### ABSTRACT

High wheat (*Triticum aestivum* L.) grain yield and desirable quality must be considered to avoid market price penalty. 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 randomized within the five N levels over contrasting environments (rainfed and irrigated) in northwestern Montana. 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 was 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 hot and dry 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.

### Core Ideas
- Egan (*Gpc-B1* gene cultivar) had superior grain protein with relatively no yield penalty
- Vida (stay-green trait cultivar), Alturas, and UI Stone are more resilient under varied growing conditions and management
- Soft white market class had higher grain yield and stronger protein dilution than hard red

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**HEAT (Triticum aestivum L.)** is the most widely grown staple crop worldwide and is primarily for human consumption (Hanson et al., 1982). 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 (Curtis, 2002; Stone and Savin, 2000). However, wheat production is greatly reduced by drought, which is one of the most yield-limiting abiotic stressors in crops (Morris et al., 1991; Fahad et al., 2017). Plants under drought stress reduce photosynthetic efficiency (Earl and Davis, 2003). Supplemental irrigation, which attenuates the large year-to-year grain yield variation due to erratic rainfall events and amounts, can minimize the impact of drought. Reliable water supply maintains transpiration, allowing plants to be photosynthetically active much longer (Acededo et al., 2002).

Nutrient availability, particularly N, is also crucial in producing high grain yield and quality in wheat. Plants need N for healthy canopy growth to intercept solar radiation effectively for photosynthesis (Barracough et al., 2014). In wheat, N is essential for the production of biomass; N stored in this biomass remobilizes later to the grain. It is estimated that up to 95% of the remobilized N is taken up prior to anthesis (Bogard et al., 2010; Masoni et al., 2007; Palta and Fillery, 1995; Slafer et al., 1990; Waters et al., 2009). In some instances, N is over-applied to achieve as close as possible to the grain yield potential and ensure a desirable quality (Diacono et al., 2012).

The excessive N application is not only to ensure the desired wheat quality but also to prevent wheat market price discounts. Grain quality parameters such as grain test weight, grain protein content, and falling number are important end-use quality indicators with marketing implications. N levels and weather conditions during reproductive phase can influence the test weight, a traditional standard grain quality measurement (Pushman and Bingham, 1975). Abiotic factors influence the grain protein, which can be diluted with increased yield, a common concern in wheat production (Barneix, 2007; Iqbal et al., 2016; Kibite and Evans, 1984; Lollato and Edwards, 2015; Slafer et al., 1990). The falling number (Hagberg, 1960, 1961) values in wheat flour have an inverse relationship with α-amylase activity (Finn, 1985). Alpha-amylase breaks down grain starch into sugar, reducing end-product quality.
A distinct feature of SWSW is its relatively low grain protein and higher yields due to an inherited stay-green trait from the cultivar Reeder (Lanning et al., 1981). Multiple factors interact impacting α-amylase activity, including seed coat color (Groos et al., 2002; McCrate et al., 1981), N application (Kettlewell, 1999; Kindred et al., 2005; Morris and Paulsen, 1985), grain drying rate (Kettlewell and Cashman, 1997), oscillating temperature near grain maturation (Farrell and Kettlewell, 2008), and applying irrigation near soft dough stage (Torrion and Stougaard, 2017).

Moisture stress affects wheat grain quality. For instance, the yield-reducing effect of limited moisture causes a rising grain protein concentration associated with its inverse relationship with grain yield (Kibite and Evans, 1984; Slafer et al., 1990). Recent reports also described a potential increase in grain protein when irrigating later in the grain-fill period. However, this response is of no guarantee because the grain protein content is in a complex association with irrigation, environment, and cultivar (Torrion and Stougaard, 2017). These authors also reported that availability of moisture increases test weights, though lowers falling number values during an extended occurrence of physiological maturity with available moisture. When maturing, heads are exposed to the continuous hot daytime and cool nighttime temperatures (Farrell and Kettlewell, 2008) later in the growing season. As reported by Torrion and Stougaard (2017), some cultivars are resistant to lowering falling number at a given environment and conditions.

