
GF						1	NS	-0.42**
PTN							1	NS
SPH								1

GY, grain yield; AGB, aboveground biomass; KN, kernels number; TKW, thousand kernel weigh; PM, physiological maturity days after emergence; GF, grain-fill duration; PTN, productive tiller number; and SPH, spikelets per head. NS, not significant at $\alpha = 0.05$; *significant at $\alpha < 0.05$; and ** significant at $\alpha < 0.01$.

Table 3.4. Correlation coefficients between grain yield and its components and related traits across cultivars under irrigated environment in 2017.

Irrigated 2017								
	GY	AGB	KN	TKW	PM	GF	PTN	SPH
GY	1	0.68**	0.94**	0.33**	NS	NS	0.5**	NS
AGB		1	0.64**	0.22**	NS	NS	0.39**	NS
KN			1	NS	NS	NS	0.5**	NS
TKW				1	-0.18*	-0.26**	NS	NS
PM					1	0.85**	NS	NS
GF						1	NS	NS
PTN							1	-0.17*
SPH								1

GY, grain yield; AGB, aboveground biomass; KN, kernels number; TKW, thousand kernel weigh; PM, physiological maturity days after emergence; GF, grain-fill duration; PTN, productive tiller number; and SPH, spikelets per head. NS, not significant at $\alpha = 0.05$; *significant at $\alpha < 0.05$; and ** significant at $\alpha < 0.01$.

Table 3.5. Correlation coefficients between grain yield and its components and related traits across cultivars under rainfed environment in 2017.

Rainfed 2017								
	GY	AGB	KN	TKW	PM	GF	PTN	SPH
GY	1	0.53**	0.9**	0.42**	0.31**	0.48**	0.41**	NS
AGB		1	0.47**	0.23**	0.19*	0.19*	0.32**	0.19*
KN			1	NS	NS	0.35**	0.46**	NS
TKW				1	0.43**	0.37**	NS	NS
PM					1	0.88**	NS	-0.18*
GF						1	NS	NS
PTN							1	NS
SPH								1

GY, grain yield; AGB, aboveground biomass; KN, kernels number; TKW, thousand kernel weigh; PM, physiological maturity days after emergence; GF, grain-fill duration; PTN, productive tiller number; and SPH, spikelets per head. NS, not significant at $\alpha = 0.05$; *significant at $\alpha < 0.05$; and ** significant at $\alpha < 0.01$.

Main Effects and Interactions

There was no four-way interaction among main effects of all traits (Table 3.6).

The N x C interaction was not significant and neither the three-way interactions involving C and N effects (N x C x Y and E x N x C) for any trait indicating that cultivars responded similarly to N levels. The E x N x Y interaction was significant for grain yield,

kernel number, maturity, and grain-fill duration (Table 3.6; Fig. 1). No significant differences were observed among N levels in either environments during 2016 for these traits, except for kernel number. There was also no response to N under rainfed conditions in 2017 for any trait. The interaction occurred through an inconsistent response of grain yield, kernel number, maturity, and grain-fill duration to N applications beyond the 155 kg N ha⁻¹ treatment observed under irrigated environment in 2017 (Fig. 1).

Table 3.6. Analysis of variance for the 2-yr split-plot experiment with five nitrogen levels as main plot and eight cultivars as subplots over two environments (irrigated and rainfed). Table shows the source of variation, numerator degrees of freedom (ndf), and probability values for the *F*-test of each main effect and interactions.

