On-farm surveys and field experiments identify genotype and management practices to increase dryland winter wheat grain yield

by

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B.S., University of Nebraska-Lincoln, 2015 M.S., Kansas State University, 2017

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Agronomy College of Agriculture

KANSAS STATE UNIVERSITY Manhattan, Kansas

Abstract

Wheat yields are variable in dryland environments due to the erratic weather regime and the consequent conservative management practices adopted by producers, leading to large yield gaps. Our objectives were to disentangle management \times genotype interactions and identify management practices associated with increased wheat yield in dryland Kansas environments. Producer-reported yield and management data were collected from 656 commercial fields during the 2016-18 harvest seasons, including 43 management practices, five weather, and two soil variables. Grain yield ranged from 0.3 to 7.1 Mg ha⁻¹ with yield gap averaging 44%. Foliar fungicide, nitrogen (N) rate, and method were the most common management strategies to affect yield. Two field experiments were conducted during 2018, 2019, and 2020 in several Kansas environments. In experiment one, we evaluated the grain yield response of four commercial wheat varieties to six different management intensities in six environments. Across environments and genotypes, managing for the yield potential increased yield by 1.4 Mg ha⁻¹ (30%) as compared to the farmer practice. Aboveground biomass and kernel number related more strongly to yield than harvest index and kernel weight. Experiment two evaluated the colimitation of nitrogen (N) and sulfur (S) to wheat yield and its effects on N and S use efficiencies (and its components of uptake and utilization) in eight environments. Across environments, wheat grain yield increased with increases in N rate; however, S application only increased grain yield at two environments. Minimum N and S uptake to maximize yield at 5.7 Mg ha⁻¹ was 120 and 7 kg ha⁻¹. Nitrogen limitation impacted S use efficiency and vice versa, and the limitation of both nutrients increased the wheat yield gap. This research identified several genotype \times management practices associated with wheat yield in commercial and experimental settings, and reinforced the need for integrated management practices according to site-specific limitations to improve wheat yields.

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2021

Approved by:

Major Professor Dr. Romulo Lollato

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Abstract

Wheat yields are variable in dryland environments due to the erratic weather regime and the consequent conservative management practices adopted by producers, leading to large yield gaps. Our objectives were to disentangle management \times genotype interactions and identify management practices associated with increased wheat yield in dryland Kansas environments. Producer-reported yield and management data were collected from 656 commercial fields during the 2016-18 harvest seasons, including 43 management practices, five weather, and two soil variables. Grain yield ranged from 0.3 to 7.1 Mg ha⁻¹ with yield gap averaging 44%. Foliar fungicide, nitrogen (N) rate, and method were the most common management strategies to affect yield. Two field experiments were conducted during 2018, 2019, and 2020 in several Kansas environments. In experiment one, we evaluated the grain yield response of four commercial wheat varieties to six different management intensities in six environments. Across environments and genotypes, managing for the yield potential increased yield by 1.4 Mg ha⁻¹ (30%) as compared to the farmer practice. Aboveground biomass and kernel number related more strongly to yield than harvest index and kernel weight. Experiment two evaluated the colimitation of nitrogen (N) and sulfur (S) to wheat yield and its effects on N and S use efficiencies (and its components of uptake and utilization) in eight environments. Across environments, wheat grain yield increased with increases in N rate; however, S application only increased grain yield at two environments. Minimum N and S uptake to maximize yield at 5.7 Mg ha⁻¹ was 120 and 7 kg ha⁻¹. Nitrogen limitation impacted S use efficiency and vice versa, and the limitation of both nutrients increased the wheat yield gap. This research identified several genotype \times management practices associated with wheat yield in commercial and experimental settings, and reinforced the need for integrated management practices according to site-specific limitations to improve wheat yields.

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Acknowledgements

First, I would like to thank my major advisor, Dr. Romulo Lollato for giving me the opportunity to be a PhD student in the winter wheat production program. Dr. Lollato helped me become a better scientist and researcher over the years in his program. The knowledge I received him will be with me the rest of my life. In addition, I learned that mistakes will happen and it is important to grow from those mistakes. Also, for pushing me to become a better agronomist and better person. Second, I would like to thank my committee members, Drs. Chris Vahl, Krishna Jagadish, and Dorivar RuizDiaz, for being on my graduate committee and answering all my agronomic and dissertation questions. Thirdly, I would also like to thank fellow graduate students, Amanda de Oliveira Silva, Kavan Mark, the research experiment field managers, Dustin Ridder, Andrew Esser, and Gary Cramer, and their crew for all of their time and hard work.

Finally, I would like to thank my family and friends for all of their support over the years. First, my parents, Marvin and Candice, for all of the support during my college degrees, which totaled nine years. In addition, the importance in having faith and believing that I could accomplish anything I put my mind too. Also, my brother and sister, Aaron and Justine, for the phone calls to discuss how life was going in Kansas and their words of encouargement. And last but not least, Jaenisch Farm's, for teaching me the definition of hard work and the ability to preserve when things don't go my way. Likewise, a very special thank you to my grandparents, Harold and Marie Jaenisch and Robert and Gloria Sulflow, who taught me that to achieve things in life you have to work extremely hard and make sacrifices in life.

Dedication

"I can do all things through Christ which strengthens me" - Philippians 4:13.

Chapter 1 - General introduction

Wheat (*Triticum aestivum* L.) is one of the most important crops in the world behind rice (*Oryza sativa* L.) and maize (*Zea mays* L.) (FAO, 2014). Within the U.S., the central Great Plains region (Kansas, Oklahoma, Colorado, Nebraska, and Texas) is the largest producing region of winter wheat. In Kansas, winter wheat is sown on more than 2.7 million hectares which produced 9.9 million metric tons in 2020 (USDA-NASS, 2020). However, wheat yields have been stagnant in this region and range between 2.2 and 3.4 Mg ha⁻¹ (USDA-NASS, 2017) which is well below the rainfed yield potential of 5.0-6.8 Mg ha⁻¹ (Patrignani et al., 2014; Lollato et al., 2017; Jaenisch et al., 2019). While a number of independent field experiments have been conducted to improve the current knowledge about wheat yield response to management intensification, no attempts have been made to do so with on-farm surveys. These surveys offer an opportunity to test the association of wheat yield with a number of independent management practices, as well as to quantify the magnitude and potential causes of yield gaps; and are currently missing in this important wheat-growing region of the world.

Winter wheat grain yield is determined by its yield components (i.e., biomass, harvest index, heads m⁻², kernels head⁻¹, kernels m⁻², and kernel weight) and their association has been researched for decades across a wide range of environments (Evans et al., 1980; Austin et al., 1989; Calderini et al., 1999; Acreche et al., 2008; Slafer et al., 2014). Wheat yields are often limited by the sink rather than the source with increases in wheat yield coming from the contribution of kernels m⁻² rather than kernel weight (Slafer and Savin, 1994; Borrás et al., 2004; Slafer et al., 2014; and citations therein). Thus, management practices that affect kernels m⁻² as compared to kernel weight would result in larger increases in grain yield (Cruppe et al., 2021). Despite the current knowledge about the importance of yield components to maximize wheat yields, research is lacking to understand the effects of increasing management intensity on crop development that determine wheat yield components.

Among important management practices adopted during the season, the application of nitrogen (N) and sulfur (S) essential nutrients can increase wheat grain yields (Girma et al., 2005; Lollato et al., 2021) and quality (Wilson et al., 2020). Nitrogen management has been studied extensively over the decades (Goos et al., 1982; Moll et al., 1982; Sinclair and Rufty, 2012), but few experiments have evaluated N and S interaction on N and S use efficiencies, especially through the lenses of its components of uptake and utilization efficiency (de Oliveira Silva et al., 2020). Additionally, no attempts have been made to identify the contribution of N and S colimitation to minimizing wheat yield gaps. Sulfur fertilization has shown to increase NUE in wheat through increases in N recovery efficiency (Salvagiotti et al., 2009). Similarly, to NUE, few experiments have evaluated S rates on SUE and its components of uptake and utilization efficiency in Kansas.

The main objectives of these research projects were to fill the knowledge gaps above through 1) performing an on-farm survey to determine the magnitude of the yield gap in commercial wheat fields in Kansas, as well as management practices associated with increased wheat yields; 2) conducting a field experiment to determine the contribution of wheat yield components and their effects on wheat yield across a range of management intensities and associated yield gaps; and 3) conducting another field experiment to determine the effects of different N and S rates on the grain yield, N and S use efficiency, and yield gaps of different winter wheat varieties through a colimitation theory.

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Chapter 2 - On-farm data-rich analysis explains yield and quantifies yield gaps of winter wheat in the U.S. central Great Plains

Highlights

- Wheat yield (Ya) and management data were surveyed from 656 wheat fields.
- Water-limited yield potential (Yw) was simulated for each field using crop models.
- Ya ranged from 0.34 to 7.1 Mg ha⁻¹ and yield gap (YG) averaged 44%.
- Clustering the data by crop zone accounted for regional-specific crop management
- Data-rich analysis highlighted many management × weather interactions impacting Ya

Abstract

With an annual production of ~60 Mt, the U.S. accounts for about 8% of the global wheat (*Triticum aestivum* L.) production. Still, quantification of the yield gaps (YG) and major management factors to reduce it are scarce. We used Kansas, the largest wheat producing state in the U.S. located in the central Great Plains, for an initial assessment of on-farm yield and YG. We collected field-level management (37 variables), weather (8 variables), soil (two variables) and yield data from 656 commercial wheat fields over three harvest years (2016-2018) to (i) quantify management adoption levels, Ya, and YG, and (ii) identify interactions among management practices and weather variables using a data-rich approach. We also used our data as a case-study to detect whether differences in crop management among regions justified data clustering by crop zones. Water-limited yield potential (Yw) was simulated for each field-year using actual soil and weather data and the SSM-Wheat model. Fields were grouped in three climate zones based on their long-term climatology and important differences in cropping

systems between zones. Grain yield averaged 3.8 Mg ha⁻¹ and ranged from 0.3 to 7.1 Mg ha⁻¹ across all regions and years. The YG averaged 44%, with seasons with high Yw resulting in greater YG. Management practices most often associated with grain yield were management of nitrogen (N), phosphorus (P), and sulphur (S) fertilizer, as well as foliar fungicide and its interaction with variety reaction to major diseases, although these depended on in-season weather. Our analyses highlighted many other genotype × management × environment interactions explaining winter wheat Ya, such as regional-specific cultivar maturity and the dependency of sowing date (and its relation to seeding rate) on cropping system.

Introduction

Water-limited yield potential (Yw) is the yield of a crop grown with no limitations other than water (Neumann et al., 2010). In rainfed cropping systems, Yw is an important benchmark as the difference between the Yw and the average yield (Ya) defines the yield gap (YG), which can identify environments where grain yield can increase economically (Lobell et al., 2009). Many methods have been proposed to quantify Yw for YG analysis, with crop simulation models being the most robust (Grassini et al., 2011b; Van Ittersum et al., 2013). In a context in which food production must increase to feed a growing global population (Tilman et al., 2001; Foley et al., 2005), reducing the YG of staple crops through management (e.g., Herrera et al., 2020) will be essential for food security (Cassman, 1999), especially in regions with large YG, such as winter wheat (*Triticum aestivum* L.) in the U.S. Great Plains (Patrignani et al., 2014).

The U.S. central Great Plains (Kansas, Oklahoma, Colorado, Nebraska, and Texas) is the largest contiguous winter wheat producing region in the world (Fischer et al., 2014). Winter wheat Ya ranges between 2.2 and 3.4 Mg ha⁻¹ (USDA-NASS, 2017a) and evidence suggests that it is well below the Yw of ~5.0-5.5 Mg ha⁻¹ estimated through modeling (Patrignani et al., 2014;

Lollato et al., 2017) or well conducted field experiments (de Oliveira Silva et al., 2020; Jaenisch et al., 2019; Lollato and Edwards, 2015). A comparison between YG estimates using government-reported yield data (YG of ~50%, Lollato et al., 2017) versus YG in highly managed fields (YG of ~15%; Lollato et al., 2019b) suggested that management practices are currently the main limitation to Ya. A range of practices has the potential to increase Ya in this region, from foliar fungicides (Jaenisch et al., 2019), plant population (Bastos et al., 2020), agricultural lime and variety selection (Lollato et al., 2013; 2019b), increased N rates (de Oliveira Silva et al., 2020b), seed treatment (Pinto et al., 2019), etc. However, these experiments evaluated few practices at a time, and a more comprehensive analysis of yield-limiting factors is warranted.

On-farm surveys provide a unique opportunity to evaluate a number of sensitive practices potentially associated with crop Ya (Rattalino Edreira et al., 2017; Mourtzinis et al., 2018; Lollato et al., 2019b). While some previous work evaluated the explanatory power of a relatively large number of management factors to Ya (e.g., Grassini et al., 2015; Mourtinzis et al., 2018b), a review of studies investigating YG in different crops suggested that the average number of variables investigated was three, ranging from zero to 29 (Beza et al., 2017). Among the studies considered, fertilization was the most often evaluated factor (45% of the studies), with fewer studies evaluating other managerial practices such as planting practices, crop protection, weeding, etc. Additionally, while most studies focused on the quantity of input applied; when considered, timing of input application explained the YG more often than quantity (Beza et al., 2017). Here we hypothesize that a data-rich approach, evaluating a large number of management factors, can provide further insights into potential avenues to increase Ya.

A challenge when using farmer-reported yield data spanning large and/or heterogenic geographies are management \times environment interactions in which the optimal agronomic

practices preclude the combination of fields (Rattalino Edreira et al., 2017; Mourtzinis et al., 2018). While smaller and more homogenous geographies might not require data stratification (e.g., Grassini et al., 2011a; Silva et al., 2017), studies spanning large and variable regions have clustered fields into smaller homogenous regions based on climate and soil characteristics (Lobell et al., 2005; Van Wart et al., 2013; Mourtzinis et al., 2018; Rattalino Edreira et al., 2018; Munaro et al., 2020). This approach is static, thus it has succeeded for crops grown in regions with small year-to-year variation such as soybeans (*Glycine max* L. Merr.) in North Central U.S. where it accounted for up to 96% of the variability in Ya (Rattalino Edreira et al., 2017). However, for crops grown in less predictable environments such as winter wheat in the U.S. Great Plains (Couedel et al., 2021), clustering based on long-term annual weather only accounted for 46% of the Ya variability, with up to 37% assigned to year (Munaro et al., 2020).

While explaining a lower proportion of Ya variability, this regional stratification might still be warranted as it can capture important differences in crop management among regions. For example, the range in sowing dates among 798 winter wheat yield trials conducted in three states in the U.S. central Great Plains varied from an early and short sowing period (i.e., from day of year [DOY] 245 to 286, optimum: 266) in cooler, semi-arid, high altitude sub-regions; to a later and wider sowing period (from DOY 252 to 327, optimum: 296) in warmer, subhumid, low altitude regions (Munaro et al., 2020). Other region-specific management factors included crop sequence (e.g., fallow in semi-arid regions *versus* more intense rotations in subhumid regions), genotypes, and row spacing (Munaro et al., 2020). Thus, failure to cluster the data into regions with distinct levels of management adoption could confound the interpretation of the outcome.

