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Winter wheat response to plant density in yield contest fields

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Abstract

Seeding rate recommendations for wheat (*Triticum aestivum* L.) are often 150–450 seeds m^{-2}. However, we hypothesize that wheat grown with high resource availability (i.e., fertility and moisture) can maximize yield under considerably lower rates. Our objectives were to explore winter wheat response to low populations under high resource availability using yield-contest fields as a case study. A factorial experiment evaluated four wheat varieties (i.e., Joe, WB-Grainfield, Langin, and LCS Revere) exposed to five seeding rates (50, 100, 150, 200, and 250 seeds m^{-2}) during five seasons in commercial wheat fields managed by yield-contest winning producers near Leoti, KS. Fields were silt-loam soils with high available water-holding capacity, long-term history of manure application with non-limiting fertility, and adopted a sorghum [*Sorghum bicolor* (L.) Moench]–fallow–wheat rotation. Plant density ranged from 26 to 341 plants m^{-2} and yield ranged from 3.2 to 6.8 Mg ha^{-1}. Water use efficiency of 19.5 kg ha^{-1} mm^{-1} suggested no management limitations to yield. Quadratic models portrayed the grain yield–plant density relation well, with 95% of the maximum yield reached at 68 to 91 plants m^{-2} for crops sown at the optimum date (4 out of 5 years), and at 312 plants m^{-2} for a late-sown crop. Greater fall temperature accumulation reduced the relative yield between the maximum and minimum seeding rates. There was no variety × plant density interaction and Langin was the most consistent yielding variety across environments. Optimum plant density for winter wheat in environments with high resource availability may be considerably lower than current recommendations.

1 | INTRODUCTION

Wheat (*Triticum aestivum* L.) responses to seeding rate are inconsistent, ranging from positive linear, quadratic-plateau, plateau-negative linear, quadratic, to inexistent (Bastos et al., 2020; Fischer et al., 2019; Holliday, 1960; Holman et al., 2021; Jaenisch et al., 2019, 2022; Lloveras et al., 2004; Lollato, Ruiz Diaz et al., 2019; Mehring et al., 2020; Whaley et al., 2000). The quadratic response suggests that there is an optimum population to maximize yields (Whaley et al., 2000). In this case, populations below the optimum may limit crop yields due to suboptimal plant density and reduced radiation interception, water usage, and yield components per unit area (Bastos et al., 2020; Fischer et al., 2019); while populations above the optimum may limit crop yields due to increased disease and insect pressure, lodging, insufficient resources such as fertility, or excessive early season crop growth and water use (Lloveras et al., 2004; Salgado et al., 2017; van Herwaarden et al., 1998).

Abbreviations: ANOVA, analysis of variance; ETc, crop evapotranspiration; PAWS, plant available water at sowing; SSM, Simple Simulation Model; WUE, water use efficiency.

In most wheat growing regions of the world, recommended seeding rates range from 150 to 350 seeds m^{-2} (Frederick & Marshall, 1985; Lloveras et al., 2004; Staggenborg et al., 2003), with some studies indicating benefits of rates as high as 450 seeds m^{-2} (Beres, Clayton et al., 2010; Beres, Harker et al., 2010; Lloveras et al., 2004). However, recent empirical evidence suggests that wheat responses to seeding rate were dependent on the level of resource availability of the environment (Bastos et al., 2020). In high-yielding environments (greater than 6.0 Mg ha^{-1}) where crop growth is likely not limited by resources (e.g., nutrient and water availability and optimal temperature and moisture for tillering), crop yield was unresponsive to plant population within the evaluated range (i.e., 50–500 plants m^{-2}). Similar results where maximum yields were achieved in populations as low as 90 plants m^{-2} were observed in winter wheat yield contests (Lollato, Ruiz Diaz et al., 2019) and replicated field experiments with intensively managed winter wheat in Kansas (Jaenisch et al., 2019, 2022). Moreover, there is evidence for spring wheat maximizing grain yield with as few as 16–44 plants m^{-2} when arranged to capitalize on resource usage (e.g., honeycomb or squared arrangements; Fischer et al., 2019; Hasan et al., 2022). Meanwhile, in average- and low-yielding environments (i.e., 4.5 and 3.0 Mg ha^{-1} average yield), Bastos et al. (2020) suggested that yield plateaus at 296 and 334 plants m^{-2}, respectively. The authors argued that crops exposed to conditions not ideal for tiller production and maintenance (e.g., late sowing and drought stress) required greater plant populations to maximize yield.

Previous studies in cereals suggest that the optimum plant density depends on variety (Anderson & Barclay, 1991; Baker, 1982; Briggs & Ayten-fisu, 1979; Faris & De Pauw, 1981; Mehring et al., 2020; Pendleton & Dungan, 1960; Wiersma, 2002), reinforcing the need to further understand genotype × management × environment interactions (Beres et al., 2020). In general, semidwarf varieties with lower tillering potential and insensitive to photoperiod require greater population to maximize yields compared to their counterparts with contrasting characteristics (Jaenisch et al., 2022; Mehring et al., 2020). The often significant variety × seeding rate interaction led researchers to recommend that every variety released by breeding programs should be tested at a range of seeding rates so that variety-specific seeding rate recommendations are available upon public release (Faris & De Pauw, 1981).

The majority of the studies evaluating wheat yield response to seeding rate were performed under standard management conditions (i.e., enough fertility levels for average yield goals [e.g., 4.7 Mg ha^{-1}, Bastos et al., 2020], lack of foliar fungicide applications, and other management factors adopted under "normal" management levels; Holman et al., 2021; Lloveras et al., 2004; Wall & Kanemasu, 1990a,b; Whaley et al., 2000). However, in a context in which substantial increases in food production are needed to feed an increasing global population (Parry & Hawkesford, 2010), exploring management practices under intensively managed scenarios that maximize grain yield is crucial. This is especially relevant in regions characterized by yields well below their respective potential yields (i.e., large yield gaps), since these cropping systems offer the most immediate potential to increase food production with current technologies (van Ittersum et al., 2013). Winter wheat grown in Kansas and neighboring states is a good case study for potential increases in yield through management since there is evidence of recent yield stagnation concomitant with substantial yield gaps (Jaenisch et al., 2021; Lollato & Edwards, 2015; Lollato et al., 2017; Lollato, Ruiz Diaz et al., 2019; Patrignani et al., 2014).

The framework adopted in this research is that in water-limited systems where stored soil water is important for grain yield, optimum plant density for wheat tends to be lower because increased crop evapotranspiration (ETc) early on with higher populations reduces water availability around flowering and grain filling (van Herwaarden et al., 1998). Under intensive management systems with ample resources, solar radiation and temperature modulate grain yield (Evans & Fischer, 1999); therefore, the crop requires enough plants to reach full radiation interception before the critical period for grains m^{-2} (Fischer et al., 2019), which for wheat starts just before flag leaf emergence (Fischer, 1985). Alternatively, denser crops can reduce yield slightly due to potential post-flowering water limitation even without lodging (Fischer & Kohn, 1966). A caveat to the above framework is that optimal plant density is often greater with later sowings because crop development is accelerated more than growth. While this is clearly illustrated in case of spring wheat (Fischer, 2016), it is also true for winter wheat (Staggenborg et al., 2003) and can be exacerbated by conditions that lead to winterkill (Beres, Harker et al., 2010). Given this framework, our

Core Ideas

- Winter wheat response to plant density depends on resource availability.
- Under high resource (fertility and moisture), winter wheat response to density relied on fall temperature.
- Note that 68–91 plants m^{-2} reached 95% maximum yield in four out of five seasons under optimum sowing time.
- Note that 312 plants m^{-2} reached 95% maximum yield in one out of five seasons with late sowing.
- Current seeding rate recommendations could be lowered for intensively managed fields.

central hypothesis is that winter wheat will be less responsive to plant density in yield contest fields, since these are intensively managed scenarios with virtually no manageable resource limitation (e.g., nutrient, pests, weeds, and diseases). The exceptions to this hypothesis would be in cases of untimely sowing that could result in less temperature accumulation in the fall and therefore less fall tillering potential. With this, our objective was to evaluate the grain yield response of different winter wheat varieties to seeding rate, including extremely low seeding rates, in an intensively managed field in semiarid western Kansas.