Source of variation	ndf	GY	AGB	KN	TKW	PM	GF	PTN	SPH
Environment (E)	1	0.001	0.007	0.030	0.001	0.001	0.001	0.014	0.314
Nitrogen (N)	4	0.821	0.523	0.801	0.586	0.294	0.163	0.322	0.077
Cultivar (C)	7	0.001	0.007	0.001	0.001	0.001	0.001	0.001	0.001
Year (Y)	1	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
E x N	4	0.333	0.379	0.408	0.666	0.875	0.814	0.436	0.546
N x C	28	0.001	0.190	0.133	0.050	0.001	0.002	0.367	0.586
E x C	7	0.975	0.896	0.948	0.346	0.987	0.981	0.795	0.305
C x Y	7	0.010	0.049	0.217	0.001	0.001	0.008	0.378	0.001
E x Y	1	0.001	0.001	0.003	0.001	0.382	0.198	0.001	0.001
N x Y	4	0.692	0.249	0.338	0.400	0.487	0.031	0.423	0.760
E x N x C	28	0.915	0.672	0.937	0.734	0.998	0.964	0.852	0.576
E x N x Y	4	0.003	0.208	0.016	0.078	0.026	0.004	0.209	0.080
E x C x Y	7	0.126	0.504	0.516	0.282	0.010	0.013	0.146	0.895
N x C x Y	28	0.933	0.884	0.914	0.980	0.432	0.897	0.475	0.197
E x N x C x Y	28	0.994	0.758	0.996	0.822	0.979	0.989	0.969	0.905

GY, grain yield; AGB, aboveground biomass; KN, kernels no.; TKW, thousand kernel weigh; PM, physiological maturity days after emergence; GF, grain fill duration; PTN, productive tiller no.; and SPH, spikelets per head.

