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Historic trends and sources of year-over-year stability in Montana winter wheat yields

Jennifer Lachowiec  | James E. Berg | Meng Liang  | Fernando H. Correr 

Plant Sciences and Plant Pathology,
Montana State University, Bozeman,
Montana, USA

Correspondence

Jennifer Lachowiec, Montana State
University, 119 Plant Bioscience Building,
Bozeman, MT 59717, USA.
Email: jennifer.lachowiec@montana.edu

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Abstract

Producers desire cultivars that consistently perform with high yields and end-use qualities. Unlike easily recognized average yield improvements, yield stability over time is less examined, especially when considering the role of breeding relative to other factors like management and changing climatic conditions. Our study system was a 70-year historical dataset from which we estimated the year-over-year stability of winter wheat (*Triticum aestivum* L.) cultivars released by Montana's Agricultural Experimental Station. We examined yield stability within six locations representing diverse growing conditions across Montana and found no evidence that breeding has improved stability, that stability may be decreasing over time at one location, and that the year-over-year stability of a cultivar is sensitive to location. We examined the role of climatic conditions, including temperature, and rainfall to understand if increased climatic variability was masking improved patterns of stability. However, the lack of impact of breeding remained. These findings suggest that Montana's winter wheat may benefit from selective breeding for increased stability within locations.

1 | INTRODUCTION

Volatile crop yields caused by environmental extremes threaten our global food supply (Lobell et al., 2008). Further, producers lose economic value when crops grow variably across fields, due to increased difficulties in management and harvest and meeting end-use quality requirements. To counteract these obstacles, multiple approaches are taken to optimize yield stability and quality, including breeding and agronomic practices (Reckling et al., 2021). Crops grown at a specific geographic location experience not only varied weather and disease pressure year-over-year but also microenvironmental differences within a field and stochastic errors during development (Lachowiec et al., 2015). Genotype greatly influences how plants withstand collective perturbations (Hill & Mulder, 2010), herein referred to as robustness.

Because genotypes associated with differing degrees of robustness have been identified in plants (Hall et al., 2007; Jimenez-Gomez et al., 2011; Sangster et al., 2008), including crops (Fisher & Zamir, 2021; Makumburage & Stapleton, 2011; Ordas et al., 2008; Tollenaar & Wu, 1999), we hypothesize that breeding has increased crop robustness to such perturbations.

Defining and measuring robustness is a complicated task. Not to be confused with the stability (or conversely, the plasticity) of a trait across geographic location, robustness is a way to describe the uniformity, repeatability, intra-genotypic variability (Bruijning et al., 2020), and predictability of a genotype within a location. In many studies examining agronomic traits, the coefficient of variation (CV) of a trait is calculated. CV traditionally is used to identify undesired high levels of variability to determine experimental

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validity (Bowman, 2001) but also potentially holds information about robustness (Fasoula & Fasoula, 2002). In agriculture, robustness also has been captured using many statistics like environmental variance (V_e , Schou et al., 2020) and heterogeneity of environmental variance (Hill & Mulder, 2010), adjusted CV (aCV; Döring & Reckling, 2018), among many others (Reckling et al., 2021), revealing how different genotypes can influence robustness. Using these and similar robustness statistics, the underlying genetic architecture and genetic loci controlling robustness have been identified (Fisher & Zamir, 2021; Hall et al., 2007; Sangster et al., 2008).

Like most quantitative traits, robustness is affected not only by genotype, but also by the environment and the interaction of genotype and environment (Falconer & Mackay, 1996). Most commonly, how the environment affects robustness is measured within a single cultivar to assess the impact of different agronomic practices. Varied planting density (Lu et al., 2020), application of fertilizers, and irrigation (Kristensen et al., 2008; Kukul & Irmak, 2018) are examples of agronomic practices examined for impacts on robustness. Long-term studies have produced mixed findings regarding how robustness has changed over time in crops. An economic study of global *Triticum aestivum* L. (wheat) and *Zea mays* L. (maize) yields produced since the Green Revolution showed an increase in robustness over time (Gollin, 2006). In contrast, an agronomic study of a single, highly controlled, long-term site found both *Hordeum vulgare* L. (barley) and wheat yields decreased in robustness, depending on fertility management (Macholdt et al., 2021). A breeding study considering the impact of a small number of specific maize hybrids released over five decades, found increased robustness is associated with greater yields, due to improved stress tolerance (Tollenaar & Wu, 1999). Additional comprehensive research is needed to understand how breeding, location, and management interact to influence yield robustness.

To explore how breeding affects robustness, we examined historical data collected on winter wheat grown in Montana. In Montana, winter wheat is one of the main cereal crops with a planting area of over 627,000 hectares in 2020, accounting for nearly \$400 M in production value (National Agricultural Statistics Service, 2021). Since 1949, Montana's winter wheat breeding program grew winter wheat systematically at multiple research centers across the state, collecting yield data. With these data, we examined yield year-over-year variability. We inspected how yield robustness varies with geographic location. Given the important role of weather variability year-over-year at a specific location, we examined the impacts of temperature and precipitation on yields and its robustness. We propose the need for breeding yield robustness based on examining the most grown Montana Agricultural Experiment Station cultivars developed over the last 100 years.

Core Ideas

- While Montana's wheat yields have clearly improved over time, overall year-over-year stability appears stagnant.
- Examining wheat cultivars reveals a need for improved year-over-year stability over time.
- Weather variability contributes to but is not the major factor affecting year-over-year stability.
- Consideration of cultivar and location is critical to understanding year-over-year stability.

2 | MATERIALS AND METHODS

2.1 | Data sets

2.1.1 | Yield data

Winter wheat yields were obtained from the Montana Winter Wheat Breeding Program, reported as bushel per acre and converted to kg ha^{-1} . The 48 exclusively inbred cultivars included those that have been planted across the state (Table S1, National Agricultural Statistics Service 1958–2019). The data include the yields of released winter wheat cultivars tested in Montana from 1949 to 2019 at six research centers (Table 1).

Extreme winterkill resulting in zero yields were excluded from all analyses as outliers (Reckling et al., 2021). Only dryland results were included with no additional irrigation.