2 | MATERIALS AND METHODS

2.1 | Field experiments

Field experiments were conducted in commercial winter wheat production fields near Leoti, western KS (38.299° N, −101.201° W, altitude 1006 m.a.s.l.), during five consecutive winter wheat seasons (2017–2018 through 2021–2022). The fields were managed by the cooperators (i.e., Horton Seed Service) following practices that often resulted in winning yield contests both at the state and national levels (Kansas Wheat, 2016, 2017, 2018, 2019). While the minimum field size to enter yield contests is 2 ha (Lollato, Ruiz Diaz et al., 2019), the size of the fields in this study where management was consistently applied ranged from 64 to 128 ha (Figure S1).

A two-way factorial treatment structure was established in a completely randomized block design with four replications to evaluate the grain yield of four commercial wheat varieties (i.e., Joe, Langin, WB-Grainfield, and LCS Revere) exposed to five seeding rates (50, 100, 150, 200, and 250 seeds m^{-2}). Since treatments were established as seeds m^{-2}, the range in variety- and season-specific seed size was 26.7–43.2 g 1000 seeds^{-1}, ranging from 30.5 to 37.9 g 1000 seeds^{-1} as function of season and from 33.1 to 40.1 g 1000 seeds^{-1} as function of variety. These winter wheat varieties were selected for their representativeness of growers' adoption in the region since Joe, Langin, and WB-Grainfield were ranked within the top five varieties in terms of area sown in Kansas, and within the top three varieties sown in the West-Central Agricultural District of Kansas (where the study was conducted) during the study period (USDA-NASS, 2018, 2019, 2020, 2021, 2022). LCS Revere was selected for this study since it was released as a replacement to the variety T-158, which has similar importance in area planted to the other three varieties. Each variety occupied as much as 5.9% of the wheat area planted in Kansas and as much as 11.1% of the area planted in the district. More information about these varieties' agronomic characteristics is provided in Table S1.

Field experiments were sown on October 13, 2017; September 27, 2018; and September 25, 2019, 2020, and 2021. We note that September 19–27 is the optimum sowing date for this region (Jaenisch et al., 2021; Munaro et al., 2020). While we were able to sow the trial in this window most years, wheat sowing was delayed in the 2017–2018 season due to rainfall at the optimum period impeding timely field operations. All experiments were sown using no-tillage practices after an 11-month fallow period in sorghum [*Sorghum bicolor* (L.) Moench] residue. This crop rotation (winter wheat–sorghum–fallow) is the predominant cropping system in western Kansas (Jaenisch et al., 2021) as it allows for soil water recharge and timely sowing prior to both crops (Schlegel et al., 1999). Fallow periods were maintained weed free with the use of commercial herbicides and aided by large residue left in the field by both crops (Simão et al., 2024). Seeds were treated with insecticide and fungicide (15 mL 100 kg seed^{-1} of imidacloprid and with 0.74 mL 100 kg seed^{-1} of tebuconazole) to avoid potential stand losses due to pests and diseases (Pinto et al., 2019). The research plots were sown using a 606NT Great Plains commercial drill adapted for small plot research. Experimental units consisted of seven 19-cm spaced rows wide and were 9.1-m long. Within the context of this experiment, winter wheat was the second crop after conditioned manure application at 11.2 Mg ha^{-1}, which provided about 163 kg ha^{-1} of N and 179 kg ha^{-1} P_2O_5 to the system. In-furrow diammonium phosphate (18-46-0) was applied with the seed at 56 kg of product per hectare despite high soil-testing P levels since it may result in increased crop yields (Maeoka et al., 2020). Management of the wheat crop consisted of 45 kg N ha^{-1} applied with 260 mL ha^{-1} Rave herbicide (8.8% Triasulfuron, 55% sodium salt of dicamba) during the winter (typically in February), 99–256 kg N ha^{-1} of N as urea-ammonium nitrate (28-00-00) applied at spring greenup (Feekes 4, typically in March), single mode of action foliar fungicides applied at the double ridge stage (Feekes 5, usually in April; product and rate varied per year but typically ~60 g ha^{-1} azoxystrobin-class), and dual mode of action foliar fungicides applied when flag leaf was fully emerged (Feekes 9–10; product and rate varied per year but typically 80 g ha^{-1} azoxystrobin- and 40 g ha^{-1} Cyproconazole-classes). In some years, cytokinin plant growth hormone (146 mL ha^{-1} at 0.04% concentration) and slow release nitrogen fertilizer were applied together with the foliar fungicides. Combined with the soil fertility available at sowing, all manageable stresses were likely limited and therefore growing conditions were representative of nonirrigated potential conditions. Experimental units were trimmed before harvest for a total length of 7.3 m, and harvest occurred using a Massey Ferguson XP8 small-plot, self-propelled combine in early July to mid-July.

2.2 | Measurements

A total of 15 individual soil cores (0- to 15-cm and 15- to 61-cm depth) were collected immediately prior to sowing each year of the study. Within each depth, samples were mixed into a composite sample, dried, and ground for initial soil fertility analysis. Analyses included soil pH analyzed via 1:1 soil–water Sikora buffer, soil organic matter analyzed via loss on ignition, KCl extraction inorganic nitrate-nitrogen (NO_3-N), Mehlich III soil phosphorus extraction, ammonium acetate extraction for potassium, calcium, magnesium, and sodium, DTPA (diethylenetriaminepentaacetic acid) extraction for iron, zinc, copper, and manganese, and $Ca(HPO_4)_2$ extraction for chloride and sulfate-sulfur (SO_4-S). Cation exchange capacity was measured by summation, and soil texture was measured via particle size distribution with a hydrometer. In-season measurements included plant density measured at Feekes 1–2, about 20–30 days after sowing by counting all plants emerged in one linear row meter; and grain yield which was measured by harvesting the entire experimental unit after edge trimming. To account for potential edge row effect, grain yield calculation considered plot width from the center of one plot to the center of the neighboring plot (as specified at sowing by GPS) to include the path's width (25 cm). Grain yield was corrected to 130 g kg^{-1} moisture basis.

2.3 | Weather data and crop simulation modeling

Daily weather data for maximum and minimum air temperatures, incident solar radiation, and precipitation were collected from an agro-climatological station located ∼23 km from the study fields pertaining to the Kansas Mesonet (Patrignani et al., 2020). Soils data on depth and available water-holding capacity were retrieved from the Web Soil Survey (Soil Survey Staff, 2023). Plant available water at sowing (PAWS) was estimated for the 120-cm soil depth by initiating simulations on January 1 of the sowing year assuming 80% plant available water, allowing for enough time for values to converge to actual PAWS (Lollato et al., 2016). These variables were used to run the mechanistic crop model "Simple Simulation Model" (SSM)-Wheat (Soltani & Sinclair, 2012) for each studied year as well as for the 30-year period preceding the experiment. The SSM-Wheat model has been validated for phenology (i.e., days to emergence, anthesis, physiological maturity, and harvest maturity); growing season dynamics for shoot biomass, leaf area index, and rootzone plant available water; and harvested grain yield and harvest index under non-limiting management conditions in the US southern Great Plains using data from Lollato and Edwards (2015). We used crop parameters detailed in Lollato et al. (2017).