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 widely grown in the state of Montana, the third largest spring wheat producer in the country. However, this class’ demand for high grain protein contributes to applying more N, especially under irrigated condition in avoidance of the known grain yield and protein tradeoff. Recent 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 (Tabbita et al., 2017; Torrion et al., 2019).

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). In 2015, the market price for this class in the Pacific Northwest was 1.5 US dollars higher for 27 kg⁻¹ of wheat (of only 95–108 g kg⁻¹ grain protein requirement) than HRSW with 140 g kg⁻¹ grain protein (US Wheat Associates, 2019). Because of the relatively high grain yield potential and low grain protein requirement of SWSW (<105 g kg⁻¹; Boke and Dubetz, 1986; Sowers et al., 1994) compared with potential and low grain protein requirement of SWSW (<105 g kg⁻¹; Bole and Dubetz, 1986; Sowers et al., 1994) compared with HRSW (>140 g kg⁻¹; Brown et al., 2005), the SWSW could be an alternative to HRSW for wheat growers in high-yielding regions of Montana, potentially 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. Recently available HRSW cultivars, such as Egan, with the Gpc-B1 gene, which upregulates grain protein, and Vida, containing the stay-green gene, warrant similar investigation.

This study analyzes a 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 of northwestern Montana. The specific objectives were to: (i) characterize grain yield and protein relationship in each market class, (ii) assess grain yield and protein of various HRSW cultivars showing distinct genotypes (Gpc-B1 gene, non-Gpc-B1, and stay-green cultivars), and (iii) 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 Pacific 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 randomized within each block; and eight cultivars (four HRSW and four SWSW), were the subplots randomized within each N levels.

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- to 15-, 15- to 60-, and 60- to 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 and estimated organic matter mineralization, MAP fertilization, and alfalfa previous crop credit, respectively; Jones and Kurnick, 2016). 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 long fertilizer boom spreader calibrated for the amount of urea needed to a summed total N of: 155, 200, 244, and 289 kg ha⁻¹ for both years. 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 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., 2018).
Planting and Pest Control

The experiment was planted on 21 Apr. 2016 and 1 May 2017 using a seven-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 mfenoxam) 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 and insecticides were applied at flag leaf stage. Insecticide (a.i. lambda-cyhalothrin) application was only necessary in 2016.

Environment

Two environments were set to investigate grain yield and quality under limited and nonlimited moisture regimes; 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 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) ~500 m 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. No irrigation was applied after medium-milk stage, as the final irrigation event was sufficient for the rest of the season (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 (Infratec 1241 Grain Analyzer, Hilleroed, Denmark), which was also used to determine grain protein and grain test weight. The falling number values were obtained using an FN 17 (Perten, Hagersten, Sweden). Falling number, in seconds, is a measure of α-amylase activity (Finney, 1985).

Statistical Analysis

Data were first analyzed for normality using PROC univariate in SAS 9.4 (SAS Institute, 2014) following the Shapiro-Wilk test of normality hypothesis. PROC GLIMMIX was used for its efficiency in computing complete analysis for split-plot experiments (Littell et al., 2006). Year 2017 deviated from the 30-yr 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 performed to examine trends of LSMEANS using GraphPad Prism 7 (La Jolla, CA).

Table 1. Selected semi-dwarf cultivars under each spring wheat classes.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Pedigree</th>
<th>Plant identification</th>
<th>Year of release</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hard red</td>
<td>Egan</td>
<td>CAP19/Choteau/McNeal*7/Glupro</td>
<td>671855</td>
<td>2014</td>
</tr>
<tr>
<td></td>
<td>McNeal</td>
<td>RS 6880/Glenman</td>
<td>574642</td>
<td>1995</td>
</tr>
<tr>
<td></td>
<td>Vida</td>
<td>Scholar/Reeder</td>
<td>642366</td>
<td>2006</td>
</tr>
<tr>
<td>Soft white</td>
<td>Alpowa</td>
<td>Fielder/Potam 70/Walladay/3/walladay/Potam 70</td>
<td>566596</td>
<td>1994</td>
</tr>
<tr>
<td></td>
<td>Alturas</td>
<td>Whitebird/Centennial</td>
<td>620631</td>
<td>2002</td>
</tr>
<tr>
<td></td>
<td>Penawawa</td>
<td>Poram 70/Fielder</td>
<td>495916</td>
<td>1985</td>
</tr>
<tr>
<td></td>
<td>UI Stone</td>
<td>Pomerelle*2/Tui</td>
<td>660550</td>
<td>2013</td>
</tr>
</tbody>
</table>