2.2 | Weather data

Weather data were obtained using the web interface and search capabilities provided by the National Oceanic and Atmospheric Administration's National Centers for Environmental Information (NCEI, 2021). The datasets chosen were "Global Summary of the Month" and "Global Summary of the Year" ranging from January 1949 to December 2019. Higher resolution data were not available for the full duration of the study. Weather stations were chosen for their proximity to the research centers and data availability. Data were obtained from Kalispell Glacier Airport (Station ID USC00244558), Sidney (Station ID USC00247560), Huntley Experimental Station (Station ID USC00244345), and Moccasin Experiment Station (Station ID USC00245761). In Bozeman, two stations were needed to obtain desired weather data. From January 1949 to October 1966, data were

TABLE 1 Research centers in this study.

Name	Research center	Location	Soil type
Havre	Northern Agricultural Research Center	48° 30', 109° 48'	Silt loam
Kalispell	Northwestern Agricultural Research Center	48° 10', 114° 15'	Silt loam
Moccasin	Central Agricultural Research Center	47° 03', 109° 57'	Clay loam
Huntley	Southern Agricultural Research Center	45° 55', 108° 15'	Silt loam
Sidney	Eastern Agricultural Research Center	47° 40', 104° 08'	Clay loam
Bozeman	Post Research Farm	45° 41', 111° 00'	Silt loam

obtained from Bozeman Montana State University (Station ID USC00241044), and from November 1966 to December 2019, data were obtained from Bozeman 6 W Experimental Farm, (Station ID USC00241047). In Havre, two stations were used to obtain data spanning the focus period: January 1949–February 1961 Havre Weather Bureau (Station ID USW00024035) and March 1961–December 2019 Havre Airport (Station ID USW00094). From each weather station, four weather variables were obtained: monthly average (TAVG), monthly minimum (TMIN), and monthly maximum (TMAX) air temperatures, and monthly cumulative precipitation (PRCP). The percent data coverage across the weather variables as follows: Bozeman: 98.5%, Havre: 100%, Huntley: 96.4%, Kalispell: 99.4%, Moccasin: 95.8%, and Sidney: 97.8%.

2.3 | Statistical analyses

All statistical analyses were performed using R version 4.1.0 (R Development Core Team, 2011).

2.4 | Yield analyses

To examine the change in yields over time, we modeled the mean yield across cultivars at each research center as follows:

$$Y_{ij} = \alpha_i + \varepsilon_{ij}, \quad (1)$$

where Y_{ij} represents the mean yield for i th year at the j th location, α_i captures the year effect, and ε_{ij} is the residual effect. The data were also separated into locations for further analyses,

$$Y_i = \alpha_i + \varepsilon_i, \quad (2)$$

where Y_i represents the mean yield for the i th year, α_i captures the year effect, and ε_i is the residual effect.

To examine the change in yield robustness over time, we utilized multiple approaches. First, we visually examined the residuals of the linear model capturing the relationship

between yield and year (Equations 1 and 2). Second, we calculated each cultivar's yield coefficient of variation ($CV = s/\bar{x}$), where s is the sample standard deviation and \bar{x} represents the sample mean) across the years it was grown (Ray et al., 2015) and examined the relationship to release year as follows:

$$CV_{jk} = \beta_k + \varepsilon_{jk}, \quad (3)$$

where CV_{jk} represents the CV for the j th location and cultivars with the k th release year, β_k is the release year effect, and ε_{jk} is the residual effect. Models were also made for each location separately as follows:

$$CV_k = \beta_k + \varepsilon_k, \quad (4)$$

where CV_k represents the CV for cultivars with the k th release year, β_k is the release year effect, and ε_k is the residual effect.

We examined the sensitivity of the yield CV to the number of years a cultivar was grown. First, we visually observed a threshold in the impact of number of years grown ("count") on the CV and used a quadratic plateau model to estimate the transition point, implemented with the `nlstools` package in R (Baty et al., 2015) as follows:

$$CV_i = \begin{cases} \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \varepsilon_i & \text{if } x < x_m \\ CV_m & \text{if } x \geq x_m \end{cases}, \quad (5)$$

$$x_m = \frac{\hat{\beta}_1}{2\hat{\beta}_2},$$

and

$$CV_m = \hat{\beta}_0 - \frac{\hat{\beta}_1^2}{4\hat{\beta}_2},$$

where CV_i is the value of the CV for each count value i , x_m is the transition point to where CV no longer increases, and CV_m is the maximum CV. Values for initializing the model were the estimated intercept and slope from a linear regression of the CV on count, and the value 10 for the transition point based on

visually examining the relationship of CV on count. The 95% confidence interval for x_m was 6.57–12.14, with an estimate of 9.36. Therefore, we used a threshold of greater than 9 years grown to estimate CV values for cultivars using Equations (3) and (4).

An alternative measurement of robustness, aCV was calculated following the method of Döring and Reckling (2018). Briefly, the logarithms of the variances are regressed on the logarithm of the means are calculated. Based on the regression line, an adjustment to the variance is determined by rotating the slope (b) to $b = 2$ to satisfy the Taylor Power Law allowing for constant scaling between the variance and mean. With the adjusted variance, the aCV is calculated.

In another approach, data were sampled using the bootstrapping method, to eliminate the effect of number of years sampled on the aCV. Cultivars were filtered to those that included measurements from at least 5 years. For each bootstrap sample, 5 years of yield data were randomly selected with replacement for each cultivar. For the bootstrap samples that did not have variances of 0, the linear relationship between the aCV of the bootstrapped samples and release year was computed, using Equations (3) and (4) with the bootstrap replication aCV at the response variable. A new bootstrap sample was created 1000 times, and model estimates from each sample were recorded, b (regression coefficient), R^2 (coefficient of determination), and p -value for b .

2.5 | Weather analyses

To understand trends in weather variables between 1949 and 2019, we examined annual mean values obtained for each location. The relationship between variables and year were modeled with linear regression for each location as follows:

$$W_i = \alpha_i + \varepsilon_i \quad (6)$$

where W_i represented either TAVG, TMIN, TMAX, or PRCP for the i th year, α_i captures the year effect, and ε_i is the residual effect. The change in each weather variable was calculated per decade using the slope estimate. Annual weather variability was examined by calculating a “moving CV” with a moving window of 30 years using the annual mean values for each weather variable. Seasonality in the weather variables were also examined at each location to understand if certain months were highly variable in temperatures relative to others. The monthly means were calculated between the years 1949 and 2019. Weather variability over time was examined by using the statistic CV after transforming the data to only include positive values by adding 30 to all values. The CV was then calculated for the monthly weather variables obtained for each month.