For the purpose of the current work, crop simulation output was used to determine the typical weather conditions experienced in important phenological stages of wheat development and their relation to measured grain yield, in an attempt to better contextualize the measured responses. Here, we calculated mean temperatures and cumulative precipitation and ETc for the sowing to maturity, sowing to jointing, jointing to heading, and heading to grain filling developmental phases, using simulated crop phenology. This was performed for weather data during the experiment, as well as for the preceding 30 years. Simulation output also provided an opportunity to evaluate water use efficiency (WUE) and whether yields were limited by water availability based on the framework originally proposed by French and Schultz (1984) and widely validated (Sadras & Angus, 2006). This framework consists of fitting a linear model to the 95th yield quantile of the yield ∼seasonal water supply as $Y = \text{WUE}\,(\text{SWS} - E)$, where Y is yield, WUE is water use efficiency, SWS is seasonal water supply (calculated as in-season precipitation plus PAWS), and E is the minimum evaporative water losses. Seasonal water supply was calculated as PAWS plus growing season rainfall.

2.4 | Statistical analysis

The impact of weather variables during critical phenological phases on grain yield was evaluated using regression analyses and Pearson's correlation. Due to the limited number of observations ($n = 5$ seasons), here we considered $p \leq 0.1$ significant (e.g., Jaenisch et al., 2022). The remaining analyses were considered significant when $p \leq 0.05$. Statistical analysis of plant density and grain yield as dependent variables was performed using three-way mixed model analysis of variance (ANOVA) considering year, seeding rate, variety, and their interactions as fixed factors, while replication nested within year was a random factor. Since seed rate is continuous, linear and nonlinear regression analyses of its impact on grain yield complemented the ANOVA, with more parsimonious models preferred. These regressions were performed on the least square means from four replicates per seeding rate. Yield response to plant density was modeled as quadratic polynomial, similar to previous research (Fischer et al., 2019; Spink et al., 2000; Whaley et al., 2000; Willey & Heath, 1969). The first derivative of the quadratic models defined the plant density for maximum yield, and was used to calculate the plant density needed to achieve 95% maximum yield. These analyses were performed across varieties due to a lack of variety × seeding rate interaction (see Section 3.3) using plant density and yield observations from individual experimental units. The residuals from the yield-plant density relations within year were subjected to one-way ANOVA to test the effect of wheat variety when density was accounted for. To contextualize crop response to seeding rate and plant density, variables were related to temperature accumulation in the fall (growing degree days calculated using a base temperature of 0°C) due to its impact on tillering. Regression analyses were derived in SigmaPlot 13 (Systat Software) and ANOVAs using PROC GLIMMIX procedure in SAS v. 9.4.

3 | RESULTS

3.1 | Soil fertility status on yield contest fields

Soil pH ranged from 6.2 to 6.8 in the topsoil and from 7.0 to 7.9 in the subsoil of the silt loam soil in the study region (Table S2). Soil organic matter was 2.3 ± 0.4% in the topsoil and 1.8 ± 0.1% in the subsoil. Initial soil NO_3-N averaged 129 ± 30 kg N ha^{-1} in the 61 cm profile. Phosphorus (102 ± 35 ppm), potassium (764 ± 91 ppm), calcium (2446 ± 228 ppm), magnesium (392 ± 48 ppm), associated cation exchange capacity (20 ± 2 meq 100 g^{-1}), and the remaining macro- and micronutrients are shown in Table S2.

3.2 | Environmental influence on annual mean grain yield

Growing season precipitation ranged from 141 to 362 mm and PAWS from 153 to 199 mm, resulting in seasonal water supply of 323–539 mm (Figure 1a–e). Seasonal water distribution mismatched the patterns of ETc (range: 251–436 mm) in 2018, 2020, and 2022. Yields were lower in these years (3.2–3.7 ± 0.1 Mg ha^{-1}) in comparison with years with better agreement between precipitation distribution and ETc (6.5–6.8 ± 0.1 Mg ha^{-1}). As compared to the 30-year mean, 2019 and 2021 had above average seasonal water supply and average grain fill temperature; 2018 and 2020 had average water supply but warm grain fill conditions, and 2022 was slightly dry and cool (Figure 1f).

Seasonal water supply is related positively with grain yield (r = 0.87, p = 0.05; Figure 2a). The 95th percentile yield within each year is plotted against seasonal water supply and returned a slope (WUE) of 19.5 ± 0.4 kg ha^{-1} mm^{-1} and estimated soil evaporative losses of 117 mm (Figure 2a). Growing season rainfall ranged from 141 to 362 mm and was the main environmental source of variation influencing grain yield (r = 0.96, p = 0.01) (Figure 2b). Growing season maximum temperature ranged from 14.3˚C to 17.2˚C and was associated negatively with grain yield (r = −0.82, p = 0.09; Figure 2c). There were no other associations of weather variables and grain yield (data not shown).

3.3 | Seeding rate and variety effects on plant density

Seeding rate interacted with year to determine plant density (Table 1). While increases in seeding rate increased plant density, the final densities were closer to the target seeding rate at lower rates as compared to higher seeding rates (Figure 3a). Here, the final plant density for the 50 and 100 seeds m^{-2} rates was on average −1% from the target (range: 24% to −19%), while the final plant density for the 200 and 250 seeds m^{-2} rates was on average −30% from the target (range: −7% to −48%). This difference, in particular for the highest seed rate, related positively with the total precipitation in the 30-day surrounding crop sowing (r^2 = 0.67, p = 0.02; Figure 3b). Across years and seeding rates, there was a significant variety effect on plant density where Langin had lower population than the remaining varieties (108 ± 3 vs. 116–118 ± 3 plants m^{-2}; Figure 3c).

3.4 | Grain yield as function of seeding rate and variety

Year interacted with seeding rate and with variety to determine grain yield (Table 1). Yield increased linearly with increases in seeding rate in 2018 (Figure 4a), while the remaining years showed either nonsignificant (2020–2021) or quadratic responses to seeding rate (Figure 4b–e). While these relationships were significant in 4 out of 5 years (r^2 > 0.96, p < 0.03), grain yield was fairly insensitive to seeding rate considering that the yield penalty of the 50 seeds m^{-2} seed rate was only 15%–18% as compared to the highest yield within year. Additionally, Tukey test suggested that the highest grain yield within each site year did not differ from that attained at 100 seeds m^{-2} in 4 out of 5 years (Figure 4b–e). The only exception was 2017–2018, when each increase in seeding rate increased yield significantly, with an overall gain of 32% from 50 to 250 seeds m^{-2} (Figure 4a). Grain yield penalty due to seeding 50 seeds m^{-2} versus the maximum yield within environment was explained by an exponential gives rise to maximum as function of fall growing degree accumulation, with colder fall conditions resulting in greater yield penalty and stabilizing at around 600˚C days (Figure 4f). Further exploration of the interaction of year × variety demonstrated that the variety Langin had the highest yield across years, with the remaining varieties changing in ranking depending on year (inset, Figure 4a–e). There was no variety × seeding rate interaction (Table 1).