As an alternative to the static regional clustering, Di Mauro et al. (2018) combined fieldlevel management, soil, and weather data to identify causes of YG for soybeans in central Argentina in a data-rich analysis. While the data collected spanned four Argentinean provinces, the study region was relatively homogenous in terms of weather, with the majority of the fields classified in about two climate zones (Van Wart et al., 2013) (Di Mauro, personal communication). Meanwhile, the state of Kansas has 13 different climate zones with a much greater environmental variability (Van Wart et al., 2013). Thus, we hypothesize that the combination of the two aforementioned methods, namely regional clustering (to address region-specific management adoption) and field-level data-rich analysis (to address the static nature of regional clustering), together with YG estimates using a mechanistic crop simulation model, could enable for a realistic quantification of the magnitude and the possible determinants of YG.

Given the importance of the U.S. central Great Plains to the global wheat production and its large YG due to sub-optimal management, coupled with the need to synthesize crop yield, management, and weather data from different areas (Lobell and Asner, 2003), we conducted a survey of management practices adopted in commercial winter wheat fields in Kansas during three growing seasons. Our specific objectives were to (i) quantify field-specific level of adoption of management practices, Ya and YG; (ii) identify the interactions of environmental and management practices associated with increased Ya; and (iii) test whether a large number of explanatory variables (management, weather, soils, and simulated outputs) would provide more insights into the determinants of Ya than the usually evaluated variables (Beza et al., 2017). Additionally, we used data representing widely varying environmental conditions to demonstrate the need for subdividing a wider geography into smaller, more homogenous regions to account for differences in management adoption between regions.

Materials and Methods

Study region

Kansas is the largest winter wheat producing state in the U.S., with more than 3 Mha sown annually for a production of ~9 Mt (USDA-NASS, 2017a). Winter wheat sowing occurs from mid-September until mid-November, and harvest occurs from early June to early July, depending on location and crop sequence (Munaro et al., 2020). Kansas experiences a wide range of environmental conditions: Annual rainfall is ~450 mm in the west and ~1100 mm in the east (Lollato et al., 2020a), resulting in winter wheat growing season precipitation ranging from ~200-650 mm (Lollato et al., 2017). Average growing season temperature ranges from 7 to 12°C from west to east owing to elevation, which ranges from ~200 to 1,200 m (Lollato et al., 2017).

Database description and data quality assessment

Field-specific geo-coordinates, agronomic management, and grain yield were collected during three consecutive seasons (i.e., 2016-2018) in central and western Kansas (Fig. 1), representing ~92% of the state's wheat area. We focused exclusively on non-irrigated fields, as they represent 96% of the wheat in the region (USDA-NASS, 2019). Producers were identified by county extension agents or in extension meetings, and completed the survey by telephone, e-mail, mail, or face-to-face.

The survey consisted of questions about different management practices, input usage, and grain yield adopted in commercial winter wheat fields (i.e., field-level data; Table 1). No variables were physically measured (e.g., soil fertility status), and grain yield verbally reported by producers derived either from yield maps or from elevator tickets combined with field size. Prior to conducting the survey, the questionnaire was approved by the Committee for Research Involving Human Subjects (Kansas State University Application number 8945) and, at each

survey, producers signed a data sharing agreement permitting the use of the data and the sole presentation of aggregated data for privacy protection. Data was homologized to account for the variation in producer responses for a specific management practice (i.e., producers reported seeding rate in seeds ha⁻¹ or in kg ha⁻¹; thus, data was transformed into kg ha⁻¹ according to the majority of the responses). We collected the commercial name of the variety and used this information to retrieve year-specific variety characteristics from extension reports (DeWolf et al., 2016, 2017, 2018), including resistance to stripe rust [*Puccinia striiformis f.sp. tritici*] and leaf rust [*Puccinia triticina*], wheat streak mosaic virus, maturity, height, straw strength, and drought tolerance. All varietal ratings used a 1-to-9 scale, where one is highly resistant, early maturity, and short; and nine is highly susceptible, late maturity, and tall. The resulting database had 656 field-years (Fig. 1). A total of 37 management-related variables were either collected or calculated and used to explain wheat grain yield.

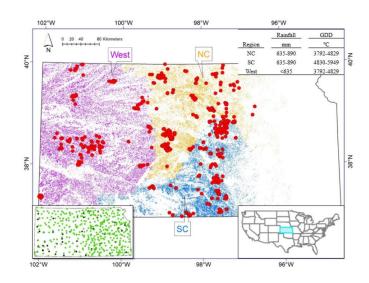


Figure 2-1.Map of the surveyed region showing the three surveyed regions in Kansas (North Central, NC; South Central, SC; and West) as different colors. The red dots represent commercial wheat fields that were surveyed during the 2016, 2017, and 2018 harvest years. Upper right inset table shows the range of cumulative rainfall and growing degree days in each region. Lower right inset panel shows the location of Kansas within the contiguous United States. Lower left inset panel shows the weather stations used to collect daily rainfall and maximum and minimum temperature (green dots) and weather stations used to collect solar radiation and reference evapotranspiration (black dots).

Variable	Unit (or classes)
Geographic coordinate	Latitute/Longitude
Previous crop	Crop species name or fallow
Sowing date	Day of year
Pre-plant control of volunteer wheat	Yes/No
Variety (or blend) name	Unitless, used to retrieve different seven variety traits
Variety traits (seven, see methods)	1-9
Seeding rate	Kg ha ⁻¹
Row spacing	cm
Fungicide seed treatment	Yes/No
Insecticide seed treatment	Yes/No
Cattle grazing	Yes/No
Tillage	Coventional or no-till
In-furrow phosphorus	Yes/No
Broadcast or banded phosphours	Yes/No
Phosphours rate	Kg ha ⁻¹
Manure	Yes/No
Lime	Yes/No
1 st Nitrogen Source	Urea, urea ammonium nitrate, or anhydrous ammonoia
1 st Nitrogen Rate	Kg ha ⁻¹
1 st Nitrogen Application Method	Streamer nozzle, broadcast, or knife
1 st Nitrogen Timing	Pre-plant, Zadoks' 20 or 31
2 nd Nitrogen Source	Urea, urea ammonium nitrate, or anhydrous ammonoia
2 nd Nitrogen Rate	Kg ha ⁻¹
2 nd Nitrogen Application Method	Streamer nozzle, broadcast, or knife
2 nd Nitrogen Timing	Pre-plant, Zadoks' 20 or 31
Total N rate	Kg ha ⁻¹
Sulfur	Yes/No
Chloride	Yes/No
Zinc	Yes/No
Zadoks' 25-31 Fungicide	Yes/No
Zadoks' 39-55 Fungicide	Yes/No
Harvest date	Day of Year
Grain yield	Mg ha ⁻¹

Table 2-1. List of variables collected from comercial wheat fields in Kansas during three crop seasons (2016-2018).

To account for the geographical influence on wheat Yw (Lollato et al., 2017) and for important region-specific management factors (Munaro et al., 2020), we clustered fields into three surveyed zones based on long-term annual cumulative growing degree days, aridity index, and temperature seasonality. While we followed the approach by Van Wart et al. (2013), we used coarser weather ranges to delineate crop zones in this study because 1) we were interested in capturing major regional differences in crop management (Munaro et al., 2020), and 2) we used field-specific weather data in the analyses (see next sections). These zones will be referred to as crop zones. The weather classification we adopted resulted in three crop zones: north-central (635-890 mm annual precipitation and 3,792-4,829 °C annual thermal units; n = 220), south-central (635-890 mm, 4,830-5,949 °C; n = 285), and West (<635 mm, 3792-4829 °C; n = 151). A power analysis suggested that approximately 150 fields were required within crop zone to detect significant effects at a power of 0.8. We note in passing that despite clustering fields by crop zones, the high year-to-year variability in growing conditions still led to a significant year effect on grain yield (~86% of the variability in the yield data was accounted for by year), but a significant zone × year interaction supported our zoning scheme.

Weather data retrieval and processing, simulated Yw, and YG calculation

Winter wheat Yw was simulated for each field-year using the Simple Simulation Model (SSM) – Wheat (Soltani and Sinclair, 2012), which is a process-based model that simulates wheat growth and development on a daily basis. We used previously calibrated parameters for winter wheat grown under non-limiting conditions in the U.S. Great Plains (Lollato and Edwards, 2015), which resulted in accurate simulation of crop phenology and Yw across a wide range of environments (Lollato et al., 2017, 2019b; Sciarresi et al., 2019). Harvest maturity dates were simulated with a ME of -2.8 days (-1.1%) and a RMSE of 8.1 days (3.2%) when compared to actual harvest dates in the current dataset ($R^2 = 0.7$, P < 0.001).

The SSM model requires daily weather data including precipitation, maximum (Tmax) and minimum temperatures (Tmin), and solar radiation, as well as relevant soil characteristics such as soil depth and available water holding capacity. The weather data were retrieved from in-

situ observations collected from federal, regional, and state weather and climate networks. For daily Tmax, Tmin, and precipitation data, we selected weather stations from the National Weather Service Cooperative Observer Program and Automated Surface Observing Systems in Kansas, which include 455 stations (inset in Fig. 1). The data quality control was implemented by Applied Climate Information System for daily maximum and minimum temperature as well as precipitation (Leeper et al., 2015). The 62 Kansas Mesonet stations (Patrignani et al., 2020) were used to collect daily solar radiation and reference evapotranspiration (ETo). All daily station's data were supported by using two standards: (i) outliers in daily maximum and minimum temperature were identified as more than 3.5 standard deviations away from climatological mean temperature for the day (Frich et al., 2002); (ii) daily homogeneity of temperature and precipitation observations were visually assessed by the monthly average time series because our study period is relatively short. Site weather data were then interpolated by using the natural neighbor interpolation method (Amidror, 2002) on a daily step.

The available water holding capacity (AWHC) and textural class of each field were collected from the Web Soil Survey (USDA-NRCS, 2015) for the 0-20 cm and 20-200 cm depths by: (i) creating an area of interest using the field boundaries, (ii) quantifying the percentage of each different soil class within each field, and (iii) calculating the weighted-average AWHC across the different soil types for each depth. A depth of 200 cm is sufficient to represent wheat rooting depth in the region (Awad et al., 2018). Soil curve number, albedo, bulk density, and drainage factor were retrieved from Soltani and Sinclair (2012) and Ratliff et al. (1983).

Simulations used actual sowing date for each field-year to account for sowing delays due to a previous summer crop, and optimal plant population (Paulsen et al., 1997). When wheat was sown following a long (11 to 14-m) or short (3-m) fallow period, the SSM-Model was initiated

in the beginning of the fallow period at 50% available water and the soil-water balance component of the model estimated the available water at wheat sowing (Lollato et al., 2016). When wheat was sown immediately after a preceding summer crop, we simulated the soil water balance under the preceding summer crop using either the soybean or the maize (*Zea mays* L.) modules of the SSM model with cultivars of appropriate maturity for the region. The available water in the soil profile at harvest of the preceding summer crop was used either as (i) the initial water at sowing for wheat following soybeans, or (ii) the initial water content at a short (15- to 30-d) fallow period prior for wheat sowing following maize. The YG was calculated for each field-year by subtracting the Ya from the simulated Yw.

Influence of management × environment interactions on wheat grain yield

On-farm surveys lack replication and experimental design, precluding the establishment of causal relationships. Thus, the association of yield and management practices is usually quantified using quantile regression (Grassini et al., 2011a, 2015; Rattalino Edreira et al., 2017) or multivariate methods such as principal component analysis (Villamil et al., 2012) or conditional inference trees (CIT)(Ernst et al., 2016; Lobell et al., 2005; Mourtzinis et al., 2018b). In our study, the interactive effects of field-level growing season weather variables, soil available water holding capacity and initial soil water at sowing, and management practices on Ya were assessed using CIT via the 'partykit' package in R software (Hothorn and Zeileis, 2015). CIT use unbiased recursive partitioning through data distribution and account for multicollineraty, interactions between treatments, interpretability, ability to handle both numerical and categorical variables (Hothorn et al., 2006), and heteroscedasticity (Tittonell et al., 2008; Lohr, 2009), which are appropriate for analyzing survey data (Hothorn et al., 2006).

The weather variables included in the CIT were cumulative rainfall and mean daily Tmax and Tmin for the growing season and for the grain filling period, cumulative solar radiation for the growing season, and the photothermal quotient [PTQ, the ratio between incident solar radiation and average temperature) (Fischer, 1985) using a $T_{\text{base}} = 0$ °C (Porter and Gawith, 1999)] for the critical period [i.e., 20 days before anthesis until 10 days after anthesis (Fischer, 1985)]. The use of field-level weather data precluded the need to use the nominal variable "year" with a more robust agronomic meaning. A total of 48 independent weather (8), management (37), soil (2), and simulated (days to anthesis) variables were used in the CIT to explain Ya.

One CIT was initially created across all 656 fields, and this CIT was evaluated for significant effects of seeding rate, previous crop, and sowing date, as these variables are regiondependent and their significance could confound the interpretation of the results (Munaro et al., 2020). Because these were significant (see results section below), individual CITs were created by crop zone. The best-fit CIT was selected by allowing the intermediate and terminal nodes to vary between 5-40% and 5-20% at five percent intervals, and CIT depth to range from 3 to 10. Coefficient of determination (r^2) and RMSE evaluated the fit of the CITs, and a more parsimonious CIT was selected when r^2 and RMSE changed less than 5% from a more complex CIT. After selecting the final model, we interrogated each node of the individual CITs for the next three surrogate splits, which in essence identifies variables that result in a good approximation of the primary results in case data for the primary split are missing (i.e., provide an insight into correlated variables within the subset of data used in the split; Lawes et al., 2021). Because our goal was to assess variable importance and conditional effects instead of future prediction, we modeled the entire dataset within each CZ without using a training and a validation dataset.

Results

Weather during the surveyed growing season as compared to historical conditions

Mean growing season rainfall ranged from 233 to 737 mm, with an overall dryer 2018 as compared to 2016 or 2017 (Fig. 2). Cumulative rainfall and plant available water at sowing were greater than the long-term mean in 2016 and 2017. These years had a mild winter and earlier spring development, resulting in earlier heading and longer grain filling period. The 2018 season was dryer and had a cool winter and early spring, which delayed the onset of wheat stem elongation in the spring, delaying wheat heading and shortening the grain fill duration.

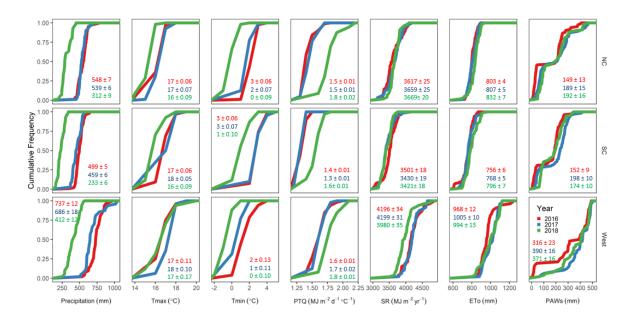


Figure 2-2. Frequency distribution of average cumulative precipitation, mean maximum (Tmax) and minimum (Tmin) temperatures, photo-thermal quotient during the growing season (PTQ), solar radiation (SR), total grass-based reference evapotranspiration (ETo), and plant available water at sowing (PAWs) for the winter wheat growing season for all fields collected in three Kansas regions (North Central, NC; South Central, SC; and West).