2.6 | Combined weather and yield analyses

Because weather data were available each year at each location, we examined the relationship between the weather variables and yields. Using principal component (PC) analysis, we examined how the four weather variables, release year (capturing the impact of breeding), and year grown (capturing, at least, changes in agronomic practices) were acting in concert. We then calculated the residual aCV (aCV_{res}) (Kukul & Irmak, 2018; Schou et al., 2020) after modeling the effects of temperature and precipitation using the following approach:

$$Y_{in} = \tau_i + \rho_i + \tau_i\rho_i + \varepsilon_{in}, \quad (7)$$

where Y_{in} represents yield each i th year for each n th cultivar, τ_i is the mean annual temperature, ρ_i is the cumulative annual precipitation (contributed most strongly to PC1 and PC2), and $\tau_i\rho_i$ captures the interaction between mean annual temperature and cumulative precipitation.

The residuals (ε_{in}) from this model, after transformation to positive values by adding the minimum residual, were used to calculate the aCV_{res} for each cultivar. Finally, the relationship between aCV_{res} and release year was examined using Equation (4).

3 | RESULTS

3.1 | Montana wheat yields have increased with little impact on yield robustness

To assess how winter wheat yields have changed historically, we focused on the most tested cultivars in Montana's winter wheat breeding program since 1920s. We examined 48 cultivars ranked on acreage planted in Montana after their release (Table S1, Montana Agriculture Statistics Service 1958–2019), assessing the results of yield trials across six research centers representing different production environments in Montana. We first examined winter wheat's interannual improvement between 1949 and 2019 by calculating the mean yield each year. On average across the six locations, yields increased 43.55 kg ha⁻¹ year⁻¹ based on fitting a linear model (Figure 1a). Depending on location, yields showed over a fivefold average improvement over the last 70 years (Figure 1b). Huntley and Kalispell had the largest year-over-year gains (Figure 1c). These yield changes are not only dependent on breeding improvement but also on improvement in agronomic practices (Lanning et al., 2010) and changing climatic conditions and atmospheric CO₂ (McGrath & Lobell, 2013).

In addition to observing increased yields over time, we hypothesized increased year-over-year yield stability. To distinguish stability year-over-year within a location from the

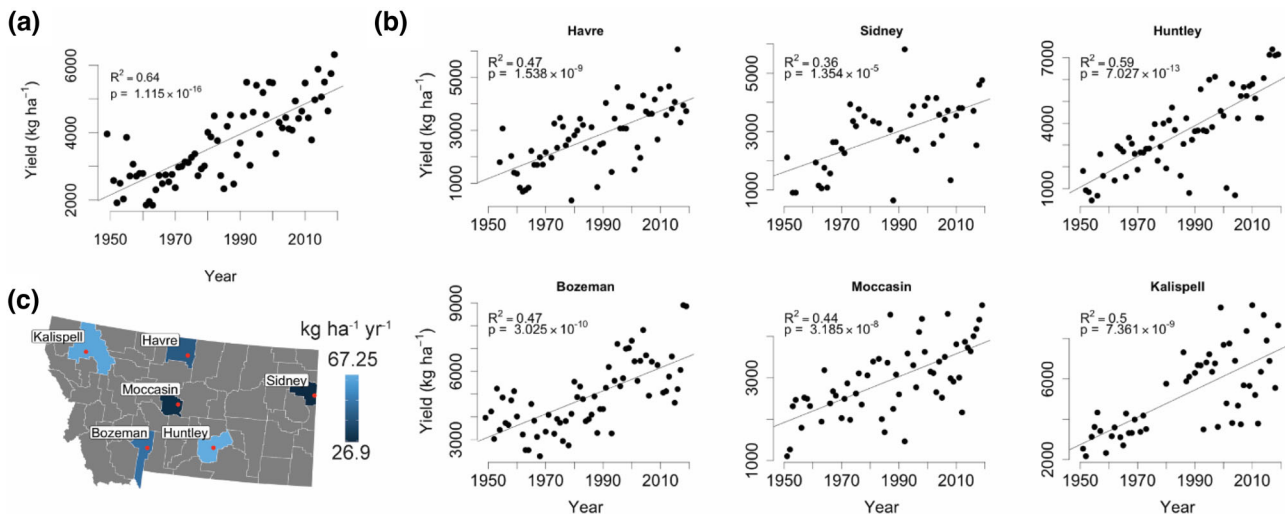


FIGURE 1 Winter wheat yield increases across Montana from 1949 to 2019 (a) The average yields from Montana's released cultivars from breeding nurseries across six research centers is shown from 1949 to 2019. The linear regression fit is indicated with the solid black line, with R^2 and p -values for the slope shown, (b) Yields from 1949 to 2019 is shown for each research station. The linear regression fit is indicated with the solid black line, with R^2 and p -values for the slope displayed, and (c) The linear regression coefficient for yield and year for each research center from panel (b) is indicated with the color scale for the corresponding county.

more common definition of stability across geographic locations (Becker & Leon, 1988; Finlay & Wilkinson, 1963), we will use the term robustness to refer to year-over-year stability. In other words, within a single geographic location we can describe how robust yields are to yearly fluctuations in weather, plot location at a research center, biotic stresses, and more. We hypothesized that the residuals of the linear regression models estimating the change in yield over time at each location would decrease with time. However, the residuals showed little change over time, except at Kalispell, where they instead appeared to increase, contrary to our prediction (Figure S1). These data suggest that the collective impacts of changing agronomic practices, climate, breeding, soil chemistry, and other factors are not resulting in greater yield robustness, with Kalispell decreasing in robustness, and other locations unchanging.