3.5 | Grain yield response to plant density

The quadratic polynomial model explained the relation between grain yield and plant density within year well (Figure 5). According to the fitted equations, the maximum and 95% of the maximum grain yield, respectively, were achieved at plant densities of 459 and 312 plants m^{-2} in 2017–2018 (Figure 5a) and between 120 and 159 or 68 and 92 plants m^{-2} in the remaining years (Figure 5b–e). The minimum density needed to reach maximum yields was higher in the year

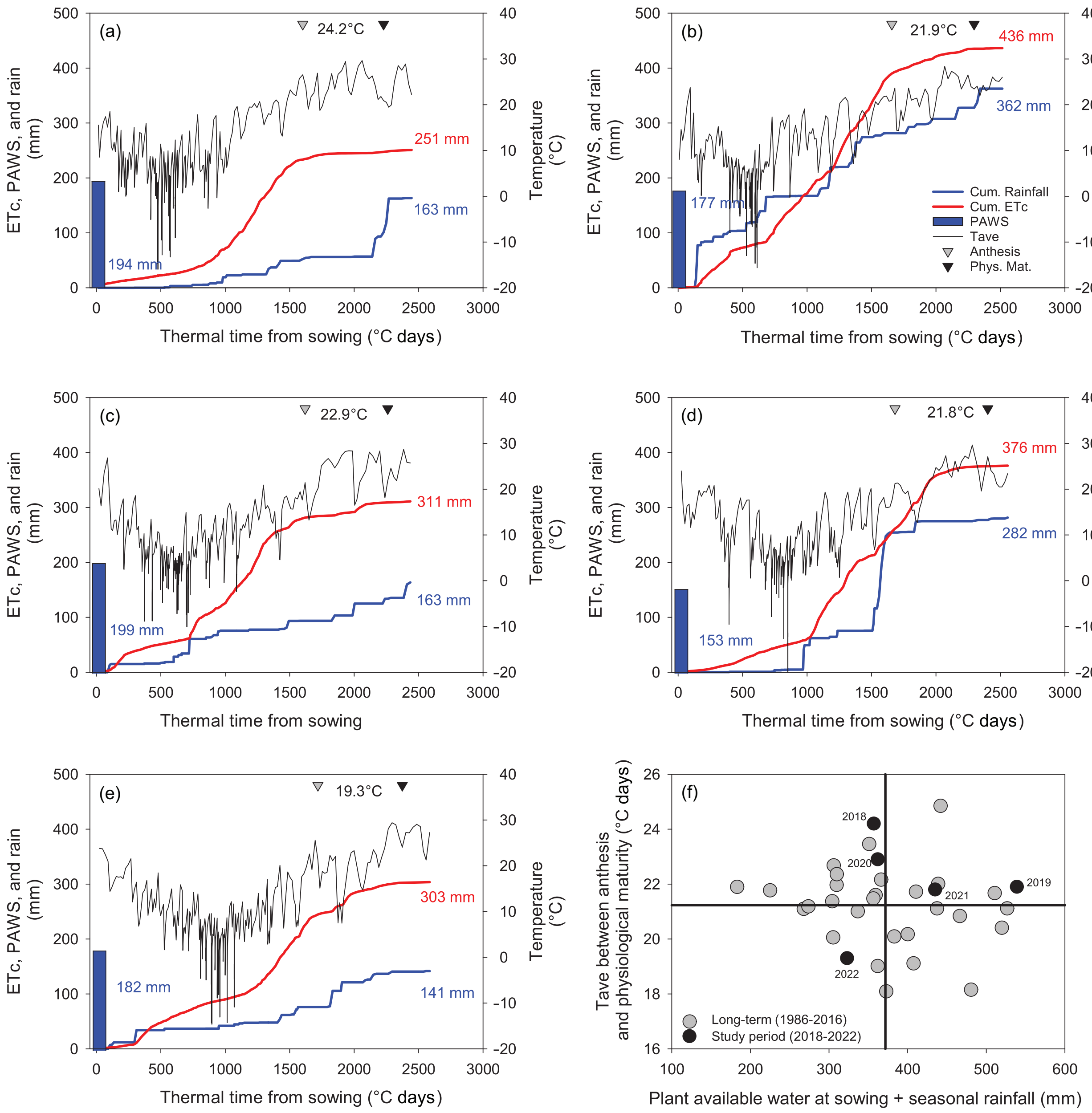

FIGURE 1 Plant available water at sowing (PAWS), cumulative crop evapotranspiration (ETc), cumulative rainfall, and average temperature (*T*ave) during the (a) 2018, (b) 2019, (c) 2020, (d) 2021, and (e) 2022 winter wheat growing seasons near Leoti, KS. Downward-facing triangles denote dates for anthesis and physiological maturity. Inset values show cumulative seasonal ETc, rainfall, PAWS, and *T*ave between anthesis and physiological maturity. Panel (f) shows the comparison of total water supply and mean grain filling temperature of the five growing seasons included in this study with the previous 30 growing seasons.

with lower temperature accumulation during the fall and similar in the remaining seasons (Figure 5f). One-way ANOVAs of the residues of the regressions shown in Figure 5a–e for the year-dependent effect of variety once differences in plant population were accounted for resulted in similar variety-effects on grain yield to those of the analyses shown in Table 1, despite some minor year-specific mean comparison changes (inset graphs, Figure 5a–e).

4 | DISCUSSION

A sample of relevant commercial winter wheat varieties managed according to practices adopted in yield contest fields and exposed to five seeding rates over the course of five consecutive growing seasons revealed environment × management and environment × variety factors driving wheat response to plant density under conditions of ample resource availability,

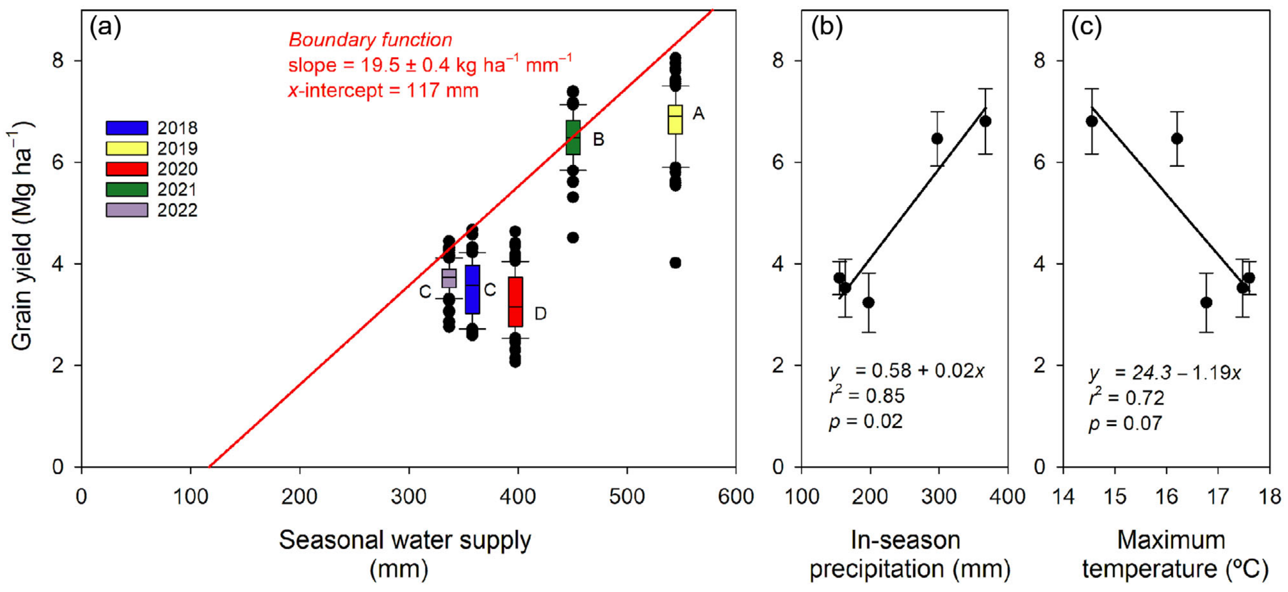

FIGURE 2 Environmental influence on winter wheat grain yield. (a) Relationship of grain yield (distribution shown as box plots of all yield observations within by year) and seasonal water supply in yield contest fields near Leoti, KS, during five growing seasons. Seasonal water supply was estimated as the sum of modeled plant available water at sowing and in-season precipitation. Parameters (slope ± SE and x-intercept) of the boundary function of maximum yield per season are shown (red line). Box plots followed by a common letter were not significantly different by the Tukey test at the 5% level of significance. Individual observations outside the box plot represent outliers from the distribution. (b, c) Relationship between environmental mean grain yield and (b) in-season precipitation and (c) average maximum temperature, both calculated from sowing to maturity. In (b, c), solid lines denote least square regressions, and error bars are standard deviation of the mean.