Winter wheat Ya, Yw, and YG

Wheat Ya averaged 3.8 Mg ha⁻¹ and ranged from 0.3 to 7.1 Mg ha⁻¹ across all fields, showing a large year \times zone variability (i.e., mean Ya ranged from 2.5 Mg ha⁻¹ in SC during 2018 to 5.0 Mg ha⁻¹ in West during 2016) (Fig. 3). The average producer-reported yields were

~19% greater than the average USDA-NASS county-level yields (3.1 Mg ha⁻¹), with a slope of 1.17 ± 0.11 , suggesting that differences were larger under higher yielding conditions. Still, the high coefficient of determination (r^2 =0.61, p < 0.001) suggested that our database was representative of the variability in conditions during the study period.

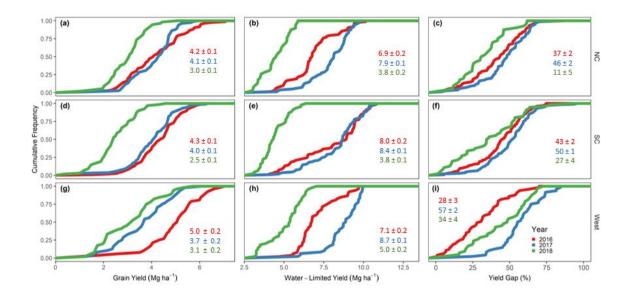


Figure 2-3.Cumulative frequency distributions of (a, f, k) actual grain yield, (b, g, l) waterlimited grain yield, (c, h, m) yield gap, (d, i, n) water productivity, and (e, j, o) transpiration efficiency for three years (2016, 2017, and 2018 shown as different colors) and regions (North Central – NC, top row; South Central – SC, middle row; and West, lower row) in Kansas. Across zones and years, crop simulation modeling suggested an average Yw of 6.8 Mg

ha⁻¹ (range: 1.2 to 10.9 Mg ha⁻¹) for an average YG of 44% (Fig. 3). These estimates were slightly greater than those using boundary function analysis of the 99th percentile yields as function of sowing dates (Box 1). The remainder of the manuscript will refer to Yw and YG as those calculated through crop modeling. The smallest YG occurred in NC during 2018, while the largest YG occurred in West during 2017. The large region × zone effect on Yw and YG was reflected on the ranges observed for these variables across fields, as mean Yw within crop zone and year ranged from 3.1 to 8.1 Mg ha⁻¹ with an associated YG range of 12 to 57%. Across regions and years, YG associated negatively with grain filling Tmin and Tmax ($R^2 > 0.25$, P < 0.25, P < 0

0.01) and positively with cumulative solar radiation during grain fill and with the ratio of ETc during grain filling over seasonal ETc ($R^2 > 0.27$, P < 0.01) (data not shown). We note in passing that the magnitude of the YG depended on crop sequence.

Wheat management in Kansas

The adoption of management practices depended on crop zone and year (Fig. 4, Table 2). Average sowing date ranged from DOY 275 in the West (range: 42-d) to 287 in SC (range: 58d). Across years, sowing date was similar in the NC region (DOY 282, range: 41-d) but varied for SC (DOY 284 in 2016 *versus* 289 in the other years) and West (DOY 280 in 2018 *versus* 272 in the other years). The regional specificity of sowing dates and its effects on wheat yield is explored in Box 1. Seeding rates also varied by 23 kg ha⁻¹ across zones, with the central zones averaging 90 kg ha⁻¹ and the West averaging 68 kg ha⁻¹. Seeding rate was similar across years in the West (68 kg ha⁻¹) but varied by year in NC (90-95 kg ha⁻¹) and SC (88-95 kg ha⁻¹). Row spacing was typically narrower in SC (75% adopted 19 cm or less) with a transition zone in NC (53% adopted 19 cm or less) and wider in the West [row spacing was mostly 25.4 (66%) or 30.5 cm (33%)]. Nitrogen rate was greater in the central zones (94 ± 2.7 kg N ha⁻¹) *versus* West (59 ± 3.5 N ha⁻¹). No-till occurred in 75, 52, and 48% of the fields in NC, SC, and West. Foliar fungicide application at GS55 occurred in 55, 56, and 42% of the fields in NC, SC, and West.

Expectedly, crop sequence varied by zone: More than 75% of the surveyed fields were in a fallow-crop rotation in the West, which was followed by 14% wheat after maize. The most common previous crop was either soybeans (44 and 30%) or wheat (42 and 51%) in NC and SC. Within a given crop zone, the adoption of management practices also depended on crop sequence. For instance, fields following a soybean crop were planted 6-8 days later and with 7-9 kg ha⁻¹ more seed than fields after wheat in the central zones; while fields following maize were

sown approximately 7 days later at 10 kg ha⁻¹ greater seeding rates than fields following a fallow

period in the West (data not shown). Within crop zone, greater seeding rates related positively

with later sowing dates (slope: 0.31-0.37 kg ha⁻¹ d⁻¹; $r^2 > 0.06$, p < 0.001).

Table 2-2. Frequency (%) or mean values of management practices and variety characteristics
adopted in the surveyed wheat fields across three regions (North Central, South Central, and
West) of Kansas. For meaning of genotype ratings, please refer to the methods section.

	Variable	Units	North Central	South Central	Wes
				– Mean –	
Wheat variety rating	Leaf rust	Unitless	5	4	6
	Stripe rust	Unitless	4	5	4
	ŴSM	Unitless	7	7	6
	Maturity	Unitless	5	5	5
	Height	Unitless	5	5	5
	Drought	Unitless	6	б	5
	Straw strength	Unitless	3	3	4
Crop management	Variety blend	%	24	12	3
	Volunteer wheat control	%	98	96	97
	Row spacing (19 cm or less)	%	53	75	1
	Seed fungicide	%	81	71	29
	Seed insecticide	%	55	62	28
	Grazing	%	3	3	1
	Conventional till	%	25	48	52
	No-till	%	75	52	48
Fertilizer	In-Furrow P	%	70	65	62
	Manure	%	0	4	9
	Lime	%	0	1	0
	Broadcast or banded P	%	20	31	7
	S	%	52	45	28
	Cl	%	6	6	1
	Zn	%	43	14	38
First N source	Anhydrous ammonium	%	9	21	11
	Urea ammonium nitrate	%	55	55	71
	Urea	%	34	22	15
First N method	Broadcast	%	45	46	48
	Knife	%	6	22	11
	Stream nozzle	%	49	32	38
First N stage	Pre-plant	%	37	45	17
-	Zadoks GS20	%	59	51	79
	Zadoks GS31	%	4	4	1
Second N source	U.A.N	%	29	44	15
	Urea	%	2	1	0
Second N method	Broadcast	%	14	24	15
	Stream nozzle	%	18	21	0
Second N stage	Zadoks GS20	%	28	34	15

	Zadoks GS31	%	3	11	0
Foliar fungicide	Zadoks GS31	%	10	4	7
	Zadoks GS39	%	55	56	42
Previous crop	Corn	%	2	11	14
	Fallow	%	10	4	75
	Other	%	1	4	5
	Soybean	%	44	30	1
	Wheat	%	42	51	4
Available water	0-15	cm ³ cm ⁻³	0.06	0.06	0.06
holding capacity	0-60	cm ³ cm ⁻³	0.16	0.15	0.18

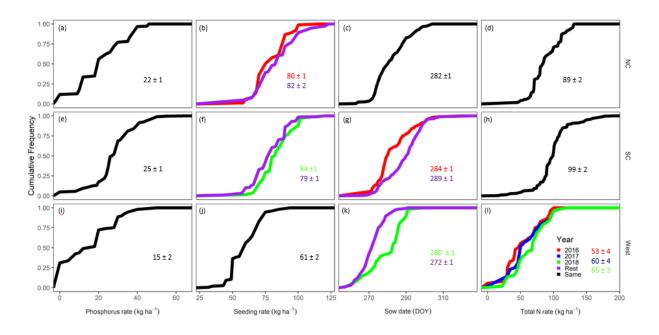


Figure 2-4. Cumulative frequency distributions of (a, e, i) of phosphorus rate (kg P ha-1), (b, f, j) seeding rate (kg ha-1), (c, g, k) sowing date (Day of Year, DOY), and (d, h, l) total nitrogen rate (kg N ha-1) for three different regions (North Central, upper row; South Central, middle row; and West, lower row) in Kansas. Black lines represent variables with no statistical difference among years. Colored lines represent statistically significant differences among years. **Interactions of weather variables and management practices on wheat grain yield**

Across all 656 field-years, the most parsimonious CIT explained 39% of the variability in yield, with a RMSE of 0.93 Mg ha⁻¹ (Fig. 5). Cumulative growing season rainfall was the most important factor associated with increased Ya, with other weather variables occurring as surrogate splits (grain filling Tmin or Tmax, or seasonal Tmax; Table 3). Yield ranged from 3.0

to 5.6 Mg ha⁻¹ in fields receiving more than 388 mm precipitation, with the highest yields resulting from fields receiving a foliar fungicide application around flag leaf and more than 87 kg N ha⁻¹ in the first N application. Grain yield ranged from 2.5 to 3.0 Mg ha⁻¹ across fields receiving less than 388 mm seasonal precipitation, depending on initial plant available water (split at 183 mm). Because five nodes either were, or had as surrogate splits, a variable that was region specific [i.e., row spacing (primary node), prior crop (three surrogate nodes), and sowing date (one surrogate node)], we further explored CIT by crop zones.

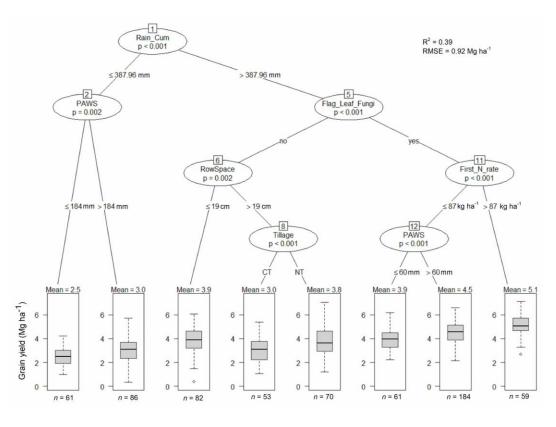


Figure 2-5. Conditional inference tree of weather, soil, and management practices winter wheat grain yield across all 656 fields surveyed. Each boxplot represents the interquartile range (gray box), median (solid line), fifth and 95th percentiles (whiskers), and outliers (empty circles). The mean, number of observations (n), and model fit statistics (R2 and RMSE) are shown. Legend: Rain_Cum, total in-season rainfall; PAWS, plant available water at sowing; Flag_Leaf_Fungi, application of a flag leaf fungicide (Zadoks GS40-55); RowSpace, row spacing; Tillage, tillage practice adopted (NT = no till; CT = conventional till); and First_N_rate, rate of N in the first application.