3.2 | Yield robustness of a cultivar depends on location

Cultivars were pooled together in the previous analyses, potentially obscuring the impact of breeding on robustness. Given that wheat is primarily released as inbred cultivars, the selection pressure to increase yields during breeding may also tend to select genotypes with more narrower trait distributions (Gavrilets & Hastings, 1994; Wagner et al., 1997)—or more predictable genotypes. We first tested whether breeding could be a component affecting yield robustness by comparing the release year of a cultivar to its robustness using the statistic CV. We calculated the yield robustness for each cultivar

across years planted at a single location (Table S2); however, we observed that robustness was sensitive to the number of years it was grown (Figure S2).

To reduce or eliminate the impact of number of years grown on robustness, we used two approaches. First, based upon an estimated plateau in decreased robustness due to number of years grown (Figure S2a), we set a conservative threshold of greater than 9 years planted for inclusion. This approach reduced the number of cultivars included and eliminated those most recently publicly released from further analysis, because they have not existed long enough to be tested for 10 years. With these filtered data, we detected a very weak negative linear relationship between CV and release year pooling across locations in this filtered dataset (Table 2).

A second aspect of the statistic CV was also examined. Due to the large range of yields examined in the study, the variance and mean yield may not scale linearly (Döring et al., 2015; Taylor, 1961). Indeed in this filtered dataset, the CV misrepresented cultivar robustness as detected by examining the estimated slope (b) between the mean and variance. If $b < 2$, artificially high CV values are estimated for low yields relative to high yields, resulting in spurious strong relationships between the release year and robustness (Figure S3, Table 2). We, therefore, used the adjusted CV (aCV) to estimate cultivar robustness. In contrast to CV, we detected no improvement in robustness due to release year of cultivar using aCV in the filtered dataset (Table 2, Figure 2a).

Given the yield of a cultivar is sensitive to geographic location in which it was grown, we hypothesized that robustness of a cultivar also would depend on location. We examined the location-specific yield aCV values for cultivars grown over

TABLE 2 Linear regression of cultivar yield CV on cultivar release year.

Location	<i>n</i>	CV			aCV		
		<i>b</i>	SE _{<i>b</i>}	<i>R</i> ²	<i>b</i>	SE _{<i>b</i>}	<i>R</i> ²
All	138	$-1.071 \times 10^{-3} **$	3.359×10^{-4}	0.0654	$+1.92 \times 10^{-4}$	3.105×10^{-4}	2.8×10^{-3}
Havre	24	$-2.589 \times 10^{-3} ***$	4.373×10^{-4}	0.6145	-5.90×10^{-5}	4.207×10^{-4}	9.0×10^{-4}
Sidney	17	$-3.069 \times 10^{-3} ***$	9.891×10^{-4}	0.4006	-1.11×10^{-4}	7.672×10^{-4}	1.4×10^{-3}
Huntley	25	$-1.776 \times 10^{-3} **$	6.205×10^{-4}	0.2606	$+2.90 \times 10^{-4}$	6.273×10^{-4}	9.2×10^{-3}
Moccasin	26	-4.75×10^{-4}	3.297×10^{-4}	0.0795	-4.10×10^{-5}	3.271×10^{-4}	7.0×10^{-4}
Bozeman	27	-3.40×10^{-4}	4.239×10^{-4}	0.0251	$+2.02 \times 10^{-4}$	4.083×10^{-4}	9.7×10^{-3}
Kalispell	19	$+3.141 \times 10^{-3} *$	1.137×10^{-3}	0.3099	$+2.89 \times 10^{-3} *$	1.195×10^{-3}	0.2566

Abbreviations: *b*, slope of the regression; aCV, adjusted coefficient of variation; CV, coefficient of variation; *R*², coefficient of determination; SE_{*b*}, standard error of *b*. Asterisks ** and *** denote significant at the 0.01 and 0.001 probability levels, respectively.

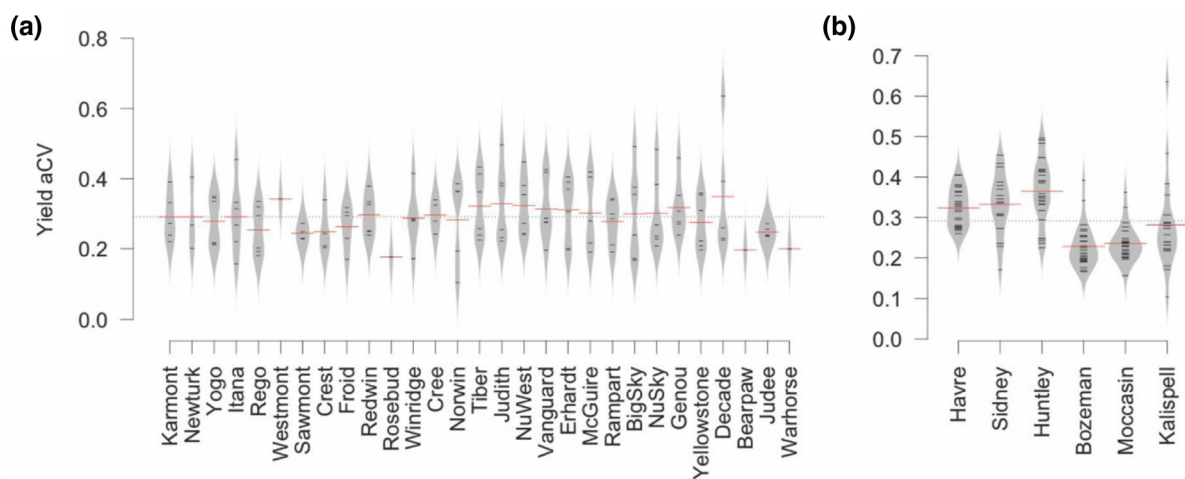


FIGURE 2 Yield robustness depends on location. (a) The yield aCV (adjusted coefficient of variation) for each cultivar is shown. Black lines indicating the yield aCV from each research center for which the cultivar was grown for at least 10 years. The red lines indicate the mean yield aCV for each cultivar, and the dotted black line shows the grand mean yield aCV. The cultivars are arranged in order of release and (b) The yield aCV is shown for each cultivar grown at least 10 years at each research station (black lines). The mean yield aCV for each research station is indicated with the red lines, and the grand mean is indicated with the dotted black line.

9 years and found that Kalispell exhibited robustness decreasing in more recently released cultivars (Table 2), but no relationship was detected in other locations. Using the aCV was critical as strong relationships were observed for the CV in this dataset.