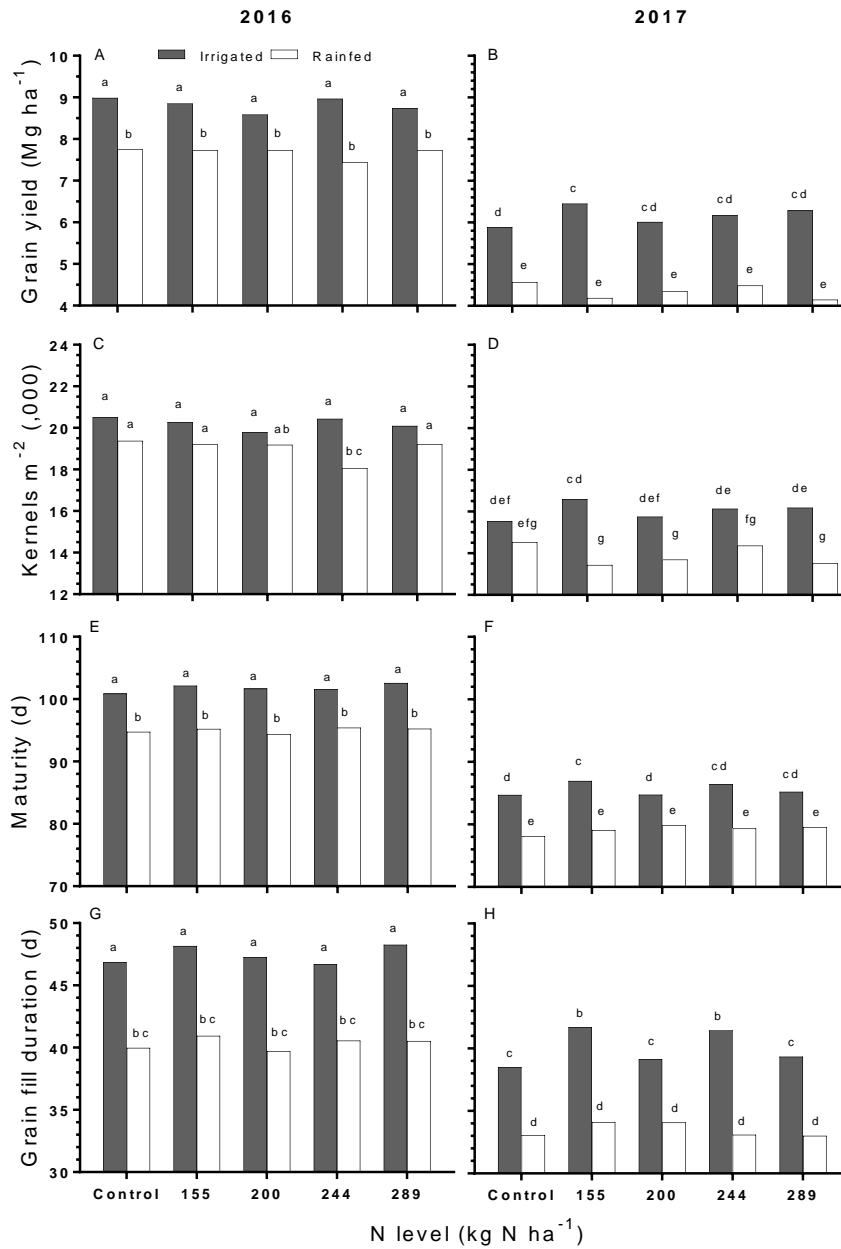


Figure 3.1. Three-way interaction means of environment, nitrogen (N), and year for grain yield (A, B), kernels m^{-2} (C, D), physiological maturity (E, F), and grain fill duration (G, H). Error bars are the standard error of the differences across the three-factor interaction means. Same letter assignment indicates the lack of significant differences across the three factors interaction ($\alpha = 0.05$).

Physiological maturity and grain-fill duration had an E x C x Y interaction (Fig. 2) showing a response variation of these two traits to environments and years. The cultivars Vida, Solano, and Alturas had the longest maturity under 2016 irrigation whereas Alpowa, Penawawa, UI Stone, and Egan showed the shortest maturity duration (Fig. 2A). In 2016 rainfed, Vida and Solano had the longest maturity. In 2017 irrigated environment, Vida had similar maturity to all cultivar but Penawawa that had the longest maturity duration. However, under rainfed Vida had the longest maturity. Alpowa, Egan, and UI Stone had the shortest maturity in 2017 rainfed (Fig. 2B).

The E x C x Y interaction for grain-fill duration occurred mostly because Vida had a longer duration when subjected to heat or water stress (Fig. 2C, D). All cultivars had similar grain-fill duration under rainfed environment in 2016 and irrigated in 2017, except for Vida that had a longer grain-fill duration under 2016 water-limited condition (2016). None of the cultivars statistically differed from another under irrigated environment in 2017. However, for 2017 rainfed, Vida had the longest grain-fill duration, whereas Egan had the shortest.