Table 2-3. Surrogate variables and associated splits for each node of the conditional inference trees (CIT) evaluated across all 656 field-years of winter wheat in Kansas during the 2016, 2017,

~~~						r to Figures 4 and 5.	
CIT	No de	Surrogate var. 1	Split	Surrogate var. 2	Split	Surrogate var. 3	Split
All	1	Grain fill Tmin	17.5°C	Grain fill Tmax	31.7°C	Seasonal Tmax	16.4°C
	2	Previous crop	Soybean vs. corn, fallow, wheat, or other.	Seeding rate	73 kg ha ⁻¹	First N method	Broadcast or stream vs. knife or no.
	5	Seasonal Tmin	2.1°C	Second N rate	15 kg ha ⁻¹	First N method	Broadcast, knife, or stream vs. no.
	6	Seasonal solar radiation	3827 MJ m ⁻²	Previous crop	Soybean or wheat vs. corn, fallow, or other.	Total N rate	73 kg ha ⁻¹
	8	Presence of S fertilizer	Yes/no	Presence of Zn fertilizer	Yes/no	First N source	AA or UAN vs. urea or no
	11	Total N rate	108 kg ha ⁻¹	Seasonal Tmax	16°C	Presence of insecticide seed treatment	Yes/no
	12	Previous crop	Soybean vs. corn, fallow, wheat, or other.	Sowing date	DOY 281	Seasonal solar radiation	4874 MJ n 2
NC	1	First N rate	92 kg ha ⁻¹	Rate of P	21 kg ha ⁻¹	Second N stage	No or tille vs. jointing
	2	Presence of in-furrow P fertilizer	Yes/no	First N stage	Jointing or tiller vs. pre-plant.	Presence of Zn fertilizer	Yes/no
	3	Seasonal Tmin	1.3°C	Grain fill Tmax	31°C	Critical period PTQ	1.18 MJ m d ⁻¹ °C ⁻¹
	5	Seeding rate	75 kg ha ⁻¹	Second N method	Broadcast vs. no or stream.	Variety stripe rust resistance	2.8
	7	Grain fill Tmin	15°C	First N rate	15 kg ha ⁻¹	Presence broadcast P	Yes/no
	10	Seasonal Tmin	1.9°C	Cumulative rainfall	544 mm	Days to anthesis	217 days
	11	Plant available water at sowing	92 mm	Variety stripe rust resistance	5	Variety wheat streak mosaic resistance	7
	15	Critical period PTQ	1.3 MJ m ⁻² d ⁻¹ °C ⁻¹	First N method	Knife or stream vs. broadcast	First N source	AA or UAN vs. urea
SC	1	Grain fill Tmin	16°C	Grain fill Tmax	30°C	Critical period PTQ	1.14 MJ m d ⁻¹ °C ⁻¹
	2	First N rate	80 kg ha ⁻¹	First N source	No, UAN or urea vs. AA	First N method	Broadcast no, or

and 2018 growing season ("All"), and individually per crop zone for north central (NC), south central (SC), and West. For identification of node number, please refer to Figures 4 and 5.

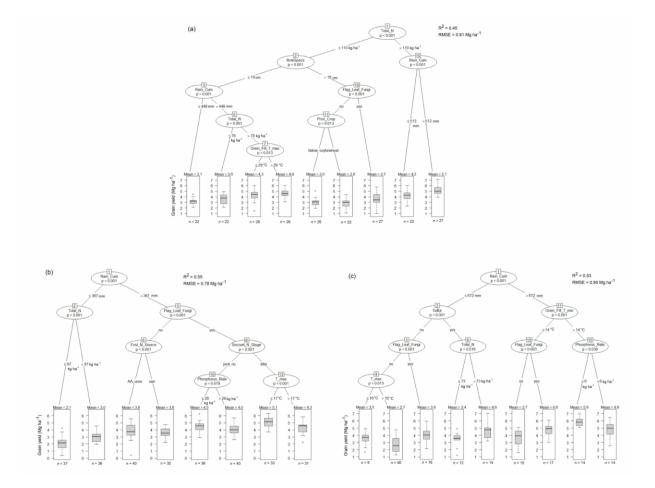
stream vs. knife Knife or no
vs. broadcast or stream
Pre-plant vs. tiller
Jointing or tiller vs. pre-plant.
Yes/no
Knife or stream vs. broadcast
389 mm
35 kg ha ⁻¹
2
Tiller vs. no
4
4
192 mm
Yes/no

In NC, the most parsimonious CIT had an  $R^2$  of 45% and a RMSE of 0.81 Mg ha⁻¹ (Fig. 6a). The first node was total N rate, splitting at 110 kg ha⁻¹ with yields ranging between 2.9-4.6 Mg ha⁻¹ and 4.2-5.1 Mg ha⁻¹ in the low and high N ranges. Surrogate splits first N rate or second N timing, or P rate (Table 3). In fields receiving more than 110 kg N ha⁻¹, the next node was growing season rainfall, splitting at 512 mm (alternative splits: PTQ, or first N application method or source). In fields receiving less than 110 kg N ha⁻¹, row spacing of 19 cm or narrower were higher yielding (3.1-4.6 Mg ha⁻¹) than wider row spacing (2.9-3.7 Mg ha⁻¹). Alternative

splits were in furrow P; stage of first N application; or Zn application. Yields of fields adopting narrow row spacing depended on seasonal rainfall (surrogate splits: Tmin, grain fill Tmax, or PTQ), total N (alternative splits: seeding rate, second N method, or variety stripe rust resistance), and grain fill Tmax (alternative splits: grain fill Tmin, first N rate, P fertilizer). For fields adopting wide row spacing, flag leaf fungicide associated with higher yields (3.7 Mg ha⁻¹; alternative splits: Tmin, cumulative rain, and days to anthesis – with later simulated anthesis out yielding earlier ones). For fields not receiving fungicide, wheat after fallow or soybeans yielded more than after wheat (3.0 versus 2.9 Mg ha⁻¹). In fields absent of fungicide, a surrogate split suggested that varieties resistant to stripe rust out yielded susceptible ones.

In SC, the most parsimonious CIT explained 55% of yield variability, with a RMSE of 0.78 Mg ha⁻¹ (Fig. 6b). The first node was seasonal precipitation, splitting at 367 mm for low yielding (2.1-3.0 Mg ha⁻¹, depending on total N rate) or high yielding fields (3.6-5.1 Mg ha⁻¹, depending on the presence of foliar fungicide). Surrogate splits for the first node were grain fill Tmin or Tmax, or PTQ (Table 3). For the second node, surrogate splits were first N rate, source, and method. Surrogate splits for the foliar fungicide node were second N application rate, crop stage, and method. In the absence of foliar fungicide, grain yields (3.6 to 3.8 Mg ha⁻¹) depended on N source used in the first application (surrogate splits: method and stage of first N application, or presence of S fertilizer). For fields receiving foliar fungicides, yields ranged between 4.0 and 5.1 Mg ha⁻¹ depending on stage of second N application (surrogates: method or source of second N application, or stage of first N application), P rate (surrogates: simulated days to anthesis – with early simulated anthesis outyielding late ones; and broadcast or in furrow P fertilizer), and seasonal Tmax (surrogates: seasonal Tmin, days to anthesis, and first N method).

In the West, the most parsimonious CIT explained 53% of yield variability with a RMSE of 0.95 Mg ha⁻¹ (Fig. 6c). The first node was seasonal precipitation, splitting at 672 mm. Surrogate splits were PTQ, Tmin, and precipitation during grain fill (Table 3). For fields receiving less than 672 mm precipitation, yield ranged from 2.7 to 4.6 Mg ha⁻¹, with the highest yielding fields receiving S fertilizer and more than 73 kg N ha⁻¹. Surrogate splits for S fertilizer included presence of Zn or P rate (note that usually S is supplied in combination with Zn and P); and surrogate splits for total N rate included first N rate, tillage, and variety's straw strength. For fields not receiving S fertilizer, higher yields (3.9 Mg ha⁻¹) associated with presence of foliar fungicide at flag leaf (surrogate splits grazing, Tmin, and stripe rust resistance). In the absence of foliar fungicide, growing season Tmax influenced yields between 2.7 and 3.5 Mg ha⁻¹ (surrogate variables: seeding rate, and second N rate and stage of application). Grain yield in fields receiving more than 672 mm season precipitation ranged from 3.7 to 5.9 Mg ha⁻¹, mostly depending on grain fill Tmin, presence of foliar fungicide at flag leaf, and P rate. Surrogate splits for grain fill Tmin were grain fill Tmax, seasonal Tmin, and variety maturity (later maturing varieties out yielding early maturing ones). Surrogate splits for flag leaf fungicide were first N method, sowing date, and rainfall during grain filling; while surrogate splits for P rate were presence or absence of S, P, and Zn fertilizer.



1

Figure 2-6. Conditional inference tree of management practice impacts on normalized wheat grain yield (i.e., difference from the mean
within each year x CZ combination) for the North Central (a), South Central (b), and West (c) regions. Each boxplot represents the
interquartile range (gray box), median (solid line), fifth and 95th percentiles (whiskers), and outliers (empty circles). The mean,
number of observations (n), and model fit statistics (R2 and RMSE) are shown. Legend: Total_N refers to total N applied during the

6 growing season in kg ha-1; Phosphours_Rate refers to total P applied during the growing season in kg ha-1; SeedInsect refers to the

7 application of a seed insecticide to the seed before sowing; Flag_Leaf_Fungi refers to the application of a flag leaf fungicide during

8 approximately at Zadoks GS55; Sow_Date refers to the sowing date in day of year.

9

## Discussion

10	A survey of management practices adopted in a large number of commercial rainfed
11	winter wheat fields in Kansas exposed to a range of environmental conditions during three
12	consecutive growing seasons, coupled with detailed crop simulation modeling, revealed
13	environmental factors and management $\times$ environment interactions affecting yield and YG of
14	winter wheat. Beyond the local implications of our findings to improve wheat management in
15	dryland regions, our analyses have implications for future YG analyses for other crops and
16	regions.
17	Implications for future yield gap analyses
18	Our analysis has a few major implications for future YG analyses: (i) we highlighted the
19	importance of region-specific agronomic practices in supporting the need for regional
20	subdivision of survey data; (ii) we combined the use of crop zones (to account for the region-
21	specific nature of particular agronomic practices) with growing season weather data (that
22	determines the crop's Yw and the impacts of weather $\times$ management interactions on Ya) to
23	explain Ya; and (iii) the large number of agronomic practices evaluated demonstrated that many
24	management factors beyond the ones most usually evaluated in yield gap analyses (e.g., sowing
25	date or fertilizer rates) helped to better defined the YG.
26	An original contribution of our work is that we explicitly highlighted the need to
27	subdivide a heterogeneous region in smaller and more homogeneous crop zones with the specific
28	goal of accounting for agronomic practices that are region-specific and can be confounded
29	otherwise. The use of crop zones was justified by the presence of management variables that
30	were region-dependent in primary and surrogate splits when a single tree represented all data
31	(Fig. 5, Table 3), as well as by the better fit of individual trees by crop zone as compared to the

32 single tree, despite a smaller number of observations in each crop zone CIT ( $R^2$  of 0.45-0.55 vs. 33 0.38). The addition of field-specific weather variables during different periods of the growing 34 season was justified due to the high importance of year, which explained 86% of the variability 35 in grain yield. This approach builds on previous efforts that evaluated grower-reported data by 36 pre-determined crop zones across years without accounting for season-specific weather (e.g., 37 Mourtzinis et al., 2018b, 2020; Rattalino Edreira et al., 2017), as well as on efforts evaluating 38 YG in thousands of fields using field-specific management and weather data in a large but rather 39 homogenous region (Di Mauro et al., 2018).

40 The subdivision of large geographies into smaller, more homogenous zones can account 41 for spatial variation in the biophysical determinants of the crop's Yw (i.e., soil and long-term 42 weather) (Rattalino Edreira et al., 2017). Zoning schemes based on long-term weather are static 43 and do not account for the temporal variation in weather or for its interactions with management. 44 Due to their static nature, these zoning schemes have been successful in accounting for large 45 portion of the variation in yield in studies using one or two years of data in regions with high 46 predictability in weather conditions (e.g., Rattalino Edreira et al., 2017; Silva et al., 2017), and 47 up to four years of data when all years corresponded to relatively favorable environments 48 (Mourtzinis et al., 2020). However, in regions with erratic weather pattern, the static nature of 49 crop zones can be a concern when analyzing yield data across years as it does not account for 50 year-specific weather conditions, thus potentially masking the effects of management under the 51 years with contrasting weather conditions. For instance, if the database from a given crop zone is 52 comprised by a dry and a wet year, management practices either improving yields on dry or wet 53 years might not be identified as significant when data is analyzed across years (Mourtzinis et al.,

54 2020). The inclusion of season-specific weather variables as explanatory variables in the CIT
55 helps to overcome this limitation (e.g., Di Mauro et al., 2018).

56 Supporting our results, Couëdel et al. (2021) recently showed that accounting for spatio-57 temporal variation in heat and drought stresses explained 2x to 7x larger portion of the variance 58 in grain yield of maize, soybeans, and wheat, as compared to the static zoning. Likewise, Di 59 Mauro et al. (2018) showed that field-level weather, management, and soil data explained 26-60 31% of soybean yield variability across four Argentinian provinces. We note, however that Di 61 Mauro et al. (2018) evaluated a relatively homogenous region, thus justifying the analyses across 62 all data combined, which differs from the conditions in our study region. The better explanatory 63 power of grouping fields based on clusters of more similar crop-phase specific weather as 64 compared to crop zones in more erratic cropping systems was speculated by Mourtzinis et al. 65 (2020), through their results did not support this for soybeans in U.S. North Central, a region 66 with greater environmental predictability (Couedel et al., 2021). One drawback of our approach 67 is that it requires site-specific weather data, which might not be available in many regions with 68 lower population density of weather stations.

69 Another important contribution of the current work to the YG literature is the opportunity 70 to better describe Ya with detailed data on crop management. We evaluated 37 producer-reported 71 management variables, which is a larger number of variables than many other efforts 72 investigating crop YG. For instance, Beza et al. (2017) extensively reviewed the YG literature 73 and suggested that the average number of management factors explaining YG was three and 74 ranged from zero to 29. The authors also highlighted that unavailability of data can be a major 75 limiting factor in YG analyses, as exemplified by the lack of fertilization data in the Neumann et 76 al. (2010) analysis and the limited number of experiments used to validate crop models by (Lu

77 and Fan (2013). We demonstrated how a rich management dataset, combined to field-specific 78 weather and soil data, helped to illustrate the challenges brought about by management  $\times$ 79 environment interactions in determining best management practices in regions with high year-to-80 year variability (Munaro et al., 2020). Also of interest to the YG literature is that individual splits 81 in the CIT correlated with other variables. In some cases, correlated variables were all aspects of 82 one management practice (i.e., total N rate as primary split, with surrogate variables first N rate, 83 source, or method), reinforcing that more focus should be given to improve the management of 84 that specific practice in that particular region. However, in other cases, different variables could 85 also explain particular splits, suggesting that careful agronomic interpretation is needed to further 86 improve Ya.

Finally, we note that the first (and most important) split in the CIT as well as its three surrogate variables were related to weather conditions in SC and in the West (Fig. 6, Table 3), regions typically more exposed to water deficit stress and heat stress, respectively (Couedel et al., 2021). Meanwhile, the first split and surrogate variables in NC, a region with cooler weather than SC and greater moisture availability than the West, were related to crop management (i.e., N or P rate). This offers insights into the greater relative importance of management practices in determining wheat yields in favorable environments as compared to harsh environments.

#### 94 Wheat grain yield, yield variability, and yield gap in the U.S. central Great Plains

The surveyed fields had slightly greater yields than those reported by official statistical sources, which is similar to other surveying efforts (Lawes et al., 2021). The high end of winter wheat grain yield in our database (maximum: 7.1 Mg ha⁻¹) was lower than values reported for the same region in fields entered in the Kansas Wheat Yield Contest during 2010-2017, which were as high as 8.3 Mg ha⁻¹ (Lollato et al., 2019b). The high end of the simulated Yw (>8.5 Mg ha⁻¹)