We also performed a second, similar analysis using bootstrapping to understand the relationship between robustness and release year. In this approach, we calculated robustness using five randomly chosen yield values for each released line measured at least 5 years. Then we modeled the relationship between release year and robustness. We performed 1000 bootstraps and examined the summary statistics' distributions for evidence of a relationship between release year and robustness. Using the data across locations, we detected no relationship between aCV and release year (mean

of 1000 bootstraps: $b = 0.00319$, $p = 0.449$, $R^2 = 0.025$, Figure S3a–c), a very similar outcome as the threshold approach. Next, we performed this same bootstrap procedure for each location (Figure S3d–i). Similar to the previous approach using a 10 year filter, we again found no support for a relationship between release year and robustness overall and at five of the six locations. In contrast, again at Kalispell we detected a loss of robustness with release year, consistent with the examination of overall residuals when fitting yield over time and in the filtered dataset (Figure S1).

To begin to understand why locations showed differences in the relationship between robustness and release year, we first examined the range of aCV values. We noted that cultivar robustness varied with geographic location, with higher

aCV values at Huntley, Sidney, and Havre (Figure 2b). Thus, this analysis suggests that robustness of a cultivar is sensitive to location and that breeding for robustness may have larger impacts on particular locations.

We also found evidence that biotic perturbations influenced levels of robustness in a location-specific manner. At Kalispell, the cultivar Decade exhibited the lowest robustness in yield of the entire dataset (yield aCV > 0.6, Figure 2b). This is due to very large range of yields produced over 12 years of testing, ranging from 605.25 kg ha⁻¹ to 9280.5 kg ha⁻¹. The low yields for Decade were location specific and not observed at other sites. Examining the breeder's notes, we found that the second lowest value (1076 kg ha⁻¹) measured was associated with stripe rust at Kalispell. The lowest value (605.25 kg ha⁻¹) was measured during the following year, which we speculate is also due to stripe rust that was not recorded in the breeder's notes. In addition to the abiotic conditions, agronomic practices, and breeding impacts considered, biotic stresses also can greatly impact the robustness measured. In this case, however, we observe that the robustness is associated with genotype, and conclude that Decade represents a genotype particularly susceptible relative to others tested at the same location and year (Kertho, 2014; Riveland et al., 2011).

3.3 | Assessment of weather variability across locations

We hypothesized that evidence for improved yield robustness may be masked because of the weather conditions experienced by a cultivar the years it was grown, given that we detected location specific effects on aCV. Therefore, we assessed mean weather patterns at the six locations at multiple scales, focusing on temperature and precipitation, both of which are critical inputs to crop yield (Kukul & Irmak, 2018). Between 1949 and 2019, average annual temperature and precipitation varied at the six locations, with Huntley having the highest average annual temperatures and Havre having the lowest precipitation (Figure S5a–d). At the same time, the maximum annual temperatures increased between 1949 and 2019 (Table 3). Sidney had the largest average annual temperature change between 1949 and 2019, increasing 0.41°C per decade. Sidney, Bozeman, and Moccasin also had increasing minimum average annual temperatures during this time. Precipitation trends also varied per location. Bozeman and Moccasin, which tended to have higher precipitation among these locations, were unchanged or tending towards decreasing during this time period, but Sidney had an annual average precipitation increasing 1.33 cm per decade between 1949 and 2019. For a better resolved perspective of seasonal temperatures at each location, we calculated the monthly means from 1949 to 2019 (Figure S5e–g). Havre and Sidney experienced the most extreme temperatures, not only facing high mean, minimum

and maximum temperatures in the summer months, but also the lowest temperatures in the winter months relative to the other four locations. Monthly total precipitation means were also calculated for each month from 1949 to 2019 (Figure S5g). Kalispell has higher rainfall, especially during the winter and early spring, relative to the other locations. Total monthly precipitation varied much more from month to month and across locations relative to temperature (Figure S5d).

Using these monthly and annual weather variables, we examined weather variability over time in the dataset. We calculated monthly CV statistics for the mean, minimum, and maximum temperatures, and the precipitation at each location from 1949 to 2019 (Figure 3a–d). For all three summaries of temperature, we observed high CV in the fall and winter months, with a peak in January. Across locations, Havre and Sidney ranked as having the highest CV values during these winter months. In contrast, during the spring and summer months of winter wheat growth, the temperature CV were indistinguishable among locations, indicating little year-over-year variation in monthly temperatures. These patterns suggested that if year-over-year variability is impacting yield robustness, the source may be the variation in the fall and winter months. Because winter wheat is planted in the fall and vernalizes over winter, temperature throughout winter also has direct impacts on the plants, including winter kill. Year-over-year precipitation showed a different pattern from temperature, with more CV values ranging from 0.40 to 1.15, again with Sidney and Havre exhibiting a tendency for more variability.

Overall Montana's weather variability is projected to increase based on climate models (Whitlock et al., 2017). We used two approaches to examine historical trends in weather variability at the six locations examined. First, we calculated a “moving CV”, based on the annual temperature and precipitation values, using window sizes of 30 years, a standard in calculating climate normal (U.S. Climate Normals, 2021). Contrary to our expectation that weather variability is generally increasing, we observed that historic weather variability depended on location (Figure 3e–h). Fitting a linear model to the moving CV values, we found that Bozeman weather in fact was converging for minimum temperature variability but showed no change for other weather variables (Table 4). At Kalispell, all measures of temperature were converging, with precipitation variability remaining steady, consistent with previous patterns observed in Montana (Zhang et al., 2021). At Havre, Sidney, Huntley, and Moccasin, the different weather variables showed mixed patterns of variability (Table 4). Sidney, for example, was diverging in all temperature variables but converging for precipitation. Moreover, an abrupt upward variability shift in all three temperature variables occurred in Sidney in approximately 1986 (Figure 3e–g). We confirmed this shift was not due to changes in equipment at the Sidney weather station

TABLE 3 Linear regression coefficients (b) from regression of weather variables on year from 1949 to 2019.