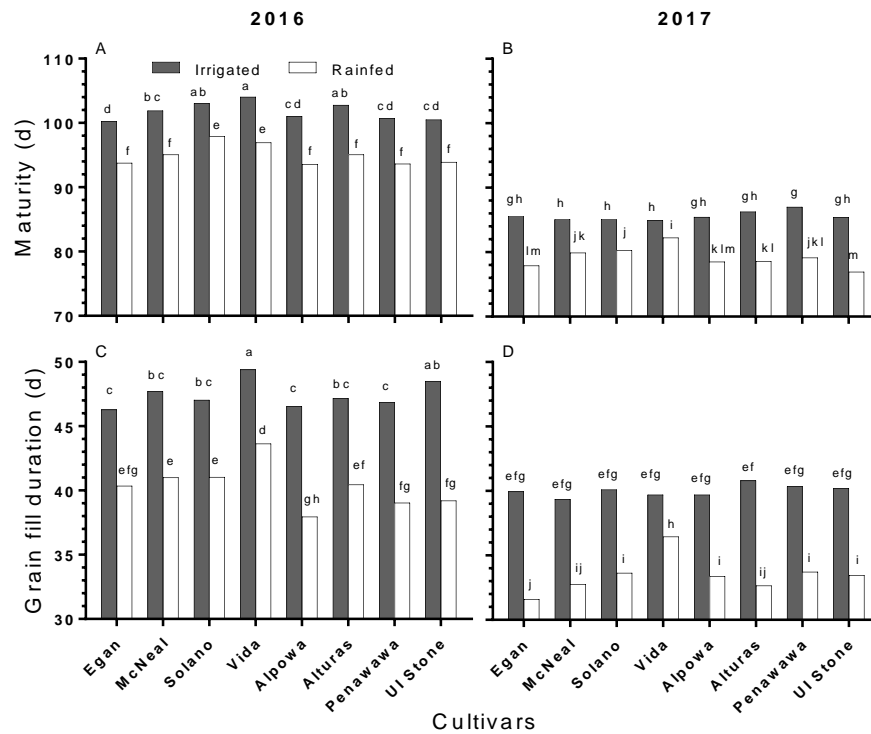


Figure 3.2. Environment x cultivar x year interaction means for physiological maturity (A, B), and grain fill duration (C, D). Error bars are the standard error of the differences across the three factors interaction means. Same letter assignment indicates lack of significant differences across the three factors interaction ($\alpha = 0.05$).

The aboveground biomass, kernel weight, productive tiller number, and spikelets per head response to environment was different between years, without any significant three-way interaction (Tables 3.6, 7). No significant difference was observed between irrigated and rainfed environment during 2016. However, irrigation resulted in 31% increase of aboveground biomass during the 2017 growing season in relation to rainfed that year. In both years, the irrigated environment had higher kernel weight and spikelets per head compared with the rainfed. The biomass E x Y interaction was caused because of a higher degree of response to irrigation during the more limiting year (2017)

compared with the near-average year (2016). The E x Y interaction for productive tiller number was attributed to similar response under irrigated environment for both years, but varied response in rainfed between years (Table 3.7).

Table 3.7. Environment x year interaction means for aboveground biomass, thousand kernel weight, productive tiller number, and spikelets per head. Same letter assignment indicates the lack of significant differences across environment and year for each trait ($\alpha = 0.05$).

Year	Environment	Biomass (kg ha ⁻¹)	1000 kernels (g)	Productive tiller (no m ⁻²)	Spikelets head ⁻¹ (no.)
2016	Irrigated	17.6 a	43.9 a	574.8 b	13.6 a
	Rainfed	16.8 a	40.6 b	606.6 a	12.9 b
2017	Irrigated	10.3 b	38.5 c	577.7 ab	11.0 d
	Rainfed	7.9 c	31.3 d	465.3 c	11.5 c

Cultivar interaction with year was significant for grain yield, biomass, kernel weight, and spikelets per head. Cultivars UI Stone and Alturas were the top yielding in 2016, but during the hot and dry year Vida yielded similarly to them (Fig. 3.3A). The soft white cultivars Alpowa and Penawawa had lower grain yield than Vida during the hot and dry year, but had higher yield than the remaining hard reds. Overall, soft whites had higher yield than hard reds in either years. The aboveground biomass in 2016 was near double (17 Mg ha⁻¹) than in 2017 (9 Mg ha⁻¹). All cultivars, except Solano, had similar aboveground biomass during 2017, whereas the cultivars UI Stone, Alturas, and Egan produced more aboveground biomass than other cultivars during near-normal 2016 (Fig. 3.3B).

In 2016, Solano and McNeal had similar kernel weight, which were the heaviest among cultivars. In 2017, Solano and Alpowa had the heaviest kernels followed by Vida, McNeal, Alturas and Penawawa with similar kernel weight. Egan had the lightest kernels during 2017 and UI Stone the second lightest (Fig. 3.3C). Spikelet per head response of

some cultivars varied between years (Fig. 3.3D). The cultivars Alpowa, Penawawa, and Solano had the highest spikelets per head in 2016 whereas Penawawa, UI Stone, and Alpowa were the highest during hot and dry 2017. Vida had the lowest spikelets per head among cultivars in each year (Fig. 3.3D).