100 occurred in 32% of the cases, mostly during 2016 or 2017 when seasonal water availability was 101 not limiting to yields (mean growing season rainfall among these 213 high Yw fields of  $825 \pm 6$ 102 mm). Still, only 13% of the simulated Yw were greater than the highest reported winter wheat 103 yield in variety performance tests in the region (i.e., 9.4 Mg ha⁻¹; Lingenfelser et al., 2019, 2016). 104 Wheat YG averaged 44%, which is similar to a comprehensive estimate of 36% by 105 Fischer et al. (2014); however, with substantial differences in Yw and Ya. Fischer et al. (2014) 106 used government reported data to estimate Ya of 2.8 Mg ha⁻¹ and variety trial data to estimate an 107 attainable yield of 3.8 Mg ha⁻¹, while our respective estimates were 3.8 and 6.8 Mg ha⁻¹. The 108 differences between these estimates result from a few features of both the current research and 109 Fischer et al. (2014). First, the group of growers included in our survey had ~19% greater yields 110 than those reported by the government, resulting in a slight overestimation of Ya in our analysis. 111 Second, we used crop simulation modeling to derive Yw while Fischer et al. (2014) used variety trial data to estimate attainable yield. Our estimate of attainable yield was 6.0 Mg ha⁻¹, which 112 113 results in more similar YG estimates to Fischer et al. (2014) (i.e., 35%, Box 1). We also note that 114 two out of three years included in our survey (i.e., 2016 and 2017) had historical state-level record wheat yields (USDA-NASS, 2016, 2017b), which suggests that the optimal weather 115 116 conditions increased the Yw estimates as compared to long-term Yw (6.8 versus 5.2 Mg ha⁻¹, 117 Lollato et al., 2017). Finally, the conditions experienced in the current research are perhaps not 118 representative of the technology levels and weather conditions of those reported by Fischer et al. 119 (2014), as their estimates reflected the year of 2010. Using the progress in Yw and Ya reported by Fischer et al. (2014) to update their calculations, Ya is estimated as ~3.1 Mg ha⁻¹ and Yw as 120 ~4.0 Mg ha⁻¹ for the last year included in this research. While this Ya estimate agrees with 121 122 current yield levels (USDA-NASS, 2018), recent evidence suggests that the yields reported in

variety performance tests in the region are  $\sim 0.9 \text{ Mg ha}^{-1}$  below their potential due to suboptimal 123 124 management (Munaro et al., 2020; de Oliveira Silva et al., 2020b). This would increase Fischer et al. (2014)'s Yw estimate to 4.9 Mg ha⁻¹, which is closer to yields from highly-managed wheat 125 126 yields in the region (Lollato and Edwards, 2015; Jaenisch et al., 2019; Lollato et al., 2019a; de 127 Oliveira Silva et al., 2020b). We note that Fischer et al. (2014) acknowledged that their analysis 128 could have underestimated Yw depending on the management of the variety performance tests. 129 About 23% of the surveyed fields had YG less than 25%, threshold below which might 130 not be economical to increase Ya (Lobell et al., 2009). This suggests that 77% of the fields 131 included in our survey could still economically improve yields through management. Conditions 132 leading to high Yw (i.e., low grain filling Tmin and Tmax, high grain filling solar radiation, and 133 high ratio of ETc during grain fill over crop cycle ETc) partially explained the larger YG, which 134 is similar to reports for wheat in other parts of the world (e.g., Lawes et al., 2021) and further 135 discussed in Box 2. A larger YG in higher yielding conditions highlights the risk-averse behavior 136 of the majority of the wheat producers in this region due to the inconsistent environmental 137 conditions (Couëdel et al., 2021) coupled with the assumption that other limiting factors will 138 provide reduced return to management intensification (de Oliveira Silva et al., 2020b).

#### 139 Implications for agronomic management of winter wheat in dryland regions

Management of N (rate, timing, source, and placement), P (rate and placement), as well as other nutrients such as S and Zn offer opportunities to improve winter wheat yield in the U.S. Great Plains. These results are consistent with previous research from field experiments in this (Lollato et al., 2013, 2019a; Wilson et al., 2020) and other wheat growing regions (Rodríguez et al., 1999; Salvagiotti and Miralles, 2008; Hochman and Waldner, 2020; Lawes et al., 2021). Additionally, these results align with the YG review by Beza et al. (2017), that suggested that

146 fertilization practices are among the most important factors reducing YG. We also demonstrated 147 that producers in the semi-arid West used lower N rates than those in the sub-humid central crop 148 zones, despite similar yield levels. The lower N rate in the semi-arid region might be associated 149 with reduced N losses (Schlegel et al., 2003; Edwards et al., 2009) or greater N carryover 150 (Hergert, 2015; Meier et al., 2021). Additionally, our survey identified that foliar fungicides 151 applied around GS40-55 associated with increased yields, likely due to stripe rust in 2016 and in 152 2017 which casued statewide yield losses of 9.1 and 8.6% (Hollandbeck et al., 2019). These 153 findings are also similar to replicated field experiments (Wegulo et al., 2011; Thompson et al., 154 2014; Cruppe et al., 2017; Jaenisch et al., 2019). Historically, producers in this region relied more in the genetic resistance of cultivars than in foliar fungicides (Kelley, 2001) reflecting in a 155 156 lingering reluctance to invest in this input to date (only 42-56% adoption), suggesting that it may 157 be an opportunity for future wheat yield improvements in Kansas. 158 Beyond the perhaps expected effects of fertility and fungicide management on wheat Ya 159 (Beza et al., 2017), our analyses including detailed management data exposed other interesting 160 management  $\times$  environment as well as management  $\times$  cropping sequence interactions. For 161 example, the association of narrower row spacing (or the presence of in-furrow P/Zn fertilizer) with increased Ya in fields receiving less than 110 kg N ha⁻¹ in NC (Fig. 6; Table 3) likely relates 162 163 to earlier canopy cover and radiation interception in these fields, which is also consistent with 164 experimental data (Rodríguez et al., 1999; Soltani and Galeshi, 2002; Shoup and Adee, 2014). 165 Along the same lines, fields sown later (i.e., after soybeans in central Kansas and after maize in 166 the West) were sown at higher seeding rates than earlier sown fields. The decreased fall tillering 167 potential is a severe yield-limiting factor of late sown winter wheat (Dahlke et al., 1993), 168 justifying increased seeding rates (Staggenborg et al., 2003). These results also suggest that

169 growers are adapting their management practices based on their cropping system. Another 170 example of how our detailed management data expands on the usual factors leading to increased 171 Ya included the results suggesting that later variety maturity was beneficial in NC and in the 172 West, while earlier maturity was beneficial in SC. While there are only slight differences in 173 maturity among modern winter wheat varieties in the U.S. Great Plains (Maeoka et al., 2020), 174 these results align with the evaluation of hundreds of thousands yield data points from variety 175 performance trials in the region (Munaro et al., 2020) with one important difference: The current 176 report uses real farm data to confirm the previous results from field trials, which not always 177 represent real farms regarding crop management and soil properties (Beza et al., 2017).

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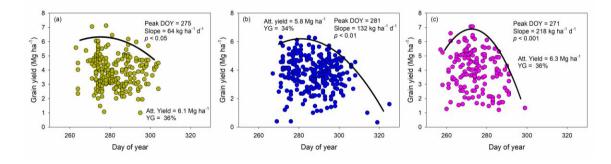
#### Conclusion

179 The analysis of 656 commercial winter wheat fields allowed for quantification of current 180 levels of technology adoption, evaluation of Ya, Yw, and YG, as well the interactions between 181 management and weather driving grain yield in Kansas, the largest winter wheat producing state 182 in the U.S. An average YG of 44% suggests room for future improvement, even for producers 183 yielding slightly above the state average. Management of fertilizer (N, P, S, and Zn) rate, timing, 184 source, and placement, as well as adoption of flag leaf foliar fungicide, associated with increased 185 grain yield across all crop zones and offer opportunities to improve yield in this region. Our data-186 rich analysis also provided greater insights into other management  $\times$  weather and management  $\times$ 187 cropping systems opportunities to increase wheat Ya, such as row spacing, seeding date and rate 188 interactions, and variety maturity. Finally, this survey also contributes to the YG literature by 189 suggesting that clustering of data by crop zone could be justified by the different levels of 190 management adoption and cropping sequence among regions.

# Box 1. Regional specificity of crop response to sowing date: A boundary function analysis

193 Previous research has demonstrated the potential of boundary functions to delineate the 194 impact of sowing date on crop attainable yield for soybeans (Grassini et al., 2015; Rattalino 195 Edreira et al., 2017), rice (Duarte et al., 2021), and spring wheat (Hajjarpoor et al., 2018), as well 196 as using long-term variety performance data for winter wheat (Munaro et al., 2020). At present, 197 we used quantile regression (Cade and Noon, 2003) to derive boundary functions between 198 attainable yield and sowing date to demonstrate (i) the regional specificity of winter wheat 199 response to sowing date, (ii) the impact of sowing date on winter wheat attainable yield using 200 grower-reported survey data, and (iii) alternative YG calculations using attainable yield instead 201 of Yw. First, the ranges in sowing dates (41, 58, and 42 days for NC, SC, and West) were 202 divided in 10 equally spaced intervals, then the 99th yield percentile in each interval was 203 identified, and a quadratic function was fitted against the mean sowing date in each range. The 204 boundary line was assumed to be the attainable yield and YG were calculated for each field 205 based on actual sowing date. The quadratic nature of winter wheat attainable yield in response to 206 sowing dates results from different yield-reducing factors on each side of the peak (Sacks et al., 207 2010). The optimum sowing date was day of year (DOY) 275 in NC, 281 in SC, and 271 in the 208 West, with average daily losses in attainable yield (calculated as the difference between the yield 209 predicted at the peak and at the last sowing date included in each crop zone's database) were 64, 210 132, and 218 kg ha⁻¹ d⁻¹ in NC, SC, and West. The estimates of optimum sowing dates agree with 211 those reported for same region using long term variety trial data (optimum DOY: 272, 284, and 212 268 for NC, SC, and West; Munaro et al., 2020). However, the loss in attainable yields due to 213 later sowing was greater in SC and West as compared to Munaro et al. (2020) (range: 42-93 kg

ha⁻¹ d⁻¹). This discrepancy is likely due to a database with a wider spread in sowing dates and more studied years reported by Munaro et al. (2020). We note that the average attainable yield across regions using this approach was 6.0 Mg ha⁻¹ with a YG of 35%, which is lower than those estimated using crop simulation models (6.8 Mg ha⁻¹ and YG = 44%).



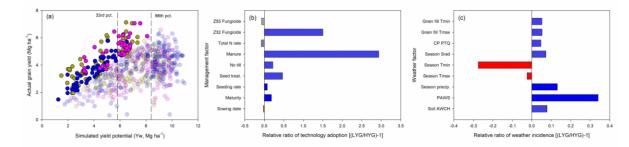
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Box Figure 2-7. Producer-reported winter wheat grain yield and attainable yield (solid line) as
function of sowing date in three distinct crop zones in Kansas: (a) North Central, (b) South
Central, and (c) West. Solid line represents the fitted boundary function using quantile regression
(99th percentile). Peak of the boundary function, derived as the first derivative of the convex
quadratic equation, as well as slope between the peak and the last sown crop, significance of the
quadratic equation, average attainable yield, and yield gap (YG) are shown.

#### **Box 2. Is it possible to narrow the yield gap in high-yielding seasons?**

227 It is well established that the YG increases with increases in Yw (Hochman et al., 2016; 228 Lawes et al., 2021; Lollato et al., 2019b; Silva et al., 2017, 2020). At question here is whether 229 fields exist that achieve narrow YG in seasons with high Yw. To answer this question, we 230 subdivided the data into Yw terciles (lower tercile,  $Yw < 5.8 \text{ Mg ha}^{-1}$ , mid, and upper tercile, Yw > 8.4 Mg ha⁻¹) and, within terciles, identified fields with YG < 25% (Lobell et al., 2009). For the 231 232 lower, mid, and upper Yw terciles, 52, 20, and 0% of the fields had YG < 25% (Box Fig. 2a), 233 supporting previous literature that no fields in the upper tercile were within 25% of the Yw. We 234 note, however, that the Yw in the mid-tercile was relatively high (5.8 to 8.4 Mg ha⁻¹), so we 235 further explored how the management of fields with YG < 25% (mean yield: 5.6 Mg ha⁻¹) differed from fields with YG > 25% (mean yield:  $3.9 \text{ Mg ha}^{-1}$ ). Overall, fields attaining small 236

237 YG in the mid tercile were sown earlier, to later maturing varieties, at a lower seeding rate, had 238 greater adoption of insecticide and fungicide seed treatments, greater adoption of no-tillage 239 practices, manure, and of an early fungicide application (Zadoks 32), but did not differ in N rate 240 or fungicide adoption at Zadoks 55 (Box Fig. 2b). All evaluated weather variables also differed 241 between groups, as fields with low YG had greater available water holding capacity, plant 242 available water at sowing, growing season rainfall and solar radiation, critical period PTQ, and 243 had lower growing season Tmin and Tmax (Box Fig. 2c). This analysis highlighted that seasons 244 with relatively high Yw require an overall more sophisticated management to narrow the YG. 245 Thus, we propose that the greater YG in high Yw seasons results from farmers that are likely 246 unwilling to apply sufficient inputs to achieve the high Yw; and that obtaining narrow YG is 247 further complicated in these seasons due to a higher disease pressure.





249 Box Figure 2-8. (a) Actual grain yield and its relationship with simulated rainfed yield potential (Yw) across the entire 656 field-years database. Dark yellow circles represent the NC region, 250 251 blue circles the SC region, and pink circles the West region. Solid circles are fields with YG < 25% and transparent circles are fields with YG > 25%. Dashed lines show the  $33^{rd}$  and  $66^{th}$ 252 percentile Yw. (b) Relative ratio of technology adoption and (c) incidence of weather variables 253 254 in fields with low yield gap (LYG) over high yield gap (HYG) for the mid-tercile Yw as shown in panel (a). Blue and red bars indicate positive and negative significant difference, grey bars 255 256 indicate no significant difference between groups, as suggested by two-tailed t-tests or Wilcoxon 257 test.

#### 258 Acknowledgments

259 We thank the Kansas wheat growers who provided their time and data by participating in

260 the survey, as well as the County Extension Agents within the Kansas State University Research

261	and Extension system who provided contact for representative growers in their regions. We also
262	thank Dr. Rattalino Edreira from Dr. Grassini's lab at University of Nebraska-Lincoln for
263	sharing shape files for the Technology Extrapolation Domains (TED) initially used in our region
264	delineation, and for his help defining coarser climate zones based on available water holding
265	capacity. This research is contribution no. 21-254-J from the Kansas Agricultural Experiment
266	Station.
267	Funding
268	This research was funding primarily by the Kansas Wheat Commission. This research
269	was partially sponsored by the Kansas Agricultural Experiment Station and by the Kansas
270	Cooperative Extension Service.
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540	Chapter 3 - Modulation of wheat yield components in response to