Location	$b \times 10^a$			
	Temperature annual mean	Temperature annual maximum	Temperature annual minimum	Precipitation annual cumulative
Havre	0.09212	0.17410*	0.01086	4.53×10^{-3}
Sidney	0.41412***	0.39452***	0.43258***	1.33099*
Huntley	0.15281*	0.19018*	0.11719	0.80292
Bozeman	0.16543**	0.19713**	0.13363**	-0.15007
Moccasin	0.22628**	0.19209*	0.24095***	-0.03251
Kalispell	0.11965**	0.16146**	0.07672	0.19277

^aTo indicate trends per decade, yearly coefficients shown are multiplied by 10.

Asterisks *, **, and *** denote significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

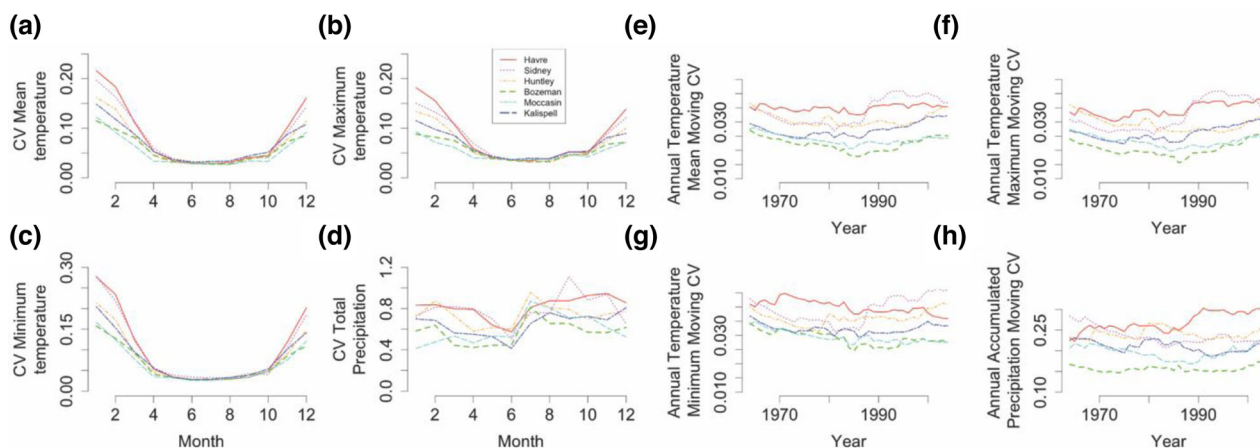


FIGURE 3 Climate variables show location-specific patterns in variability (a–d). The CV (coefficient of variation) of monthly values from 1949 to 2019 for (a) mean, (b) maximum, and (c) minimum temperatures, and (d) total precipitation are shown for each research center. (e–h) CV values calculated from a 30-year moving window are displayed for each location for the average (e) mean, (f) maximum, and (g) minimum temperatures, and (h) total precipitation.

or missing weather data (only found in 2010s), but we have not identified sources of this shift. Out of the 24 weather–location combinations, eight showed convergence in weather variability, eight with divergence, and eight with no change.

3.4 | Accounting for weather demonstrates remaining geographic influences on robustness

Weather, breeding, and agronomic practice are expected to impact yield robustness at all locations but are not independent of one another. For example, while year grown reflects improvement in agronomic practices, it also captures increasing temperatures and is strongly correlated to release year. Therefore, we first examined the relationships among release year (to reflect breeding), growing season (to reflect agronomic practice at least), and the four weather variables using principal component analysis. The first dimension described

47.8% of the variation (Figure 4a), primarily capturing the three temperature variables, along with a substantial contribution of year and release year. The second dimension was driven by year and release year, representing an additional 27.4% of the variation, which showed a close visual association with yield increase, as expected (Figure 4b). The third dimension describing 17.4% of the variation primarily represented precipitation differences (Figure 4a). Because of the inter-relatedness of weather, agronomic practices, and breeding due to their correlations with time, we isolated their potential impacts on yields. A partial correlation analysis showed that after accounting for the correlations between release year, weather variables, and year, a remaining correlation of $r = 0.0583$ was remaining between yield and release year of cultivars examined (Table 5) though the strongest correlation with yield was with precipitation ($r = 0.29$).

With this firmer basis of how yields were collectively affected by weather, we next aimed to parse out the impact

TABLE 4 Linear regression coefficients from 30-year moving window CV of multiple weather variables on year from 1954 to 2004.

Location	<i>b</i>			
	Temperature annual mean CV	Temperature annual maximum CV	Temperature annual minimum CV	Precipitation annual cumulative CV
Havre	3.625×10^{-5}	$1.947 \times 10^{-4**}$	$-2.460 \times 10^{-4**}$	$1.6190 \times 10^{-3**}$
Sidney	$3.411 \times 10^{-4**}$	$4.423 \times 10^{-4**}$	$2.817 \times 10^{-4**}$	$-1.2177 \times 10^{-3**}$
Huntley	-2.430×10^{-5}	$-1.332 \times 10^{-4**}$	$1.390 \times 10^{-4**}$	1.729×10^{-4}
Bozeman	-4.244×10^{-5}	7.501×10^{-5}	$-2.238 \times 10^{-4**}$	1.507×10^{-4}
Moccasin	$1.766 \times 10^{-4**}$	$2.102 \times 10^{-4**}$	-5.304×10^{-5}	$-5.766 \times 10^{-4**}$
Kalispell	$-1.069 \times 10^{-4**}$	$-7.245 \times 10^{-5*}$	$-2.398 \times 10^{-4**}$	-1.416×10^{-4}

Abbreviation: CV, coefficient of variation.

Asterisks * and ** denote significant at the 0.05 and 0.01 probability levels, respectively.