TABLE 1 Analysis of variance for plant density and grain yield based on data collected from yield contest fields near Leoti, KS, during five growing seasons.

		Plant density		Grain yield	
Source of variation	***df***	***F***	***p > F***	***F***	***p > F***
Year (Y)	4	10.3	<0.001	361.3	<0.0001
Seeding rate (SR)	4	312.9	<0.0001	65.2	<0.0001
Variety (V)	3	3.4	0.02	19.8	<0.0001
Y × SR	16	6.6	<0.0001	3.1	<0.0001
Y × V	12	1.6	0.09	7.8	<0.0001
SR × V	12	1.1	0.35	0.9	0.5805
Y × SR × V	48	1.1	0.41	1.0	0.5234

highlighting the absence of significant seeding rate × variety and seeding rate × variety × year interactions.

4.1 | Evidence for absence of management limitation to grain yield

We initiated this study after some evidence for a relative insensitivity of winter wheat yield response to density in yield-contest fields (Lollato, Ruiz Diaz et al., 2019), justifying its conduction in fields managed by growers who often win yield contests (Kansas Wheat, 2016, 2017, 2018, 2019) to explicitly avoid managerial limitations. The intensive management of pests and diseases adopted by these high-yielding producers alleviated potential biotic stresses typical in the region (Cruppe et al., 2017, 2021; Pinto et al., 2019; Sassenrath et al., 2019). Further, the yield range in this study (3.2–6.8 Mg ha^{-1}) is similar to yields reported by yield contests fields in Kansas (2.2–8.3 Mg ha^{-1}; Lollato, Ruiz Diaz et al., 2019) and from intensively managed field experiments (2.0–7.7 Mg ha^{-1}; de Oliveira Silva et al., 2020; Jaenisch et al., 2019, 2022; Lollato & Edwards, 2015).

The soil fertility data (Table S2) provides evidence for the absence of nutrient limitation to grain yield (Leikam et al., 2003). Soil pH was well above that demonstrated to reduce the wheat yield in the region (ca., 5.5; Lollato et al., 2013;

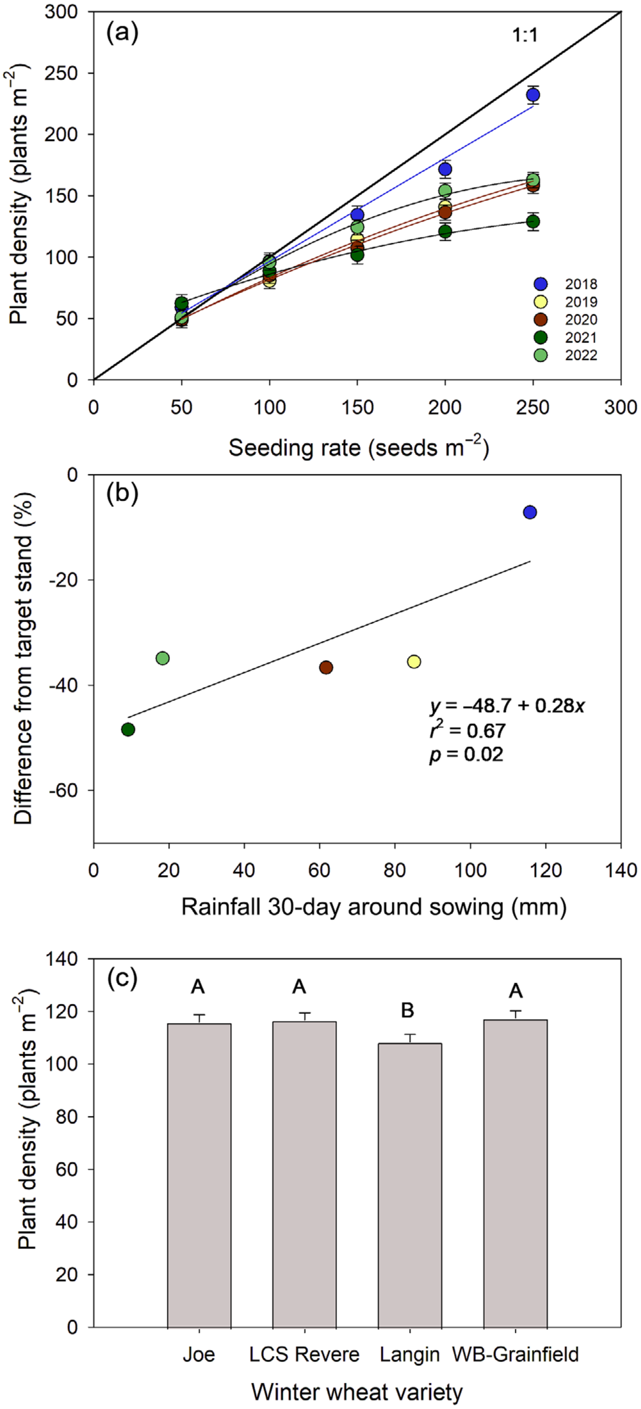

FIGURE 3 Treatment effects on plant density on a trial evaluating variety and seeding rates impact on wheat production in yield-contest winning fields near Leoti, KS, during five growing seasons. (a) Seeding rate interacted with year to determine plant population. (b) Difference from the target population varied as function of rainfall in the 30-day period surrounding crop sowing. (c) Winter wheat variety significantly impacted plant density across years and seeding rates. Solid lines (a, b) denote significant least square regressions. Least square means followed by a common letter (c) were not significantly different by the Tukey test at the 5% level of significance.

Lollato, Ochsner et al., 2019). Total N available (i.e., soil NO_3-N available at sowing plus N fertilizer applied) ranged from 215 to 413 kg N ha^{-1}, which is considerably higher than the minimum grain N removal by winter wheat grain for maximum yields (i.e., ~130 kg N ha^{-1} for ~5.8 Mg ha^{-1} yield; Fowler, 2003; Giordano et al., 2024). Indeed, large amounts of N available resulted in N balances of +10 to +292 kg N ha^{-1} (calculated considering grain N removal of 24.7 kg N Mg^{-1}; Lollato, Figueiredo et al., 2019). While this suggests no limitation of N to grain yield (Tenorio et al., 2019), we note that large N balances are not environmentally ideal (Tamagno et al., 2022; van Groenigen et al., 2010) and can question the sustainability of these intensively managed crops (Spiertz, 2010). Still, recent evidence suggests that this excess N is still available to subsequent crops in semiarid regions (Meier et al., 2021; Smith et al., 2019).

The WUE analysis offers additional evidence to suggest that yields were only limited by water supply (Figure 2a). WUE of 19.5 kg ha^{-1} mm^{-1} is at or above maximum wheat WUE reported in this region. For example, Patrignani et al. (2014) suggested a wheat WUE of 19 kg ha^{-1} mm^{-1} in the Oklahoma panhandle, which is in the same approximate longitude of the current study but south (36.5–37.0° N, 100.0 to 103.0° W, elevation: 650 to 1052 m.a.s.l.). Lollato et al. (2017) suggested a wheat WUE of 15.1 kg ha^{-1} mm^{-1} in the region spanning the current study and expanding to drier and warmer regions. Sadras and Angus (2006) calculated a WUE of 16.7 kg ha^{-1} mm^{-1} in Bushland, TX; a site in the same approximate longitude but south (35.19° N, 102.06° W, 1166 m.a.s.l.). Our minimum water losses (117 mm) were also in the range reported for wheat (range: 50–170 mm; French & Schultz, 1984; Lollato et al., 2017; Patrignani et al., 2014; Sadras & Angus, 2006). These WUE levels suggest that the maximum yields in each experiment were only limited by water supply, which is a product of PAWS and in-season precipitation.