541	management intensification to reduce yield gaps
542	Highlights
543	• We investigated the modulation of yield through yield components in winter wheat
544	• Significant environment $\times$ management and environment $\times$ genotype affected grain yield
545	• Fertility and fertility plus fungicide maximized yield in dry and wet environments
546	• Wheat grain yield was modulated by kernels m ⁻² rather than kernel weight
547	• Source limitation was evident with a positive green canopy cover $\times$ yield relationship
548	Abstract
549	Appropriate genotype selection and management can impact wheat (Triticum aestivum
550	L.) yield in dryland environments, but their impact on yield components and their role in yield
551	modulation are not well understood. Our objectives were to evaluate the yield response of
552	commercial winter wheat genotypes to different management practices reflecting a stepwise
553	increase in management intensity, and to quantify how the different yield components modulate
554	wheat yield. A factorial experiment evaluated six management intensities ['farmer practice' (FP),
555	'enhanced fertility' (EF), 'ecological intensification' (EI), 'increased foliar protection' (IFP),
556	'water-limited yield' (Yw), and 'increased plant productivity' (IPP)] and four winter wheat
557	genotypes in two Kansas locations during two seasons. Average grain yield was 4.9 Mg ha ⁻¹ and
558	ranged between 2.0 and 7.4 Mg ha ⁻¹ , with significant two-way interactions (environment $\times$
559	management and environment $\times$ genotype). The EF usually maximized yields in dry
560	environments while EI, which consisted of EF plus one fungicide application, maximized yields
561	in wet environments. Kernels m ⁻² and aboveground biomass were the strongest modulators of

yield as compared to kernel weight and harvest index, while heads m⁻² and kernels head⁻¹ modulated yields at a similar magnitude. We provide evidence for source limitation of wheat yield either when fungicides were not applied or when plant population was reduced, supported by significant relationships between yield and green canopy cover. Treatments more intensive than EI were not warranted as EF or EI maximized yields at all environments, and practices that promote biomass and kernels m⁻² are to be targeted for future increases in wheat yield.

568

#### Introduction

Bread wheat (*Triticum aestivum* L.) is cultivated in more than 200 million ha across the world, being an essential component of the human diet and the primary source of calories for the world's population (Reynolds et al., 2012). Thus, increases in wheat production are crucial for global food security (Shiferaw et al., 2013), especially as yield gains fail to sustain historical rates (Grassini et al., 2013). Within this context, increasing crop yield in currently cultivated land can help to meet future food demand while minimizing the expansion of agricultural lands (Cassman, 1999).

576 The majority of global wheat production occurs under rainfed conditions. These non-577 irrigated cropping systems are subject to droughts due to insufficient and/or poorly distributed 578 precipitation (Sadras, 2002; Sadras and Angus, 2006; Torres et al., 2013; Lollato et al., 2017). 579 This leads to a more conservative approach from producers in terms of adoption of management 580 practices with the objective of increasing yield. The underlying rationale is that water availability 581 is the most yield-limiting factor and reduces the return on added inputs (Jaenisch et al., 2019; de 582 Oliveira Silva et al., 2020b), following Liebig's law of the minimum which states that the growth 583 of a plant is proportional to the scarcest of the essential nutrients available. However, empirical 584 and theoretical evidence support that crop yields might not be limited by a single factor but

585	rather determined by interactions between two or more factors (Sadras, 2004; Cossani and
586	Sadras, 2018; Carciochi et al., 2020). Thus, it can be hypothesized that improvements in crop
587	management could increase grain yield despite water limitation (de Oliveira Silva et al., 2020b).
588	The state of Kansas, U.S., provides a good case-study for testing the management- and
589	genotype- related opportunities for future yield increases in dryland wheat growing regions. With
590	3-4 Mha of winter wheat sown annually and a total production of ~8 MMt, Kansas is the largest
591	winter wheat producing state in the U.S. (USDA-NASS, 2017a). The crop is grown
592	predominantly under dryland conditions (~94%, USDA-NASS, 2018a), with a 10-yr average
593	yield of 2.8 Mg ha ⁻¹ which corresponds to only 50-55% of the dryland yield potential (~5.2 Mg
594	ha ⁻¹ ; Patrignani et al., 2014; Lollato et al., 2017). A range of genotypic traits and agronomic
595	management practices is proposed to modulate wheat yield in this region (Munaro et al., 2020).
596	For instance, improved fertility management including the adoption of in-furrow starter fertilizer
597	(McConnell et al., 2010; Lollato et al., 2013; Maeoka et al., 2020), increased nitrogen rates
598	(Thomason et al., 2002; Walsh et al., 2018; Lollato et al., 2019a, 2021), and use micronutrients
599	(Zain et al., 2015), have associated positively with yields. Likewise, genetic resistance to major
600	diseases and its interaction with fungicide management are candidate variables of interest
601	(Lollato et al., 2019b; de Oliveira Silva et al., 2020b). The role of seeding rate, however, seems
602	variable and dependent resource availability (Fischer et al., 2019; Lollato et al., 2019b; Bastos et
603	al., 2020), and thus might interact with other practices (e.g., Jaenisch et al., 2019).
604	The studies above provided insights into individual management practices to improve
605	wheat grain yield. Others attempted to quantify wheat yield response to intensified management
606	combining the prophylactic use of inputs to minimize yield gaps in wheat (Mohamed et al.,
607	1990; Jaenisch et al., 2019; Quinn and Steinke, 2019; Herrera et al., 2020; de Oliveira Silva et

al., 2020b; Roth et al., 2021; Steinke et al., 2021). However, with few exceptions (de Oliveira
Silva et al., 2020b, 2021), these efforts mostly overlooked the mechanisms behind the yield
responses and simply quantified the magnitude of yield improvements. Because organogenesis is
linked to crop developmental stages (Slafer et al., 2021), we argue that it is relevant to discuss
management opportunities to maximize yield within the timeframe of yield component
determination.

614 The relationships between wheat yield and its components (i.e., biomass, harvest index, heads m⁻², kernels head⁻¹, kernels m⁻², and kernel weight) have been researched for decades 615 616 across a wide range of environments (Evans et al., 1980; Austin et al., 1989; Calderini et al., 617 1999; Acreche et al., 2008; Slafer et al., 2014). The majority of the literature suggests that wheat 618 is mostly sink-limited, with kernels m⁻² explaining a larger variation of yield than kernel weight, 619 and with changes in assimilate supply only offering modest changes in yield (Slafer and Savin, 620 1994; Borrás et al., 2004; Slafer et al., 2014; and citations therein). Thus, management practices that affect kernels m⁻² would expectedly have a greater impact on yield. Still, some management 621 622 practices that mostly modulate kernel weight might also relate positively to yield in some 623 environments (Cruppe et al., 2021). To our knowledge, there have been no attempts to explicitly 624 manipulate management practices that match important stages of crop development when 625 different organs are produced and quantify their relationship to yield within a context of 626 management intensification, which is crucial for food security (Cassman and Grassini, 2020). 627 Organs that eventually become source and sink are initiated during different times in the 628 vegetative and reproductive stages in wheat (Slafer and Rawson, 1994; Ochagavía et al., 2021). Plants m⁻² are determined during the vegetative stage as seedlings emerge and establish; tillers m⁻ 629  2  (and thus potential heads m⁻²) are determined between seedling emergence and the terminal 630

631 spikelet stage (although less productive tillers can be produced later); potential spikelets head⁻¹ are determined prior to jointing; and kernels spikelet⁻¹ are determined between the onset of stem 632 633 elongation until harvest maturity through the process of floret development (which ends by 634 anthesis) and grain filling (Ochagavía et al., 2021). Grain weight is determined between booting 635 and maturity, with the different sensitivities between the heading and grain-setting stages (Calderini et al., 2001), ^{and} the grain filling stage (Bergkamp et al., 2018). Meanwhile, the source 636 637 capacity (i.e., leaf area index or green canopy cover) is usually maximized prior to anthesis and 638 decreases with maturity (Lollato and Edwards, 2015). Disentangling the effects of genotype, 639 environment, and management – with the specific goal of modulating different yield components 640 and tradeoffs -can provide physiological basis for future yield increases.

641 While genotypic and management factors associated with wheat yield gaps in 642 Kansas and other dryland regions have been explored individually in different studies, their role 643 to improve crop yield and its components within an integrated management perspective having 644 as goal to optimize yield components has not been explored. Thus, our objectives were to 645 evaluate the yield and yield components response in commercial winter wheat genotypes to 646 different management practices reflecting a stepwise increase in management intensity using as 647 baseline the current technology level followed by an average producer in the region; and to 648 quantify how different yield components modulate wheat yield in this dryland region. We 649 hypothesize that a more intensive management will increase grain yield, and that yield increases 650 will be genotype- and environment-specific. Additionally, we hypothesize that fertilizer-based practices will affect yield components that are coarse regulators of yield (i.e., heads m⁻² and 651 kernels m⁻²) while fungicide-based practices will affect fine regulators of yield (i.e., kernel 652 653 weight, kernels head⁻¹) (Slafer et al., 2014). Due to the importance of grain protein concentration

654	to the end-product quality (May et al., 1991) and on wheat yield potential (Lollato et al., 2020b),
655	a secondary objective was to evaluate the $G \times E \times M$ effects on grain protein concentration.
656	Materials and Methods
657	Experimental locations and agronomic management
658	Rainfed field experiments were conducted near Belleville (39.81°N, 97.67°W; 471 m) in
659	a moderately well-drained Crete silt loam, and near Hutchinson (37.93°N, 98.03°W; 468 m) in a
660	well-drained Ost loam during the winter wheat seasons of 2017-18 and 2018-19. Each
661	environment will be referred to as Bel18, Bel19, Hut18, and Hut19. Winter wheat was sown
662	under conventional tillage after a summer fallow using a Great Plains 606 no-till drill (7 rows
663	spaced at 19 cm) with plot dimensions of $1.3 \times 9.1$ m. Seeds were treated with 6.9 g a.i. ha ⁻¹
664	thiamethoxam, 1.4 g a.i. ha ⁻¹ mefenoxam, and 8.9 g a.i. ha ⁻¹ difenoconazole, to avoid early-
665	season diseases and insects. Composite soil samples (i.e., 15 individual soil cores) were collected
666	at sowing from the 0-15 and 15-60 cm depth to quantify initial soil nutrient status (Table 1).
667	Weeds were controlled and insect pressure was not observed across the study.
668 669	Table 3-1. Initial soil fertility at Belleville and Hutchinson, Kansas for the 2017-18 and 2018-19 growing seasons. Soil test includes soil pH, Mehlich-3 extractable phosphorus (P), potassium

(K), calcium (Ca), magnesium (Mg), sodium (Na), ammonium-(NH₄-N) and nitrate- (NO₃-N)
nitrogen, chloride (Cl), sulfate-sulfur (SO₄-S), organic matter (O.M.) and cation exchange

672 capacity (C.E.C). Sampling depths were 0-15 cm and 15-60 cm.

	eupueny (C.1	2.C). Dum	ping	uep	uns w			15	00 CIII.					
_	Location	Depth	pН	Р	Κ	Ca	Mg	Na	NH ₄ -N	N03-N	Cl	S04-S	O.M.	C.E.C
		cm					- mg kg ⁻¹						%	Meq 100g ⁻¹
_							- 2017-18							
	Belleville	0-15	4.9	29	321	1465	204	13	2	20	2	3	2.7	25
		15-60	5.7	8	213	2450	300	28	2	14	2	2	2.5	23
	Hutchinson	0-15	6.0	77	218	1886	238	11	4	6	7	3	2.4	20
		15-60	6.7	55	214	2665	231	10	5	8	6	4	2.4	16
_							- 2018-19							
	Belleville	0-15	5.4	-		2056	296	17	3	1	8	3	3.1	28
		15-60	6.6	8	381	4022	555	58	5	4	9	3	2.4	26

Hutchinson	0-15	8.0	27	315 4746	163	35	3	17	8	3	2.9	26
	15-60	8.1	4	194 5202	132	128	4	13	12	13	2.2	28

673

#### **Treatment structure and experimental design** 674

675	Treatments	were arra	inged in a	a complete	e factorial	structure	established	1 in a s	split-pl	ot

676 design with four replications. Whole plots were assigned to six management intensities and sub-

677 plots were assigned to four winter wheat genotypes. Treatment combinations represented

678 stepwise increases in management intensity from a baseline reflecting the level of technology

679 adoption of an average producer in the region, and will hereafter be referred to as 'farmer

680 practice' (FP), 'enhanced fertility' (EF), 'ecological intensification' (EI), 'increased foliar

681 protection' (IFP), 'water-limited yield'  $(Y_w)$ , and 'increased plant productivity' (IPP) (Table 2).

682 Table 3-2. Description of the six management intensities evaluated in the current study. Farmer

683 practice (FP) was followed by stepwise additions of five inputs: enhanced fertility (EF),

ecological intensification (EI), increased foliar protection (IFP), water-limited yield potential 684

⁶⁸⁵ (Yw), increased plant productivity (IPP).

			Management intensity					
Treatments	FP	EF	EI	IFP	Yw	IPP		
Nitrogen Rate for Yield Goal (Mg ha ⁻¹ )	2.4	6.7	6.7	6.7	6.7	6.7		
In-furrow starter N, P, S, and Zn	No	Yes	Yes	Yes	Yes	Yes		
Foliar Fungicide Feekes GS10.5	No	No	Yes	Yes	Yes	Yes		
Foliar Fungicide Feekes GS6	No	No	No	Yes	Yes	Yes		
Foliar S, Zn, Mg, and B	No	No	No	No	Yes	Yes		
Seeding rate (million seeds ha ⁻¹ )	2.7	2.7	2.7	2.7	2.7	1.1		

686

The FP consisted of a seeding rate of 2.7 million seeds ha⁻¹ plus a N application at 687

688 Zadoks GS23-25 with a rate reflecting a yield goal of the ten-year county-level wheat grain yield

689 average (~2.4 Mg ha⁻¹). Nitrogen rate was determined considering the soil NO₃-N measured at

- sowing, potential N released from the organic matter, and a 40 kg ha⁻¹ applied N per Mg ha⁻¹ 690
- 691 grain yield goal (Leikam et al., 2003). Due to the residual soil NO₃-N carry over from the
- 692 previous growing season and N released from organic matter, N rate varied across environments.

693	The first increase in intensity was the enhanced fertility (EF) treatment, which included 112 kg
694	ha ⁻¹ micro essentials (MESZ; 13 kg N ha ⁻¹ , 45 kg P ha ⁻¹ , 11 kg S ha ⁻¹ , and 1 kg Zn ha ⁻¹ ) placed
695	in-furrow with the seed, and increased N rate for a 6.7 Mg ha ⁻¹ yield goal applied at Zadoks
696	GS23-25 in the spring. The fertilizer treatments aimed at increasing tiller and biomass
697	production. The N rate in this treatment was selected so that N was not a limiting factor based on
698	the long-term wheat yield potential of ~5.2 Mg ha ⁻¹ (Lollato et al., 2017). The next step was
699	ecological intensification (EI), which consisted of EF plus one fungicide application
700	(fluxapyroxad-26 g ha ⁻¹ , pyraclostrobin-171 g ha ⁻¹ , propiconazole-107 g ha ⁻¹ ) at Zadoks GS55.
701	Increased foliar protection (IFP) was the next step, consisting of EI plus the same fungicide
702	product and rate applied at Zadoks GS31. The aim of these fungicide applications was to protect
703	the green canopy cover of the crop (i.e., source) during the different stages of development. The
704	water-limited yield potential (Yw) treatment consisted of IFP plus micronutrients (81 g S ha ⁻¹ , 90
705	g Zn ha ⁻¹ , 67 g Mn ha ⁻¹ , and 2 g B ha ⁻¹ ) applied at Zadoks GS31. The increased plant