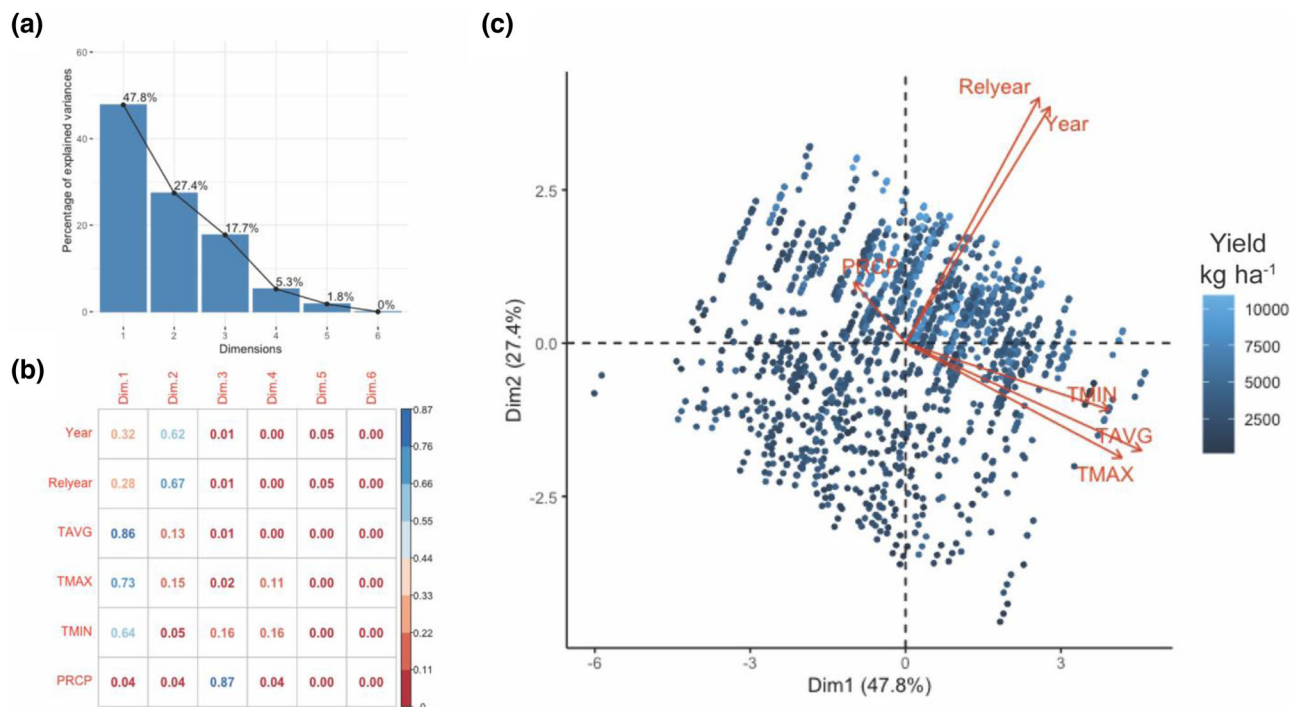


FIGURE 4 Non-independence of multiple metrics affecting robustness (a) Bar chart of percent of variance explained per principal component. (b) Loadings of metrics to each component (labeled Dim1, Dim2). (c) Biplot for each cultivar tested, colored by yield.

of weather for influencing yield robustness in these data. We revisited the filtered dataset with years grown greater than 9, to avoid the impact of years grown. We obtained the corresponding average annual temperature and annual average precipitation for each cultivar during the specific years it was grown. Due to missing weather station data, we were unable to include data for some years. We modeled how yields at each location were affected by average temperature and precipitation, the largest contributors to PC1 and PC3, as well as their interaction. Finally, we recalculated each cultivars' yield robustness as the aCV_{res} based on the residuals of the models following the approach by Schou et al. (2020). Overall, we observed similar patterns as before (Figure 5). We

detected no relationship between release year and aCV_{res} in any location but Kalispell, where again the robustness decreased with release year. Overall, even after some correction for weather differences, we continued to observe the location specific impact on robustness, pointing to many other factors involved in influencing patterns of robustness over time.

4 | DISCUSSION

Historical data collected from specific cultivars of winter wheat grown at defined locations in Montana enable

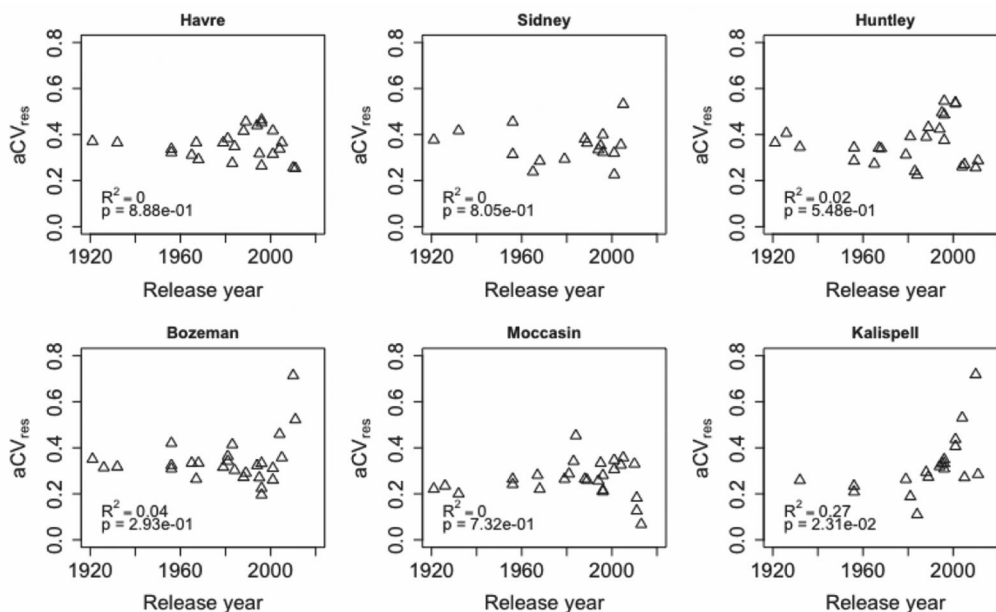


FIGURE 5 The relationship between yield aCV_{res} (residual adjusted coefficient of variation) and release year of a cultivar is dependent on location. After modeling the impact of average temperature and precipitation on yield, yield aCV_{res} was calculated at each research station for each cultivar grown at least 10 years and plotted against the cultivar release year. R^2 and p values for the regression coefficient are displayed.

TABLE 5 Partial correlations^a analysis among yield and potential explanatory factors, all locations.