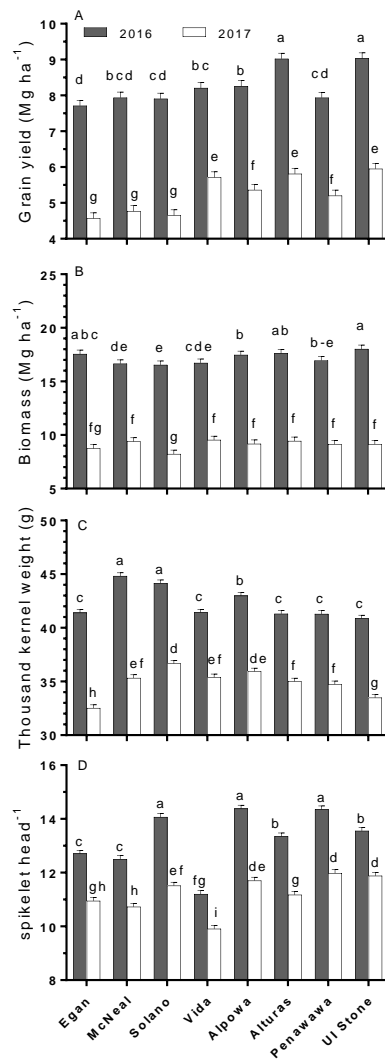


Figure 3.3. Cultivar x year interaction means for grain yield (A), aboveground biomass (B), thousand kernel weight (C), and spikelets per head (D). Error bars are the standard error of the differences across the two factors interaction means. Same letter assignment indicates the lack of significant differences across the two factors interaction ($\alpha = 0.05$).

The E x C interaction was significant for grain yield and kernel weight without any significant three-way interactions. The cultivars UI Stone and Alturas had consistently the highest grain yield across environments. Vida had similar grain yield to UI Stone and Alturas, but only under rainfed environment. Overall, soft white cultivars had a higher response to irrigation compared with hard reds (Fig. 3.4A)

The kernel weight under irrigated environment were the heaviest for McNeal and Solano whereas UI Stone and Egan were the lowest. Under rainfed environment, Solano had the heaviest kernel weight followed by McNeal and Alpowa with similar weight. Penawawa, Alturas, Egan, and UI Stone had similar and lightest kernel weight in the water-stressed environment (Fig. 3.4B).

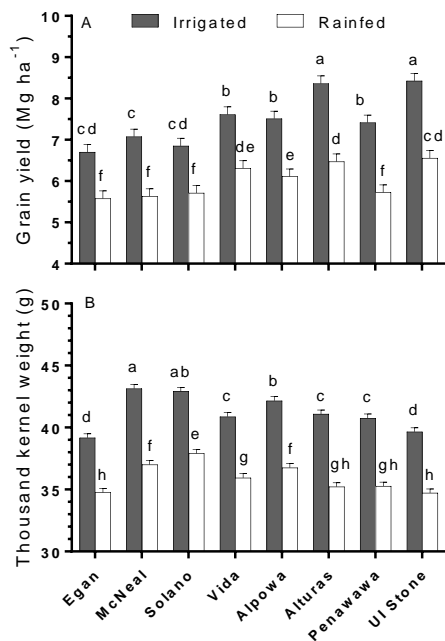


Figure 3.4. Environment x cultivar interaction means for grain yield (A), thousand kernel weight (B). Error bars are the standard error of the differences across the two factors interaction means. Same letter assignment indicates the lack of significant differences across the two factors interaction ($\alpha = 0.05$).

Cultivar main effect was significant without any association with the other main effects only for kernel number and productive tiller number. UI Stone was the cultivar with the most kernel number followed by Alturas and Vida whereas Solano and McNeal had the least (Fig. 3.5A). The cultivars Vida, UI Stone, and Alpowa had the most productive tiller number whereas Solano had the least (Fig. 3.5B). These observations were consistent regardless of environment, N levels, or years.