706	productivity (IPP) treatment consisted of $Y_w$ with a reduced seeding rate (1.1 million seeds ha ⁻¹ )
707	to explore whether a high resource availability scenario allows for reduced plant population
708	(Table 2). Wheat genotypes were selected based on their adoption by growers, adaptation to the
709	region, and contrasting performances in regional trials. The genotypes tested and their percent of
710	seeded area in central Kansas during 2020-21 were WB4303 (<1%), WB4458 (2.2%), WB-
711	Grainfield (5.5%) and Zenda (7.8%) (USDA-NASS, 2020a).
712	A pressurized CO ₂ backpack sprayer with a three nozzle boom was used to apply the N as
713	urea ammonium nitrate (UAN, 28-0-0) with a streamer nozzle (SJ3-03-VP); and foliar fungicide,
714	and micronutrients using a flat fan nozzle (XR11002) with a constant volume of 140 L ha ⁻¹ .

## 715 Measurements

716 Stand count was recorded in two linear meters per plot, three to four weeks after sowing, 717 and immediately prior to tiller initiation. Percent green canopy cover was measured 718 approximately at bi-weekly intervals from heading (Feekes GS10.1) until maturity (Feekes 719 GS11.4) from downward facing digital photographs from an area of about 1 m² processed using 720 Canopeo (Patrignani and Ochsner, 2015). Aboveground biomass was sampled from a one linear 721 row-meter area ( $\sim 0.19 \text{ m}^2$ ) from one of the center-rows of each plot same day of wheat harvest. 722 Samples were dried at 65°C until constant weight and aboveground biomass was measured. The 723 heads were counted and separated from the stover prior to threshing to remove the chaff from the 724 kernels. Grain weight was measured after threshing. The grain weight divided by the total 725 aboveground biomass weight including stover, chaff, and grain, determined the harvest index 726 (HI). A 1000 kernel weight was determined from a random kernel sub-sample. The ratio between total grain weight and 1000 kernel weight determined kernels m⁻²; and the ratio between kernels 727 728  $m^{-2}$  by heads  $m^{-2}$  determined kernels per head. The number of productive tillers per plant was calculated as the ratio of heads m⁻² and plants m⁻². Plots were trimmed prior to harvest to avoid 729 730 edge effects, and wheat was harvested using a small-plot Massey Ferguson 8XP combine. Grain moisture was measured at harvest and grain yield was corrected for 135 g kg⁻¹ water content. 731 732 Grain samples were cleaned to remove foreign material and subsampled twice and ran on a DA 7200 (Perten Instruments Inc., Springfield IL) for protein quantification (135 g kg⁻¹ water basis). 733 734 Weather data including precipitation, reference evapotranspiration (ETo), and maximum 735 and minimum temperatures, were collected from a station pertaining to the Kansas Mesonet 736 (Patrignani et al., 2020) located ~50 m from the experiments. Plant available water at sowing 737 was estimated using non-growing season precipitation and the soil's available water holding

738 capacity (Lollato et al., 2016). At each environment, the weather variables were averaged (Tmax, 739 Tmin) or accumulated (precipitation) for the entire growing season, as well as separated into four 740 distinct phases: fall (the period between sowing and December 31); winter (January 1 to March 741 31), critical period ([20-d prior to anthesis through 10 days afterwards (Fischer, 1985)], and grain 742 filling (10-d after anthesis through harvest). This sub-division intended to reflect (i) the 743 conditions surrounding sowing that affect crop establishment and fall tiller initiation; (ii) the 744 dormant period that can affect tillering and winterkill; and (iii) the yield determination period in 745 the spring, similar to previous reports in the region (e.g., Lollato and Edwards, 2015).

746 Statistical Analyses

747 Analysis of variance was performed using "ImerTest" in R software version 3.4.0 748 (Kuznetsova et al., 2017). Management, genotype, environment, and their interactions were fixed 749 effects, while block nested within environment and management intensity nested within block 750 were random effects (the latter accounted for the split-plot design). Pearson's correlation analysis 751 was performed in R using the "corrplot" package (Wei and Simko, 2017) to determine the degree 752 of linear association between variables. Because the data only derived from four environments, 753 we relaxed the assumptions of *p*-values for the correlation analysis to 0.15. For all other analyses 754 in this research, effects were considered significant at  $\alpha = 0.05$ .

We used the stability method (Eberhart and Russell, 1966) to further understand the genotypic effect on grain yield, productive tillers per plant, and grain protein concentration. This method consists of a linear regression of trait expression of each genotype versus an environmental index calculated as the mean trait expression of all genotypes at each environment minus the overall mean trait expression. Each management-by-environment combination was considered an environment (n = 24) (Ferrante et al., 2017; Lollato et al., 2021). The slope ( $\alpha$ )

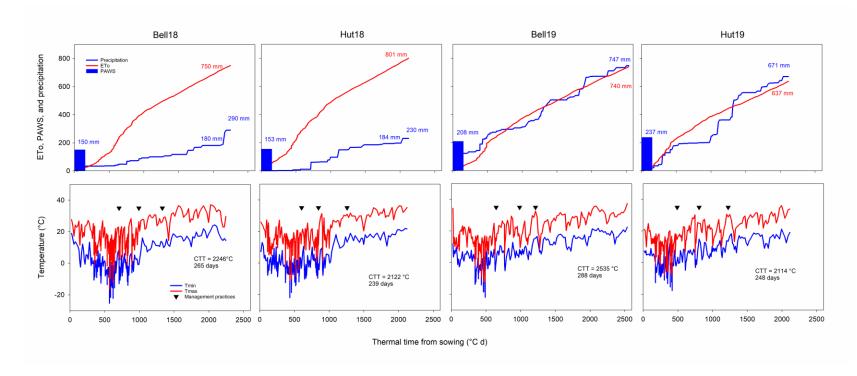
indicates whether the genotype has broad adaptability ( $\alpha = 1$ ) or adaptability specific to low ( $\alpha < 1$ ) or high- ( $\alpha > 1$ ) trait expression environments, and is associated with phenotypic plasticity (Sadras and Richards, 2014). The intercept ( $\beta$ ) is an estimate of the trait expression across environments; and a model goodness of fit index (i.e.,  $R^2$ ) quantifies stability.

The modulators of yield in response to management were quantified as the relationships between yield components and grain yield using linear regression for each management intensity, genotype, and environment (e.g. de Oliveira Silva et al., 2020b). Differences in grain yield between the FP and each management for each genotype were calculated and regressed for: (i) all environment and management practices by wheat genotype combinations (n = 96), (ii) on average of each management intensity (n = 24; 6 managements × 4 genotypes).

To understand the drivers of yield improvements in response to each step within the management intensification practices evaluated, we explored the relationships between the responsiveness of yield and the responsiveness of each yield component using linear regression (Slafer et al., 2014). Responsiveness was calculated as the ratio of each trait in a given management intensity over the same trait measured in the preceding management intensity, so that we could quantify the effects of each management addition (e.g., responsiveness calculated as EF over FP associated with changes resulting from improved fertility).

Finally, we evaluated the green canopy cover data to better interpret the effects of fungicide and plant density on grain yield in terms of source limitation (i.e., as a proxy to light interception). First, we calculated the linear slope of canopy cover dynamics between heading and maturity to detect whether the presence of foliar fungicides delayed canopy senescence, which would be indicated by a less negative slope. This comparison was made between

784	treatments EF and EI to isolate the effect of a single fungicide application at Feekes GS10.5.
785	Second, green canopy cover values at anthesis and their association with grain yield were
786	compared for the Yw and IPP treatments to detect whether grain yield limitations from lower
787	population could be explained by reduced green canopy cover.
788	Results
789	Weather conditions and associations with yield components
790	Growing season total precipitation ranged from 297 to 823 mm and corresponding
791	seasonal ETo ranged from 637 to 801 mm (Fig. 1). Environments in 2017-18 were characterized
792	by cold and dry fall, winter, and early spring, and a hot and dry late spring and early summer,
793	while environments in 2018-19 had warm and moist fall and cool and moist late spring and early
794	summer (Fig. 1), increasing disease pressure (i.e. stripe rust; Hollandbeck et al., 2019). Above
795	normal temperatures during the May and June in the 2017-18 environments (average
796	temperatures between 23 and 27 °C versus 15-23°C in 2018-19) accelerated and shortened the
797	reproductive crop development (duration of grain fill ranging from 27-29 days in 2017-18 and
798	from 33 to 52 days in 2018-19; Fig. 1), decreasing the yield potential of the crop. The contrasting
799	environments resulted in growing season length ranging from 239 to 288 days.



802 Figure 3-1. Weather conditions experienced during the winter wheat growing season at the four Kansas environments resulting from

- 803 two locations (Bell, Belleville; Hut, Hutchinson) and two growing seasons (18, 2017-18 season; 19, 2018-19 season). Upper row shows plant available water at sowing (PAWS), cumulative reference evapotranspiration (ETo) and precipitation, bottom row shows 804
- 805 maximum and minimum temperatures. Downward facing triangles show respectively dates for N application at Zadoks GS25,
- 806 fungicide and micronutrient application at GS32, and fungicide application at GS55. Inset values show cumulative ETo, precipitation,
- 807
- PAWS, cumulative thermal time between sowing and harvest (CTT), and season duration in days. Two cumulative precipitation
- 808 values are shown for 2018 environments as considerable rainfall occurred after the crop was mature.

Table 3 shows the correlations between weather variables during specific crop developmental stages and yield components and protein. Productive tillers plant⁻¹ related negatively with fall Tmin and positively with Tmin during the critical period. Harvest index related positively to winter Tmin. Heads m⁻² related negatively to Tmin and precipitation during the winter. The negative relation between winter Tmin and heads m⁻² or productive tillers plant⁻¹ reflects a delayed incorporation of the N fertilizer into the root zone until late spring in these environments, reducing the formation of spring tillers, Kernels head⁻¹ related positively to precipitation and water supply during the season, fall and grain filling precipitation, and duration of the grain filling period; and negatively to Tmax (growing season, and at each stage evaluated), and Tmin during grain filling. Kernel weight associated positively with winter Tmin and precipitation, as well as critical period precipitation. Grain protein concentration associated negatively with PAWS and critical period precipitation, and positively with grain filling Tmax and Tmin.

Table 3-3. Correlations between yield components and protein, averaged across four varieties and six management intensities, and daily average or cumulative values of environmental factors during specific crop development periods. Weather variables included in the analysis were minimum (Tmin, °C) and maximum (Tmax, °C) temperatures, cumulative precipitation (mm), plant available water at sowing (PAWS, mm), water supply (growing season precipitation plus PAWS, mm), and photothermal quotient (MJ m-2 C-1). Developmental periods evaluated were the fall (from sowing date until December 31),the winter (from January 1st until March 31st), the critical period (20-d prior to until 10-d after anthesis), and the grain filling period (from 10-d after anthesis until harvest).

Trait	Environmental factor	Period	r
Productive tillers plant ⁻¹	Tmin	Fall	-0.99
	Tmin	Critical period	0.89
Harvest index	Tmin	Winter	0.96
Heads m ⁻²	Tmin	Winter	-0.88
	Precipitation	Winter	-0.87
Kernels head ⁻¹	Tmax	Growing season	-0.99
	Precipitation	Growing season	0.97
	Water supply	Growing season	0.96
	Tmax	Fall	-0.89
	Precipitation	Fall	0.96

	Tmax	Winter	-0.91
	Tmax	Critical period	-0.86
	Tmax	Grain filling	-0.87
	Tmin	Grain filling	-0.9
	Precipitation	Grain filling	0.91
	Duration	Grain filling	0.86
Kernels m ⁻²	Tmax	Winter	-0.88
	Precipitation	Grain filling	0.9
Kernel weight	Tmin	Winter	0.9
	Precipitation	Winter	0.93
	Precipitation	Critical period	0.89
Protein	PAWS	Sowing	-0.94
	Precipitation	Critical period	-0.93
	Tmax	Grain filling	0.84
	Tmin	Grain filling	0.88

# Management effects on grain yield, yield components, and protein concentration

Across all sources of variation, mean grain yield ranged from 2.3 to 7.2 Mg ha⁻¹ (Fig. 2a). Environmental mean yield (across management and genotypes) ranged from 3.3 Mg ha⁻¹ in Hut18 to 5.6 Mg ha⁻¹ in Bel19, with overall greater yields in 2019 (5.43 Mg ha⁻¹) as compared to 2018 (4.28 Mg ha⁻¹). Mean yield across environments and genotypes with increasing management intensity was 4.02, 4.47, 5.37, 5.14, 5.39, and 4.82 for FP, EF, EI, IFP, Yw, and IPP, respectively. Mean grain yield for the genotypes was highest for WB4303 (5.19 Mg ha⁻¹), followed by Zenda (4.99 Mg ha⁻¹), WB-Grainfield (4.73 Mg ha⁻¹), and WB4458 (4.58 Mg ha⁻¹).

There were significant  $G \times E$  and  $M \times E$  interactions for grain yield, but no three-way interaction. General trends as related to the  $G \times E$  interaction were: (i) WB4303 was in the highest yielding group at all environments; (ii) Zenda was in the highest yielding group in three out of four environments; and (iii) WB4458 yielded well in dryer conditions (i.e., Hut18) but yielded poorly at the higher yielding environments (Bel19). General trends as related to  $M \times E$ interaction were: (i) the FP yielded similarly to other treatments only in one environment (Bel18); (ii) EF yielded higher from FP in three environments; (iii) increases in grain yield from foliar protection (i.e., EI) only occurred in environments with greater rainfall (i.e., Bel19 and Hut19); (iv) the addition of the early fungicide (i.e., IFP) did not increase yields compared to a single fungicide application later in the season; (v) wheat grain yield benefited from all the management practices combined (i.e., Yw) only in one environment (i.e., Hut19); and (vi) reducing plant population under an otherwise highly managed system had no effect on grain yield except in one environment (i.e., Hut19).

Further exploration of the significant interactions through the adaptability and stability indices suggested that wheat genotypes varied in stability and adaptability across the different yield environments (Fig. 2a). The wheat genotype WB4458 had the lowest slope ( $0.76 \pm 0.11$ ), suggesting that this genotype was the least adapted to high yielding environments; and was unstable with a high variation about the fitted line ( $r^2$ =0.69). Due to their slopes equal to one ( $1.17 \pm 0.09$ ,  $1.11 \pm 0.09$ , and  $0.95 \pm 0.09$  Mg ha⁻¹), the wheat genotypes Zenda, WB4303, and WB-Grainfield all showed broad adaptability and greater stability ( $R^2 > 0.83$ ).

With the exception of 1000 kernel weight, the yield components were not affected by the three-way interaction and followed the yield analysis, mostly reflecting  $G \times E$  and  $M \times E$  interactions. Briefly, management intensification tended to increase aboveground biomass as compared to the FP (magnitude: 18-100%), while the latter usually resulted in the greatest HI, while the magnitude of change was not large (16-46%). Expectedly, the IPP treatment had less plant density (149-163 plants m⁻²) as compared to other treatments (223-266 plants m⁻²) which resulted in more productive tillers per plant (3.18-4.97 versus 2.16-4.22 productive tillers plant⁻¹. The magnitude in the differences in heads m⁻² due to management and genotype was similar (38-72%) as those compared to changes in kernels head⁻¹ (39-64%). The results of kernels m⁻²

reflected those for grain yield while 1000 kernel weight was impacted by a  $G \times E \times M$  interaction.

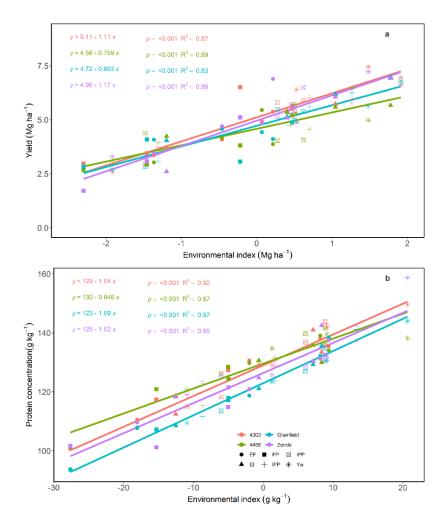


Figure 3-2. Wheat grain yield (a) and grain protein concentration (b) as affected by the environment index for each wheat genotype (WB4303, WB4458, WB-Grainfield, and Zenda). Environmental indices were calculated as the combination of environment (Bel18, Hut18, Bel19, and Hut19) and management practices (FP, EF, EI, IFP, Yw, and IPP).