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 the late 1980s. UI Stone is a recently released cultivar with high grain yield and end-use quality (Chen et al., 2013). Details of the cultivar pedigrees and sources are shown in Table 1.

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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. 1A and 1B). 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. 1C and 1D).

RESULTS

Correlations between Yield and Quality Traits

Table 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 varied association strengths (coefficients). The exception is that yield and falling number of HRSW had no significant association. A significant ($P < 0.01$) inverse relationship 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 that in SWSW. For each class and the combined data, grain yield and test weight were positively correlated ($P < 0.01$).

Main Effects and Interactions

Grain Yield

For HRSW, yield response to N was observed only under irrigated condition (significant $E \times N$, Table 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. 2A). However, no yield trends were identified in either environment in 2017. 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$^{-1}$).

![Figure 1](image1.png)

Fig. 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).

![Table 2](image2.png)

Table 2. Correlation coefficients between grain yield and quality for hard red (HRSW), soft white (SWSW) spring wheat, and the two market classes combined (All).

<table>
<thead>
<tr>
<th>Traits</th>
<th>Class</th>
<th>HRSW</th>
<th>SWSW</th>
<th>All</th>
<th>HRSW</th>
<th>SWSW</th>
<th>All</th>
<th>HRSW</th>
<th>SWSW</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>GY</td>
<td>1</td>
<td>-0.26**</td>
<td>-0.64**</td>
<td>-0.36**</td>
<td>0.83***</td>
<td>0.77**</td>
<td>0.80***</td>
<td>-0.08</td>
<td>-0.33**</td>
<td>-0.25***</td>
</tr>
<tr>
<td>GPC</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-0.34**</td>
<td>-0.44**</td>
<td>-0.38**</td>
<td>0.15**</td>
<td>0.30**</td>
<td>0.65**</td>
</tr>
<tr>
<td>GTWT</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.83***</td>
<td>0.77**</td>
<td>0.80***</td>
<td>-0.08</td>
<td>-0.33**</td>
<td>-0.25***</td>
</tr>
<tr>
<td>FN</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-0.24**</td>
<td>-0.22**</td>
<td>-0.32**</td>
<td>0.15**</td>
<td>0.30**</td>
<td>0.65**</td>
</tr>
</tbody>
</table>

** Indicates significance at $P < 0.01$. 

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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 to here as the “response breakpoint” (X₀) using an upper-plateau model.

The 2016 growing season (Fig. 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% was 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. 3A and 3C).

The cultivar main effect for HRSW in 2016 did not interact with other factors (Table 3). During this near-average year, Egan (with the Gpc-B1 gene) yielded similarly to Solano and McNeal regardless of the environment (Fig. 3A). Vida, a cultivar with the stay-green trait, was the highest yielding cultivar among HRSW regardless of environment. The E × C interaction (P < 0.01) of HRSW in 2017 is shown in Fig. 3B. From this simple interaction (no criss-cross), Vida outperformed the rest of HRSW in both environments.

For SWSW, two- or three-way associations of main effects did not exist in 2016 (Table 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. 3C).

The E × 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 (P > 0.05) under irrigation (Fig. 3D) than Alpowa and Penawawa. Moreover, Alturas and UI Stone consistently performed better in both the near-average year and the dry and hot year. Overall, the irrigation increased yield by 48% more compared with the rainfed, an approximately three-fold increase relative to 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 trend was unjustifiable. Thus treatments
means were fitted linearly in which the coefficient was insignificant from slope 0 (Fig. 2B).