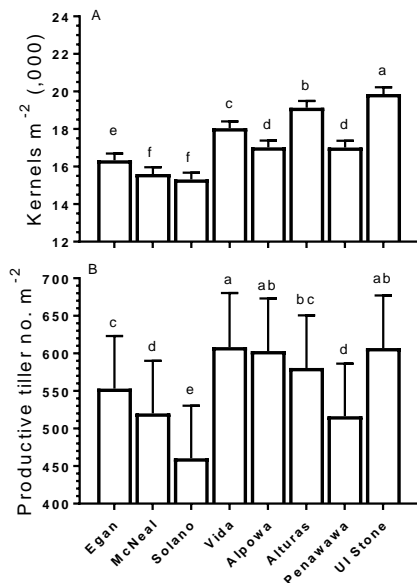


Figure 3.5. Cultivar means for kernels m^{-2} (A), and productive tiller no. m^{-2} (B). Error bars are the standard error of the difference among cultivars. Same letter assignment indicates the lack of significant differences among cultivars ($\alpha = 0.05$).

Discussion

Nitrogen fertilization is a major management practice and often times the highest input in wheat production (Diacono et al., 2013). The lack of response of grain yield to N

treatments in 2016 suggests that the lower N levels (including the control) were sufficient to achieve optimal grain yield – as this year had high residual N plus alfalfa crop credit from previous year. The grain yield was mostly limited by moisture regimes, as differences between irrigated and rainfed environments were observed. When water is adequate, grain yield can be limited by N application (Terman et al., 1969; Fowler et al., 1990). In 2017 irrigated plots, it was evident that the control N level had significantly lower grain yield than N increment up to 155 kg N ha⁻¹. Although, under rainfed environment, N fertilization did not increase grain yield, which may have been strongly influenced by drought and high ambient temperature (Long et al., 2017).

Temperature in 2016 was near to the 29-yr average, but contrastingly during 2017 Tmax was above optimal (32°C; Reynolds et al. 2016) on several days. The higher temperatures in 2017 resulted in variation in grain yield between years. Heat stress is reported as a major constraint in wheat production (Barnabas et al., 2008; Farooq et al., 2011; Fahaad et al., 2017). During reproductive phase, it may cause florets abortion (Wardlaw and Wrigly, 1994) consequently reducing the potential number of kernels per area, and may accelerate maturation, therefore reducing grain size and weight (Wardlaw and Moncur, 1995; Farooq et al. 2011).

The changing climate and the trend of rising temperatures (IPCC, 2018) make agricultural practices more uncertain and challenging. Lanning et al. (2010) showed that the rising temperatures in Montana, primarily during reproductive phase, has potential negative effect on wheat production in the region. Traditional management practices such as N fertilization can do little to reduce the effects of heat stress (Altenbach et al., 2003;

Elia et al., 2018), and irrigation could only mitigate the heat stress effects in wheat production (McDonald et al., 1984; Acevedo et al., 2002; Fahaad et al. 2017), if abortion of florets is avoided as shown in Torrion and Stougaard (2017). Therefore, identifying resilient cultivars and understanding why they are better adapted to adverse conditions could benefit wheat production and breeding programs.

Gourdji et al. (2012) reported a lack of grain yield increase in varieties bred under high-yielding environments when submitted to hot conditions, emphasizing that breeding targeting drought and heat stress tolerance is more successful when done under stressing environments. However, a cultivar should ideally not only thrive when dry and hot years occur, but also be able to take advantage of more favorable years and management practices.

In our study, we were able to replicate the study in a near-average year and evaluate the impacts of drought and heat stress with their fortuitous occurrence in 2017. For example, the consistent high grain yield for UI Stone and Alturas regardless of years or moisture regime environments was mainly attributed by their high kernel number and productive tiller number, which were well correlated to grain yield in this study as well as in the literature (Blum et al., 1990; Baum et al., 2003; Naruoka et al., 2011; Golba et al., 2018). UI Stone had significantly higher number of kernels per area, yet Alturas and UI Stone both had high yields. Distinctively, the cultivar Alturas had significantly heavier kernels than UI Stone under irrigated environment or during the dry and hot year. This difference however was unrelated with longer maturity or grain-fill duration, as these

traits were similar across years and environments for both cultivars. Likely, there was a trade-off between kernel weight and kernel number.