4.2 | Weather

All analyses related to weather conditions in this experiment were constrained to five environments, which is a limitation of the current study. Nonetheless, three of the five environments were similar to long-term seasonal water supply, and two were similar to long-term grain fill temperature (Figure 2f). The dry conditions experienced in these three seasons were characterized by an immediate pre-anthesis drought that probably limited yield the most through reducing grain number, followed by dry grain filling periods that would have reduced grain size (Figure 1). These conditions are typical of the study region, with high likelihood of water and heat stresses (Couëdel et al., 2021; Lollato et al., 2020; Sciarresi et al., 2019; Zhao et al., 2022). Passioura and Angus

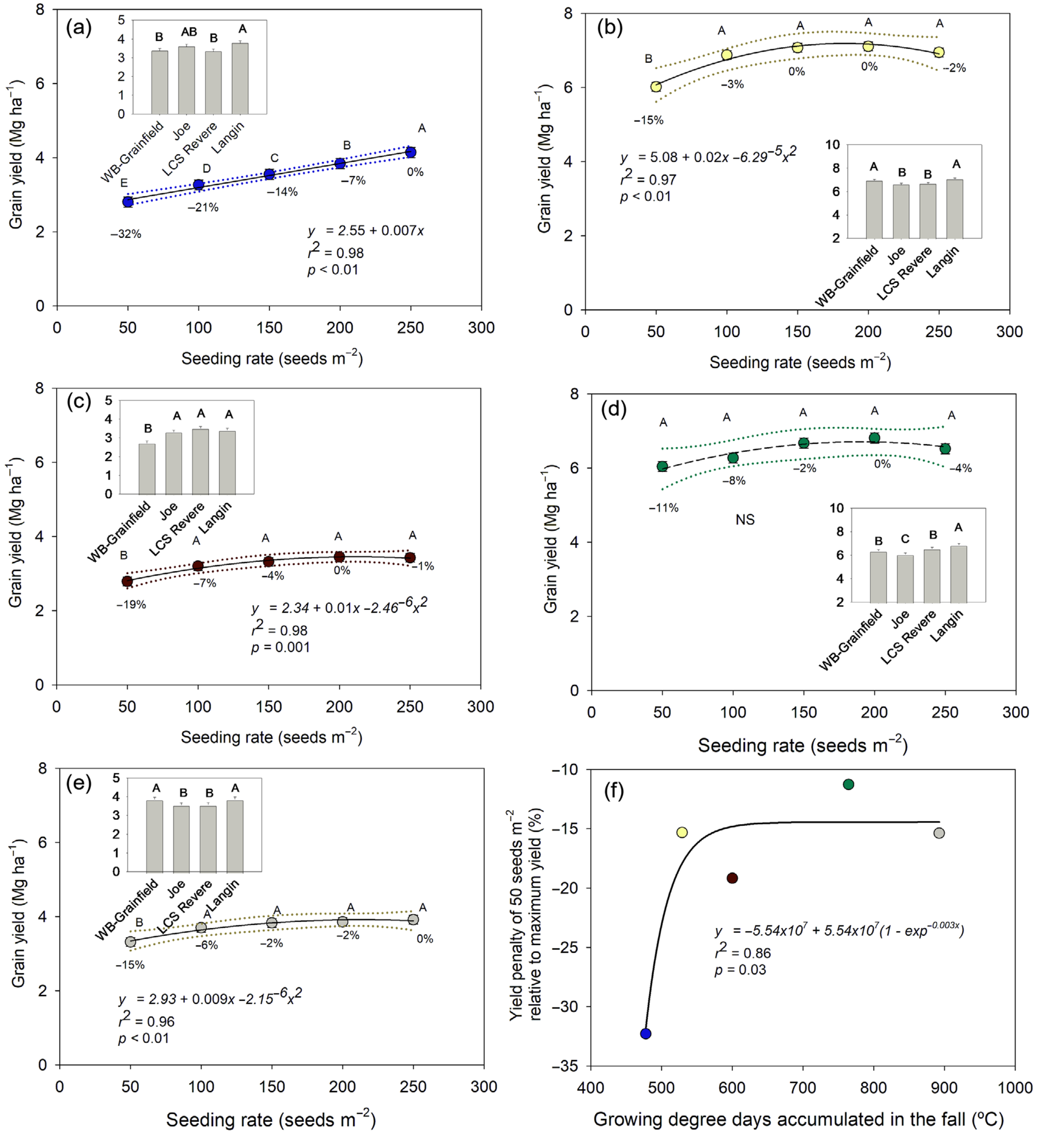

FIGURE 4 Winter wheat grain yield as impacted by the interaction of year and seeding rate, and by the interaction of year and variety in yield contest fields near Leoti, KS, during the (a) 2017–2018, (b) 2018–2019, (c) 2019–2020, (d) 2020–2021, and (e) 2021–2022 growing seasons. Inset bar charts (a–e) show year-dependent variety effect. (f) Yield penalty of the lowest seeding rate versus the maximum yield in each year as function of growing degree days accumulated in the fall. Solid lines (a–f) denote significant least square regressions, dashed lines (d) denote nonsignificant least square regression, and dotted lines (a–e) show 95% confidence interval. Density means followed by a common letter (main graph and inset, a–e) were not significantly different by the Tukey test at the 5% level of significance. Percentage shown under least square means show yield penalty relative to maximum.

(2010) suggested that wheat yields are usually limited by rainfall <500 mm, which concur with local research (Jaenisch et al., 2021; Lollato et al., 2017; Patrignani et al., 2014). High average maximum temperature adversely affected wheat yield, also aligning with previous research (Giordano et al., 2023; Sadras et al., 2022). Warmer temperatures hasten crop development (Cossani & Sadras, 2021), negatively impacting yield, which is function of the critical period's duration,