**Grain Protein Content**

There was an E × C interaction \((P < 0.05)\) for grain protein for either of the market classes and years (Table 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. 4A). During 2017, grain protein was similar in both environments for HRSW (Fig. 4B). Among SWSW cultivars, Alpowa had higher grain protein with irrigation over rainfed in 2016 (Fig. 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 than the irrigated treatment (Fig. 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 than the irrigated environment for either class (Fig. 5A and 5C). In 2017, the E × N interaction was significant \((P < 0.05)\) for both HRSW and SWSW. The grain protein-N response of rainfed HRSW was significantly higher than that of the irrigated HRSW only when N level was low (i.e., 45 kg N ha\(^{-1}\); Fig. 5B). However, 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 across N treatments in 2017 (Fig. 5D), but no significant difference was observed between environments in 2016 (Fig. 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. 5A and 5C). 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. 5B and 5D).

**Falling Number**

Falling number of each of the market classes was influenced consistently by E × C association \((P < 0.01)\) in both years (Table 3). 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 (Table 4). The observed lowering of falling number with irrigation in 2016 was not observed in 2017, except for UI-Stone SWSW. The E × 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 4). Despite the E × 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 the highest falling number among the SWSW cultivars, which was consistent across water regimes and years (Table 4).

In 2017, HRSW falling number was also influenced by N × C interaction (Table 3). Closely, this was because among
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. 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. 1C and 1D). 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. 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, and 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. 3). Within HRSW, Vida 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 (Bänziger et al., 1999; Borrell et al., 2000). Naruoka et al. (2012) related the more extended 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) under hot and dry conditions. 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treatment or N level (Fig. 3A and 3B). 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). 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 a 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 indicated in Table 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. 4A). A similar response was observed for Alpowa (Fig. 4B) whereas the other SWSW had statistically similar protein content in both environments. As expected, irrigation resulted in a higher yield. However, 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 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 affecting grain protein threshold. However, the observed rise in regional temperature (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 of SWSW, especially with increased N levels (Fig. 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. 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. 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. 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. 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 the premium for grain protein is nonexistent or low, the maximum protein-based response (X0; Fig. 5) is less meaningful. Historically, avoiding protein discounts had been more profitable than targeting a premium for higher grain protein (Baker et al., 2004).

Apprehension exists about a leading cultivar for high yield due to protein dilution. Vida, for instance, outyielded all HRSW cultivars, especially under severe drought, but had the lowest grain protein among HRSW in this study. However, its grain protein content only fell below the market threshold under rainfed conditions in 2016, which is not unprecedented. In this region of Montana, irrigation tends to have no negative impact on grain protein content compared to rainfed, during average years (Torrion and Stougaard, 2017). The protein-based market discount had been more profitable than targeting a premium for higher grain protein (Baker et al., 2004).

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 falling number under irrigated environment regardless of market class. Torrion and Stougaard (2017) suggested that lowered falling number is further triggered by irrigation application later in the season. Lowered falling number is evident during times of extreme fluctuations in day and night temperatures during grain maturation (Farrell 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 4) under unpredictable growing conditions.

Light seed-coat color of SWSW has been associated with low falling number (Groos et al., 2002; McCrate et al., 1981). On average, the HRSW (inherently darker seeds) did show higher falling number compared with SWSW (inherently lighter seeds). However, 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 falling number in this region. However, this warrants more investigations as late-season condition (rainfall, fluctuating air temperature) triggers 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 correlated
positively with grain yield for HRSW (Tables 2 and 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 short grain fill duration due to temperature stress (Hernández-Espinoza et al., 2018; Yabwalo et al., 2018) that caused the accelerated maturation. Specifically, the impact of N on test weight was observed only for HRSW during the dry year (2017). Low N resulted in higher test weight than the higher N applications. This is contradictory to what the literature reports (Pushman and Bingham, 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 air temperature did not reach to a destructive level (Fig. 1). It could be that the low-level N in 2017 influenced the reduction of the potential seed number. Consequently, 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 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 than HRSW to lowering grain protein with increased yield, which is desirable for SWSW. 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 classes. The yield of the 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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