Kernel number is referred as a coarse regulator of grain yield whereas kernel weight is responsible for fine-tuning it (Slafer et al., 2014). During 2017, the combination of more abundant and heavier kernels in the irrigated environment contributed to the higher grain yield compared with rainfed. However, in 2016, irrigated and rainfed environment produced similar kernel number, but grain yield was higher under irrigated because heavier kernels were produced in this environment. Although a minor source of variation of grain yield, the kernel weight was an important compensatory yield component especially when growing conditions were more limiting, as observed on the positive correlation with grain yield in 2017. The majority of carbohydrate reallocated to kernels is produced after anthesis (Evans et al., 1975). Rather than limited by sink, the grain yield was decreased by limited source from a shorter maturity and grain-fill duration that are usually correlated with kernel weight (Blake et al., 2018).

Although N availability can be related to longevity of canopy (Sinclair and Jamieson, 2006), in our study N had little effect on maturity or grain-fill duration. These traits were more influenced by the genotype, irrigation, and yearly weather variations. The maturity and grain-fill duration response to N only occurred in 2017 irrigated and was not consistent with N increments. Lack of moisture in the rainfed environment hastened maturity and grain-fill duration compared with the irrigated in both years. When drought was combined with heat stress, the grain development was even more compressed, which is described as a mechanism to maintain the ability to produce viable

seeds (Altenbach, 2012). Among hard red cultivars, Vida had the longest grain-fill duration, as expected due to its stay-green trait gene. The extended period of grain-fill was the main advantage to increase Vida's grain yield especially under stressed conditions (Chen et al., 2011; Naruoka et al., 2012; Semenov et al., 2014). However, kernel weight of Vida did not differ from other cultivars. Most likely, Vida reallocated the additional photoassimilate production from the longer grain-fill duration to its larger number of kernels per area, via more productive tillers (Fig. 3.5B) therefore not reflecting on the individual kernel weight but on the grain yield as a whole.

Kernel number is highly influenced by productive tiller number (Golba et al., 2018). In our study, the productive tiller number was affected by environment x year interaction and cultivar main effect, which indicates that cultivars responded to irrigation and yearly differences at the similar degree. High productive tiller number is reported as an important trait related to phenological plasticity under drought (Baum et al., 2003). This was clear in 2016 when the rainfed environment produced significantly more tillers than irrigated. Additionally, the irrigated environment in 2017 although statistically similar, had higher productive tiller number than irrigated the 2016 counterpart. However, severe heat and drought stress (2017 rainfed) may have contributed to a high mortality of sensitive young tillers (McDowell et al., 2008) hindering a higher productive tiller number response. Phenological plasticity was also observed in correlation analysis that showed negative correlation between productive tiller no. and kernel weight in the less yield limiting year (2016), but no relationship was observed during 2017.

Kernel number is a major limiting factor for grain yield potential (Fischer, 2011). The head size, here expressed as spikelets per head, is a determinant trait of potential kernels per head that essentially contribute to kernel no. per area. The spikelets per head response to irrigation or cultivar effect significantly varied between years. Heads were bigger and grain yield was higher in 2016 or under irrigated environment. However, we could not find any significant correlation between spikelets per head and grain yield, kernel number, or kernel weight in either years or environments. This suggests that, besides the differences among cultivars, years, and environments, head size was not a good selection criterion under the tested conditions.

Conclusion

Two important wheat classes to the Pacific Northwest were subjected to major agronomic managements (irrigation and N fertilization) over two contrasting years. The soft white cultivars had an overall higher grain yield than hard reds. The soft whites UI Stone and Alturas had consistently higher grain yield across environments and years. The advantage was mainly attributed to a larger number of kernels per area and high productive tiller number. Among hard reds, the cultivar Vida (stay-green) had outstanding grain yield especially under rainfed environment, mostly because of its longer grain-fill duration and high number of productive tillers.