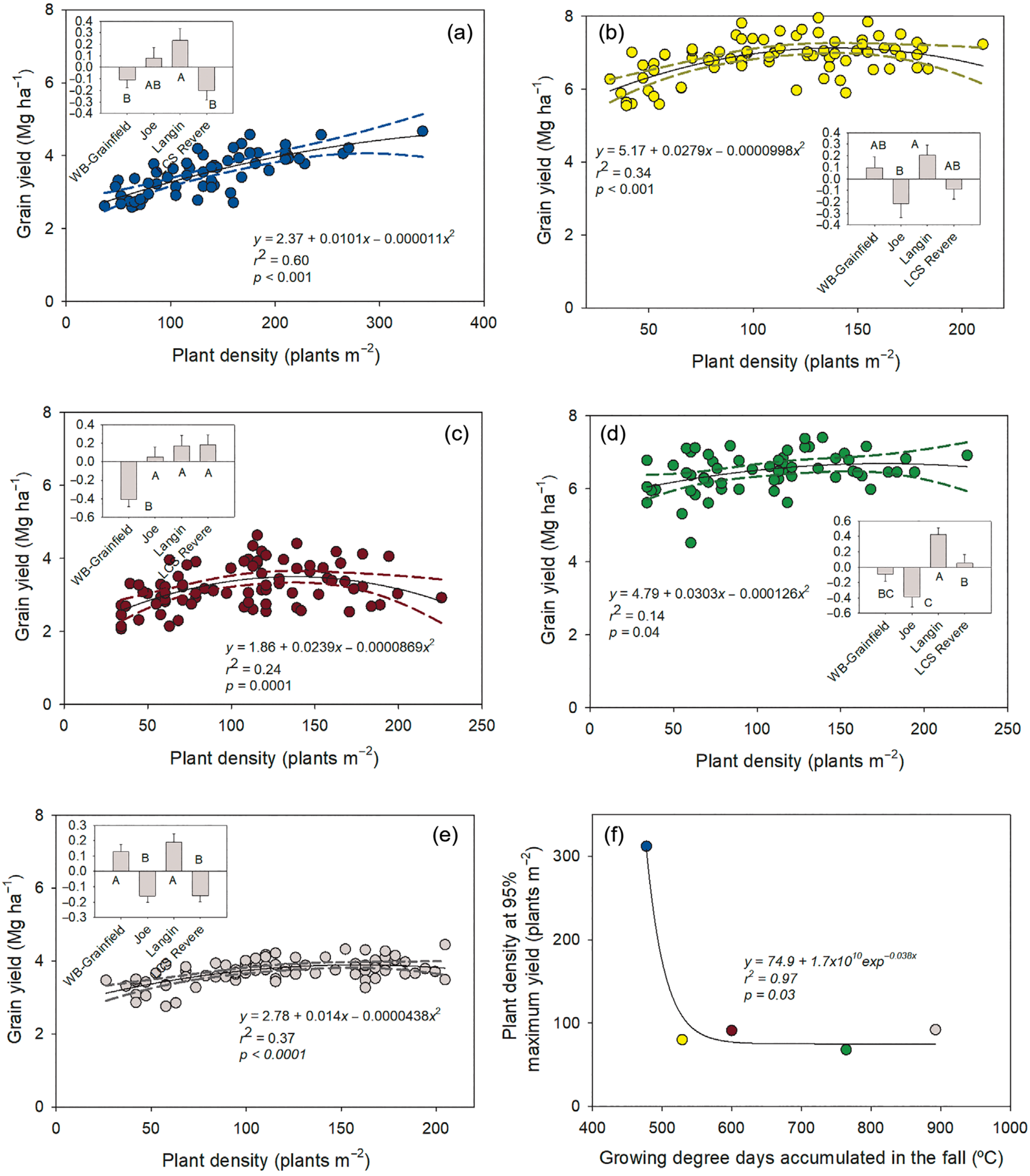

FIGURE 5 Winter wheat grain yield as impacted by plant density and variety (inset graphs) within year in yield contest fields near Leoti, KS, during the (a) 2017–2018, (b) 2018–2019, (c) 2019–2020, (d) 2020–2021, and (e) 2021–2022 growing seasons. Each symbol represents one individual datapoint collected from an experimental unit. Inset bar charts (a–e) show the mean and standard error of four replicates year-dependent variety effect. (f) Minimum plant density needed to reach 95% of the maximum yield as function of growing degree days accumulated from sowing to December 31 ("fall"). Solid lines (a–f) denote significant least square regressions and dotted lines (a–e) show 95% confidence interval. Least square means followed by a common letter (inset graphs, a–e) were not significantly different by the Tukey test at the 5% level of significance.

growth rate, and reproductive allocation (Andrade et al., 2005; Fischer, 1984; Slafer et al., 2021). Warmer temperatures during the critical period play a more important role in yield determination than growing season duration (Carrera et al., 2023; Slafer et al., 2023).

Despite low minimum temperatures measured during the winter (Figure 1), the studied seasons had smooth transitions from warmer fall temperatures to colder winter temperatures, which is typical in the region and not conducive to winterkill since they allow the crop to acclimate and increase freeze tolerance (Bridger et al., 1994). It would be important to consider spring survival in regions where winterkill is frequent, either due to larger temperature swings or prolonged colder winter temperatures. The higher potential for winterkill in northern regions could also justify higher seeding rates (Beres, Harker et al., 2010).

4.3 | Mechanisms explaining the relative insensitivity to density of winter wheat

During 2017–2018, grain yield responded to increases in seeding rate linearly and required more plants m^{-2} to reach 95% of the maximum (312 plants m^{-2}) (Figures 4 and 5). During this season, sowing occurred ∼16 days after the end of the optimum window (i.e., September 19–27; Jaenisch et al., 2021; Munaro et al., 2020). Optimal plant density is often greater with later sowings because development is accelerated more than growth (Dahlke et al., 1993; Lloveras et al., 2004; Spink et al., 2000; Staggenborg et al., 2003). Since tillering is function of the number of leaves per main stem (mostly determined by cumulative temperature prior to vernalization; Kirby et al., 1994), later sowing reduces tiller production (Dahlke et al., 1993) and fertile tillers per plant (Spink et al., 2000). The later sowing in 2017–2018 reduced fall temperature accumulation (i.e., 478˚C versus 529˚C–892˚C; Figure 4f), resulting in as many as 2.2 fewer fall tillers in 2017–2018 assuming a phyllochron of 75˚C and tiller initiation every ∼2.5 leaves (Soltani & Sinclair, 2012).

During the other four seasons, winter wheat grain yield was remarkably insensitive to density, only showing yield reductions at the 50 seeds m^{-2} rate or less than 68–92 plants m^{-2} (Figures 4 and 5). The comparison of these results with other literature is challenging, since most research on wheat response to plant density evaluated populations in higher ranges. Still, limited evidence for such comparisons exists. McLeod et al. (1996) compared two seeding rates (30 vs. 60 kg ha^{-1}) for winter wheat across 11 Canadian environments. In six environments, grain yields were significantly greater at 113 ± 29 plants m^{-2} than at ∼71 ± 20 plants m^{-2} (1.7 vs. 1.5 Mg ha^{-1}). In the other five environments, grain yield attained at 96 ± 24 plants m^{-2} did not differ from that attained at 155 ± 27 plants m^{-2} (0.9 vs. 1.0 Mg ha^{-1}). In high-yielding wheat systems of the United Kingdom (i.e., 8–10 Mg ha^{-1} maximum yields), Spink et al. (2000) and Whaley et al. (2000) evaluated seeding rates including densities lower than 100 seeds m^{-2} in winter wheat. Across nine environments, Spink et al. (2000) suggested that ∼62 plants m^{-2} maximized winter wheat yield sown late September; ∼93 plants m^{-2} maximized yield when sown mid-October; and ∼139 plants m^{-2} were needed when sown mid-November. Similarly, Whaley et al. (2000) suggested that minimum densities of ∼100–125 plants m^{-2} maximized yield of winter wheat sown at the optimum date. Darwinkel (1978) also suggested that 100 plants m^{-2} maximized winter wheat yield in high-yielding environments (8.3–8.9 Mg ha^{-1}) in the Netherlands. More recently, Hasan et al. (2022) evaluated the yield of two contrasting spring wheat cultivars to square grid planting arrangement when sown under 44 versus 350 seeds m^{-2} in high-yielding (11–12 Mg ha^{-1}) environments in southern Chile, concluding that one of the cultivars benefited from low seeding rates through increased harvest index and grain size.

The relative insensitivity of wheat yield response to seeding rate measured in four out of five seasons originates from its high plasticity—function of the potential for profuse tillering—which allows the crop to accommodate for extra space (Tokatlidis, 2014, 2017). Previous research has reported the potential for over 130 productive tillers per plant under extremely low densities (20 plants m^{-2}) at field conditions (Rodríguez-Casas et al., 2005). Since tillering potential and stability are variety-specific (e.g., Destro et al., 2001; Elhani et al., 2007; Parveen et al., 2010; Rodríguez-Casas et al., 2005) and the interaction of variety with seeding rate seems to occur in very low densities (20–160 seeds m^{-2}; Hasan et al., 2022; Rodríguez-Casas et al., 2005), the success of lower seeding rates could depend on a better understanding of wheat variety tillering dynamics under low densities (Tokatlidis et al., 2006).