	Yield	Temperature annual mean (°C)	Temperature annual maximum (°C)	Temperature annual minimum (°C)	Precipitation annual cumulative (cm)	Year
Temperature annual mean	-0.0013					
Temperature annual maximum	-0.0024	0.9994***				
Temperature annual minimum	0.0112	0.9984***	-0.9965***			
Precipitation annual cumulative	0.2929***	0.0548*	-0.0682**	-0.0400		
Year	0.2026***	0.0257	-0.0238	-0.0225	-0.1124***	
Release year	0.0583*	-0.0220	0.0218	0.0202	0.0293	0.8551***

^aPearson correlation coefficients given.

Asterisks *, **, and *** denote significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

studies of the change in year-over-year stability, or robustness, of yields over time. It is important to consider to which perturbations the trait is robust (Wagner, 2007). Examining the robustness of repeated organs formed on an individual, such as tillers in wheat, reveals robustness to stochastic errors of development. Examining individual plants within a single plot reveals robustness to microenvironmental variation as well as developmental differences. On a larger scale, mea-

suring robustness across multiple plots captures robustness to field variation, and finally, robustness has also been considered across years, revealing robustness to weather or variation in agronomic practices at the very least. In this experiment, we measured aggregate robustness across these levels (Falconer & Mackay, 1996) and detected tendencies for robustness to increase over time, dependent on breeding, but this was dependent on geographic location.

A simple examination of the residuals of a linear fit of yield over time as a proxy for robustness did not point to improved robustness over time. This approach cannot distinguish cultivars, agronomic practices, weather changes, soil quality changes, changes in atmosphere composition (including nitrogen and sulfur), or other influences on yield. For example, improved management and other non-genetic inputs at these research sites are known to affect yields. A study of spring wheat at these six research centers from 1950 to 2007 found that the cultivar “Thatcher” showed increased grain yields throughout this period, ranging from 14.8 kg ha⁻¹ year⁻¹ in Moccasin to 50.8 kg ha⁻¹ year⁻¹ in Kalispell (Lanning et al., 2010). Examining robustness of each cultivar separately by calculating a standardized variance using the statistic aCV showed that more recently released cultivars do not tend to be more robust, and even a loss of robustness at the location Kalispell (Table 2, Figure 2).

Importantly, estimating robustness requires a careful consideration of the statistic used. We found that estimates of robustness using the statistic CV were dependent on the number of years a cultivar was grown. If a cultivar was only grown for a few years, the CV was not representative of robustness. We detected a plateau of approximately 10 years of data as sufficient to estimate robustness using CV (Figure S2a). We speculate that this plateau represents the number of years needed for a cultivar to experience an extreme weather event on average. Additionally, an adjusted CV needed to be used to account for the wide range of mean yields in this historic study to avoid mathematical artifacts (Döring & Reckling, 2018).

Geographic location was an indicator of cultivar robustness. A relationship between robustness and release year was observed at Kalispell (Table 2, Figure S4i) and not at the other locations. Notably, Havre, Sidney, and Huntley represent where most of the wheat is grown in the state by producers (National Agricultural Statistics Service, 2021), possibly reflecting a focus of breeders to optimize wheat's growth to those locations. Kalispell stands out from the other locations that comprise the primary focus of the breeding program and represents a region of the state more like eastern Washington. The selected lines are not well-adapted to this region, and the decrease in robustness over time in Kalispell may reflect this. The higher robustness levels at Kalispell, Bozeman, and Moccasin (Figure 2b), support the concept that robustness could be improved at Havre, Sidney, and Huntley, the centers of wheat productivity in Montana.

Pathogen and herbivore pressure also vary over the years and were not considered in this study. Wheat stem sawfly and stripe rust have devastating impacts on yields that can be location specific and breeding has focused on producing resistant cultivars that likely contribute to improved robustness. Finally, we also note that management also did vary across research centers: during this period, Havre and Huntley transitioned from tillage to chemical fallow, increasing soil

moisture (Lenssen et al., 2007), while other sites maintained tillage, including Sidney.

Weather conditions greatly impact crops yields, evidenced by both the great impacts that droughts and floods have on yields (Ray et al., 2015) within a region and how wheat yields are sensitive to one-degree changes in temperatures in controlled conditions (Lanning et al., 2010). We surmised that variability in weather conditions from year to year should be reflected in the robustness of crops. Upon examining climate patterns of temperature and precipitation, we first found that temperatures are increasing at all research centers, and precipitation is unchanging or increasing (Table 3). Second, the variabilities of weather variables showed patterns of convergence, divergence, and no change (Table 4). No general statements could be made to relate change in robustness in yields as dependent on weather variability. After removing the effect of weather variables assessed, we still did not detect new relationships between robustness and release year. These analyses suggest that variable weather is not masking breeding improvements on robustness.

Overall, in this historical wheat dataset spanning 70 years, we can detect a signal that yield robustness is dependent on location across many levels of perturbations, from within plant to across years. Because of the extensive confounding of management, soil quality parameters, and environmental conditions, such as global CO₂ levels, the impact of breeding could best be tested compared by growing historical cultivars at the same site and time for multiple seasons to estimate robustness.

5 | CONCLUSIONS

Winter wheat yields in Montana have greatly increased over the last 70 years. However, assessing cultivars for year-over-year yield stability within single locations does not show improvements with breeding. Weather variability in Montana has been fairly stable in terms of temperatures or precipitation over the last seven decades and do not appear to mask improvements in year-over-year stability, though many other crucial factors may be implicated in future studies. Overall, certain locations tend to produce lower year-over-year stability in cultivars, demonstrating a need to improve year-over-year stability and ensure predictable yields.

AUTHOR CONTRIBUTIONS

Jennifer Lachowiec: Conceptualization; formal analysis; funding acquisition; investigation; methodology; supervision; visualization; writing—original draft; writing—review and editing. **James E. Berg:** Data curation; writing—review and editing. **Meng Liang:** Data curation; formal analysis; writing—review and editing. **Fernando H. Correr:** Data curation; software.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

Code generated and data analyzed in this study are available at <https://github.com/Lachowiec-Lab/historical-stability>.

ORCID

Jennifer Lachowiec  <https://orcid.org/0000-0003-2962-6448>

Meng Liang  <https://orcid.org/0000-0002-1467-946X>

Fernando H. Correr  <https://orcid.org/0000-0001-8562-1946>

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