As expected, kernel number was the yield component that better explained grain yield variations. However, kernel weight was an important component during 2017.

Breeding on ideal or close to ideal conditions may disguise the importance of this component, as kernel weight is usually inversely related to grain yield and kernel no. in these conditions. In a dry and hot environment, such as the 2017 rainfed, the most important traits were productive tiller number and grain-fill duration, as they related to kernel no. and kernel weight. Spikelets per head had no correlation with grain yield. In fact, the most productive cultivars had relatively low head size with low spikelet number. This trait is not a singular factor for high grain yield, but operates in combination with other components such as productive tiller number and grain-fill duration.

Acknowledgments

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CHAPTER FOUR

CONCLUSION

This study consisted in analyzing both the grain yield and quality of two spring wheat classes. Four hard reds and four soft white spring wheat were subjected to differential moisture regime environments and nitrogen fertilization over two years. Fortuitously, one year deviated from the other and from the 29-yr average regarding ambient temperature and precipitation. This allowed us to make assessments on cultivar resiliency to heat and drought stress, and how they interacted with the applied management practices. It was also possible to analyze yield component and trait plasticity aspects as the correlations among them varied with environmental differences.

In chapter two, we focused on analyzing how the differential water and nitrogen management affected each spring wheat class separately. The soft whites and hard reds are very distinct in grain yield potential and grain quality requirements and thus the management should affect them differently. We concluded that the soft whites are much more prone to lowered grain protein content than hard reds, which could be advantageous. But there is a tradeoff, because when grain yield is depressed, the protein increases. Soft white production may be risky on a dryland considering the quality aspects. Additionally, farmers should observe nitrogen fertilization for this wheat class as grain protein content may exceed the threshold. Irrigation on soft whites resulted in higher grain yields than hard reds, however this management practice should be coupled

with low nitrogen fertilization to maintain grain protein content under the required threshold.

The hard red cultivar carrying the *Gpc-B1* gene had consistently the highest grain protein content among all cultivars. Interestingly, this cultivar did not suffer yield depression compared with one of its parents (McNeal) and another well adapted cultivar. Among hard reds, Vida (stay-green) had remarkably higher yield, especially under rainfed condition, and could maintain grain protein contents at desirable levels.

In chapter three, we focused on analyzing how the yield components and traits responded to different moisture regime environments and nitrogen fertilization over two years. Identifying traits that are related to grain may accelerate the process of selecting potential parents. The main advantage is that it is not necessary to wait until harvest, and the phenological selection can be done within the first stages of breeding when seeds are not abundant. We found evidence that productive tiller per area was directly related to grain yield in both rainfed and irrigated environments and during both near-average and heat and drought stressed years. We confirmed the strong positive correlation between kernel number per area and grain yield. Also, the usual negative correlation between kernel weight and grain yield, however only during the near-average year. During the heat and drought stressed year, kernel weight was positively associated with grain yield and was not associated with kernel number.

Another important trait was the grain fill duration. Among the hard red spring wheats, Vida had outstanding grain yield. Under rainfed conditions Vida's grain yield was similar to the most productive soft whites. The main reason for this advantage under

rainfed is the inherited the stay-green trait which enable to extend the green leaves duration. Consequently, a longer grain fill duration permits the production and reallocation of photoassimilates for a longer period and thus increasing grain yield. In addition, Vida also had the highest number of tillers per area, along with UI Stone and Altura, and as a result more sink was generated.

Collectively, this research demonstrates main differences between two important spring wheat classes and their response to major management practices. Information may be useful not only for breeder who can refer to the yield components chapter to aid decision on physiological selection, but also useful for farmers that want to diversify their production and need management information on spring wheat grain yield and quality.

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