Whaley et al. (2000) suggested that winter wheat at 125 plants m^{-2} maintained yields similar to those at higher populations due to many complementary mechanisms. Low-density crops increased the duration of tiller production, green area per shoot, and shoot survival, ultimately increasing canopy nitrogen status and green area per plant. The latter led to better radiation distribution through the canopy which increased radiation capture per plant and radiation use efficiency. Greater radiation use efficiency increased relative growth rate that allowed for maintenance of crop dry matter production, which, coupled with better partitioning of assimilates to the head, increased grains head^{-1} despite reducing fertile shoots m^{-2}. Since grain number is a coarse regulator of wheat yield (Slafer et al., 2014) and it is equally dependent on heads m^{-2} and kernels head^{-1} (Jaenisch et al., 2022; Slafer et al., 2022), this balance led to maintenance of yields at populations of ∼125 plants m^{-2}. Higher plant densities, increasing fertile shoots m^{-2} but reducing kernels head^{-1}, have been widely reported for cereals (Conry, 1998; Conry & Hegarty, 1992; Darwinkel et al., 1977; Spink et al., 2000). Radiation interception to avoid yield losses due to suboptimal density must exceed 95% during the critical period (Fischer et al., 2019). However, radiation interception was only measured in the above winter wheat study by Whaley et al. (2000) who showed that intercepted radiation only reached 77% by anthesis at densities lower than 125 plants m^{-2}, resulting in corresponding yield reductions (~20%).

In wheat crops sown at 350 plants m^{-2}, 28%–32% of the yield originated from tillers (Elhani et al., 2007), with this contribution reducing 2%–12% under higher densities (Destro et al., 2001). The greater reliance of wheat yield on tillers under low densities has four major consequences: (i) Because tillers are formed progressively afterward main shoots, lower density wheat usually reduces uniformity in heading days (since different tillers head in different days) (Beres et al., 2016; Destro et al., 2001; Donald, 1968; Elhani et al., 2007) and has later heading date (Fischer et al., 2019). Less uniform heading date spreads the risk against adverse weather events such as frost (Fuller et al., 2007), heat (Ferris et al., 1998), and combined stresses (Zhao et al., 2022), and later heading can improve yield through frost escape and in seasons with cool and moist grain fill conditions. However, this also suggests that higher density crops (with shorter maturity and more uniform heading) could have greater yield under hot and dry grain fill (Flohr et al., 2017). (ii) Later heading dates increase pre-anthesis growth which can be beneficial (Fischer et al., 2019). (iii) Finally, low densities decrease plant height and potentially lodging (Hasan et al., 2022; Rodríguez-Casas et al., 2005).

4.4 | Practical implications for wheat seeding rate recommendations in environments with ample resource availability

Plant density was closer to the target at lower seeding rates as compared to higher seeding rates (Figure 3), which is usually observed in seeding rate studies (Bastos et al., 2020; Hanson & Lukach, 1992; Mehring et al., 2020; Spink et al., 2000; Wiersma, 2002) and suggested to be function of greater intraspecific competition (Masle, 1985; Puckridge & Donald, 1967) and worsened by poor seedbed (Hanson & Lukach, 1992) or adverse weather conditions (Mehring et al., 2020). We provided evidence that the larger difference in target versus attained density was at least in part function of precipitation in the 30-day period around sowing, where greater precipitation amounts resulted in greater agreement between target and actual stands. The conditions experienced in 2017–2018 (i.e., ~120 mm rainfall delaying sowing), however, are unusual in the region. Weather data from 1955 to 2010 in western Kansas suggested that the monthly precipitation around winter wheat sowing averages 24–49 mm (Holman et al., 2011). This is an important practical consideration for growers in the region since actual stands may more often be further from target.

Our results offered no evidence for variety × seeding rate interactions for yield, suggesting that in practice seeding rate recommendations may be independent of variety. While some literature supports our findings (e.g., Guitard et al., 1961; Spink et al., 2000; Teich & Smid, 1993), including an earlier study in the same region but under standard management intensity (Holman et al., 2021), this disagrees with many previous studies suggesting variety-specific seeding rates (Anderson & Barclay, 1991; Baker, 1982; Bastos et al., 2020; Briggs & Ayten-fisu, 1979; Faris & De Pauw, 1981; Hasan et al., 2022; Mehring et al., 2020; Pendleton & Dungan, 1960; Rodríguez-Casas et al., 2005; Wiersma, 2002). Some of these studies suggested that the significant variety × seeding rate interaction was mostly evident at seeding rates below the maximum yield (Hasan et al., 2022; Rodríguez-Casas et al., 2005). Since our findings were constrained to the four varieties and five seeding rates evaluated across 5 years, relatively low statistical power and/or low diversity in phenotypes could partially explain these differences. We also note that while we focused on yield, there may be important differences in varieties' competitive ability against weeds which may impact variety × seeding rate interactions in low plant densities (Beres, Clayton et al., 2010; Beres, Harker et al., 2010).

Deriving direct practical implications from our results is challenged by the limited inference space of this study, including geographical, since it is restricted to one location; temporal, since it is restricted to five growing seasons; and to some extent, regarding the treatments evaluated, since the maximum plant density evaluated was 341 plants m^{-2} which limits our ability to extrapolate potential yield responses beyond this level. While the quadratic model identified maximum yields at plant densities less than 160 plants m^{-2} in four out of five seasons, evaluating denser populations would still be particularly important in seasons such as 2017–2018 where yield had a linear response to seed rate and/or density. These findings also reinforce the need for higher seeding rates when sowing is delayed, highlighting the need for further research on the interactions of seeding rate with sowing date in reference to the onset of the winter as well as seasonal forecasts. From a practical perspective, reducing the recommended seeding rate would require producers to pay extreme attention to many practical aspects of stand establishment and canopy management to avoid yield losses (e.g., ensuring excellent seed viability and adjusting seeding rates based on seed quality). Additionally, weed control can be challenging under low seeding rates since (i) weeds become more competitive under lower seeding rates (Kristensen et al., 2008), and (ii) widely differing tiller initiation dates can pose challenges from a herbicide management perspective where more uniformity is advantageous. These and other practical challenges from low seeding rates were thoroughly reviewed by Fischer et al. (2019). While we dove into the mechanisms and potential advantages of low seeding rates in winter wheat, an alternative view to reducing rates is to consider that the highest seeding rate evaluated was the only treatment that provided consistently high yields, that is, in practice, increasing seeding rates could be a fairly simple and cost-effective method to protect yield. This viewpoint is sustained by some preliminary evidence from our own data of a greater risk of not attaining maximum yields at low rates (1 out of 5 years). Therefore, there is room for further research to explore the risks of low seeding rates returning maximum yields in a more quantitative approach with a greater number of experiments.

AUTHOR CONTRIBUTIONS

Romulo P. Lollato: Conceptualization; data curation; formal analysis; funding acquisition; methodology; project administration; visualization; writing—original draft. **Luiz O. Pradella**: Data curation; investigation; methodology. **Nicolas Giordano**: Data curation; investigation; methodology; writing—review and editing. **Luke P. Ryan**: Data curation; investigation; methodology. **Jorge R. Soler**: Data curation; formal analysis; investigation; methodology. **Luana M. Simão**: Data curation; investigation; methodology. **Brent R. Jaenisch**: Conceptualization; data curation; investigation; methodology. **Rick Horton**: Conceptualization; methodology; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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