A significant  $G \times E \times M$  interaction occurred for protein concentration. From an

environmental perspective, protein concentration was greatest (134 g kg⁻¹) in the driest environments (Hut18 and Bel18) as compared to the more moist environments (113-127 g kg⁻¹). From a management standpoint, protein concentration was lowest in the FP (range: 94-128 g kg⁻¹), with significant differences among genotypes at each environment. The greatest gain in grain protein concentration occurred when management was intensified from the FP to the EF (protein gain ranged from 2-36 g kg⁻¹) whereas, the other stepwise increases in management resulted in smaller (-28 to 17 g kg⁻¹) differences in grain protein concentration, with the lowest increases in protein concentration resulting from reductions in population and the highest values resulting from micronutrient application. From a genotypic standpoint, wheat genotypes tended to be broadly adapted ( $\alpha = 1$ ) across protein concentration levels, except for WB4458 which showed greater protein concentrations at lower protein-environments ( $\alpha = 0.84 \pm 0.07$ ; Fig. 2b). WB-Grainfield showed the lowest grain protein concentration across environments, followed by Zenda and WB4303, which all responded similarly to increases in the environmental index for protein concentration. Overall, the stability coefficient was greater for grain protein concentration ( $R^2 = 0.85-0.92$ ) than for grain yield. We note in passing that the slopes of the relationships between grain protein as affected by grain yield within environment were largely non-significant.

#### Yield component modulation of wheat grain yield

Across E, M, and G, aboveground biomass at maturity explained 77% of the variation in yield, showing a positive relationship (Fig. 3a). Although significant, a negative relationship of HI only explained 8% of the variation in yield (Fig. 3d). Across environments, differences in grain yield were dependent on differences in biomass accumulation (Fig. 3b) and independent of differences in HI (Fig. 3e). Following the same trend, differences in biomass accumulation among the different wheat genotypes under different management were also strongly related to differences in grain yield (Fig. 3c) as compared to HI (Fig. 3f). Increasing management intensity (the difference of each management practice to FP) significantly increased biomass accumulation, which resulted in a yield increase across environments (Fig. 3b, insert). Likewise, increased management intensity increased the responsiveness of biomass accumulation for wheat

genotypes, which increased grain yield (**Error! Reference source not found.**c, insert). Meanwhile, increased management intensity had limited effect on HI across environments or across genotypes (Fig. 3e, f, inserts).

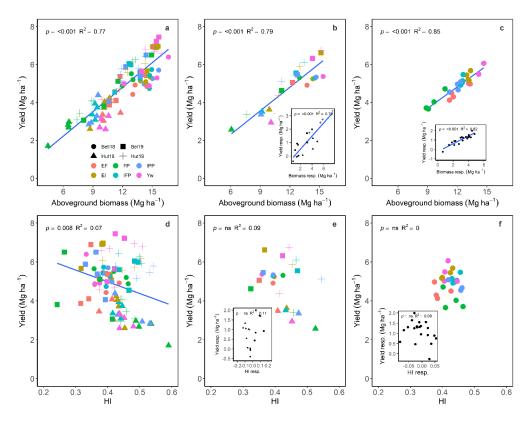


Figure 3-3. Relationship between yield and aboveground biomass (a-c) or harvest index (d-f) at maturity across environments, wheat genotypes, and management systems (n=96) (a,d), on average of each management for each environment (n=24; 6 management practices  $\times$  4 environments) (b,e), on average of each genotype for each environment (n=24; 6 management practices  $\times$  4 genotypes) (c,f). Inset graphs are the relationships between the responses of the variables to each management practices (difference between each management practice from the FP) averaged across either genotype for each management practice (n=20) or management for each environment (n=20) (c,f).

Kernels m⁻² had greater importance in increasing grain yields as compared to kernel weight (Fig. 4). Across E, M, and G, a positive relationship of kernels m⁻² explained 78% of the variation in grain yield (Fig. 4a). No relationship ( $R^2$ =0.02) between kernel weight and yield occurred across all sources of variation (Fig. 4d). Averaged across wheat genotypes, increasing management intensity increased grain yield through differences in kernels m⁻² (Fig. 4b), and yield responses to management practices were associated with increases in kernels m⁻² (Fig. 4b, insert). Similarly, averaged across management practices, wheat genotypes that had greater kernels m⁻² also had greater grain yield (Fig. 4c) and yield responses were dependent on the genotype's kernels m⁻² responsiveness (Fig. 4, inset). Following a different trend, increases in grain yield were independent of kernel weight for both management practices and wheat genotypes (Fig. 4d-f); however, increases in kernel weight due to management were associated with increased grain yield within each environment (Fig. 4e, inset). Differences in kernel weight within each genotype were not associated with increases in grain yield (Fig. 4f, inset).

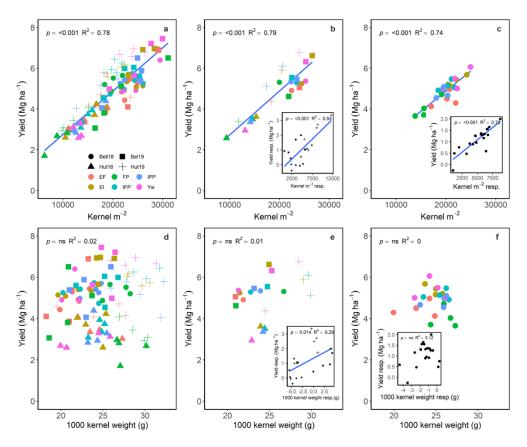


Figure 3-4. Relationship between yield and kernels  $m^{-2}$  (a-c) or 1000 kernel weight (d-f) across environments, wheat genotypes, and management systems (n=96) (a,d), on average each management for each environment (n=24; 6 management practices × 4 environments) (b,e), on each genotype for each environment (n=24; 6 management practices × 4 genotypes) (c,f). Inset graphs are the relationships between the responses of the variables to each management practices (difference between each management practice from the FP) averaged across either genotype for each management practice (n=20) or management for each environment (n=20) (c,f).

Heads m⁻² and kernels head⁻¹ both had a positive effect on grain yield (Fig. 5). Across E, M, and G, a positive relationship of heads m⁻² and of kernels head⁻¹ explained 19 and 39% of the variation in yield, respectively (Fig. 5a). Averaged across either management practices or wheat genotypes, grain yield differences were dependent on differences in heads m⁻² (Fig. 5b, c). Likewise, wheat genotype responsiveness to heads m⁻² resulted in positive differences in grain yield (Fig. 5c, insert). Interestingly, management practices resulting in greater number of kernels head⁻¹ also significantly affected yield (Fig. 5e) but there were no differences across genotypes (Fig. 5f). Likewise, the responsiveness of kernels head⁻¹ to management practices affected grain yield, with no differences among genotypes (Fig. 5f, inserts).

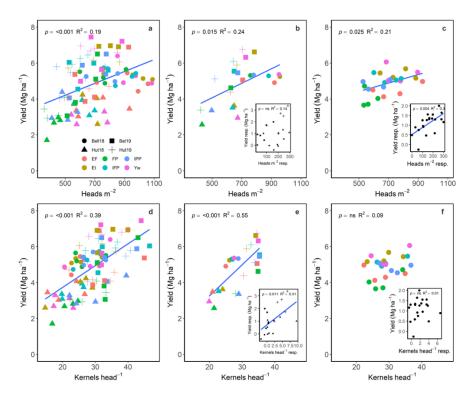


Figure 3-5. Relationship between yield and heads  $m^{-2}$  (a-c) and kernels head⁻¹ (d-f) across environments, wheat genotypes, and management systems (n=96) (a,d), on average each management for each environment (n=24; 6 management practices × 4 environments) (b,e),on each genotype for each environment (n=24; 6 management practices × 4 genotypes) (c,f). Inset graphs are the relationships between the responses of the variables to each management practices (difference between each management practice from the FP) averaged across either genotype for each management practice (n=20) or management for each environment (n=20) (c,f).

Each stepwise increase in management intensity modulated different yield components

(Fig. 6, first row). In the first step (i.e., addition of enhanced fertility to the FP), the responsiveness of yield ranged from 0.83 to 2.21 (mean:  $1.21 \pm 0.03$ ), and was positively linked to the responsiveness of biomass (range: 0.51-4.26, mean:  $1.27 \pm 0.06$ ), heads m⁻² (range: 0.53-2.75, mean:  $1.29 \pm 0.04$ ), and kernels m⁻² (range: 0.39-4.12, mean:  $1.34 \pm 0.06$ ). We also note that yield responsiveness was positively associated to grain protein responsiveness (range: 0.94-1.52, mean:  $1.12 \pm 0.01$ ) when fertility was the driving factor behind yield increases. When one fungicide application was added to the EF, yield responsiveness ranged from 0.77 to 1.82 (mean:  $1.14 \pm 0.02$ ) and associated positively to responsiveness of biomass (range: 0.61-1.90, mean:  $1.14 \pm 0.03$ ), harvest index (range: 0.48-1.72, mean:  $1.04 \pm 0.02$ ), and kernel weight (range: 0.79-1.58, mean:  $1.08 \pm 0.02$ ) (Fig. 6, second row). The addition of an early fungicide application to the EI had very weak relationships of yield responsiveness (range: 0.65-1.36, mean:  $1.0 \pm 0.01$ ) to the responsiveness of harvest index (range: 0.40-1.84, mean:  $1.08 \pm 0.03$ ) and kernel weight (range: 0.75-1.34, mean:  $1.03 \pm 0.01$ ) (Fig. 6, third row). The addition of micronutrients to the IFP treatment only suggested that responsiveness of harvest index (range: 0.62-2.35, mean:  $1.00 \pm 0.03$ ) associated with responsiveness of yield (range: 0.82-1.53, mean:  $1.05 \pm 0.01$ ) (Fig. 6, fourth row). Finally, when plant population was reduced from the Yw, responsiveness in yield (range: 0.61-1.21, mean:  $0.90 \pm 0.01$ ) was positively related to responsiveness of harvest index (range: 0.41-2.21, mean:  $1.02 \pm 0.03$ ) and kernel weight (range: 0.58-2.51, mean: 1.05  $\pm$  0.02), and negatively related to responsiveness of plants m⁻² (range: 0.32-2.75, mean:  $0.72 \pm 0.06$ ) and protein (range: 0.73-1.10, mean:  $1.00 \pm 0.01$ ) (Fig. 6, fifth row).

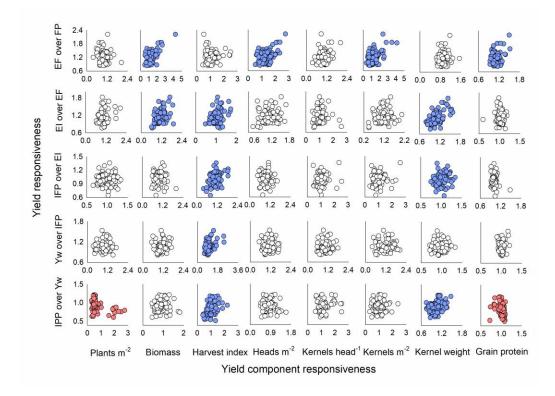


Figure 3-6. Winter wheat yield responsiveness and its relationship with responsiveness of yield components (plants m⁻², biomass, harvest index, heads m⁻², kernels head⁻¹, and kernel weight) and grain protein concentration for each step of management intensification evaluated in the current study. Responsiveness values were calculated as enhanced fertility (EF) over farmer's practice (FP)(first row); ecological intensification (EF) adding a fungicide application at Zadoks GS55 over EF (second row); increased foliar protection (IFP) adding a fungicide application at Zadoks GS31 to EI (third row); rainfed yield potential (Yw) adding micronutrients at Zadoks GS31 to the IFP (fourth row); and increased plant productivity (IPP) reducing seeding rate from Yw (fifth row). Circles in blue denote a significant positive and circles in red a significant negative relationship between variables at p < 0.05.

The slope of green canopy cover dynamics following fungicide application was

positively associated with grain yield for the selected treatments that allowed for a direct comparison between fungicide and non-fungicide application (EF versus EI) (Fig. 7a). Likewise, the difference between slopes of these treatments was highly positively related to grain yield difference (Fig. 7a, inset). Following a similar trend, green canopy cover values measured at anthesis for the Yw and IPP treatments related positively with grain yield (Fig. 7b), as did their differences (Fig. 7b, inset), suggesting that reduced plant population at the IPP could be restricting yields due to less green canopy coverage. We note that this dependency was genotype specific, as different varieties had different tillering abilities and adaptation to tillering environments; Zenda was the highest tillering variety across environments (mean: 3.81 productive tillers per plant) with even greater tillering expression in high tillering environments (slope of  $1.18 \pm 0.19$ ); which was followed by WB-Grainfield, WB4458, and WB4303 (3.5, 2.97, and 2.75 productive tillers per plant). While WB-Grainfield and WB4458 had wide adaptability of productive tillers, the ability of WB4303 to produce tillers decreased further as tillering environment increased (slope of  $0.66 \pm 0.13$ ).

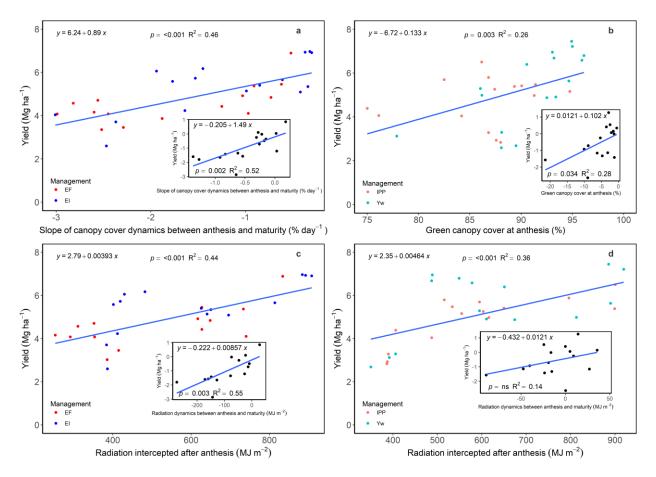


Figure 3-7. (a) Relationship between wheat grain yield and slope of the green canopy cover dynamics between anthesis and maturity for the enhanced fertility (EF) and and ecological intensification (EI) treatments across genotypes and environments. Inset panel in (a) shows the relationship between the difference in both grain yield and canopy cover dynamics slope between the two treatments. (b) Relationship between wheat grain yield and percent green

canopy cover values measured at anthesis for the 'yield potential' (Yw) and 'increased plant productivity' (IPP) treatments across genotypes and environments. Inset panel (b) shows the relationship between the difference between IPP and Yw for grain yield and percent green canopy cover. (c) Relationship between wheat grain yield and radiation dynamics between anthesis and maturity for the EF and EI treatments across genotypes and environments. Inset panel in (c) shows the relationship between the difference in both grain yield and radiation dynamics between the two treatments. (d) Relationship between wheat grain yield and radiation values measured at anthesis for the Yw and IPP treatments across genotypes and environments. Inset panel (d) shows the relationship between the difference between IPP and Yw for grain yield and radiation.

#### Discussion

We aimed to expand on the knowledge of the interactions  $G \times E \times M$  to identify opportunities for future yield increases for dryland winter wheat through yield component manipulation using Kansas, US, as a case-study. The average grain yield in the FP was 4.01 Mg ha⁻¹, which compared to 5.38 Mg ha⁻¹ in the highest yielding treatment (Yw), resulting in a yield gap of 1.37 Mg ha⁻¹. Similar yield levels and yield gaps have been reported for the area under intensified management (Jaenisch et al., 2019; de Oliveira Silva et al., 2020b), confirming the opportunity to increase current yields.

The management comprised of enhanced fertility and one foliar fungicide application around heading (i.e., EI) resulted in average yield of 5.36 Mg ha⁻¹, which was similar to the Yw treatment though the latter received an additional fungicide application and micronutrients. Thus, these additional practices might not be necessary to fill the bulk of the yield gap, although this is environment-dependent (i.e. Hut19). Additionally, in environments where water deficit limited the yield potential of the crop, EF was sufficient to maximize grain yield, precluding application of foliar fungicides. Furthermore, in one dry environment with high NO₃-N carryover (Bell18), the FP was enough to maximize grain yield. While evaluating the economics of intensified management was beyond the scope of this research, these findings support the idea that managing to reach the yield potential might not be economical (Lobell et al., 2009). Wheat genotypes responded differently to increased yielding conditions but similarly to management (Fig. 2), suggesting that selecting wheat genotypes either with performance specific to the most re-occurring environment in a given region or with broad adaptability seems more promising than genotype-specific management. We note, however, that the lack of significant G  $\times$  M interaction in this research might be due to a small sample size, as previous research with larger sample size showed significant G  $\times$  M (Thompson et al., 2014).

#### Management practices and their effects on wheat yield components

Our results align well with previous literature reporting that, across all sources of variation, wheat grain yield relates closely to aboveground biomass and kernels m⁻², and is relatively independent of harvest index and kernel weight (de Oliveira Silva et al., 2020; Slafer et al., 2014; Ferrante et al., 2017). However, an original contribution of our research is the detailed yield responsiveness analysis and its relation to yield component responsiveness, for each individual step in management intensification (Fig. 6). To our knowledge, this has not been previously attempted in the existing literature of wheat response to management intensification. From this analysis, it was clear that yield responsiveness of 1.21 and 1.14) as compared to the remaining practices (mean responsiveness of 0.9-1.0). The added fertility drove improvements in yield mostly through greater biomass, heads m⁻², and kernels m⁻²; while the added fungicide modulated yield through biomass, harvest index, and kernel weight (Fig. 6). All the remaining practices that had little effect on yield only modulated harvest index and kernel weight.

The modulation of yield thought kernels m⁻² driven by the added fertilizer (EF) is justified as both in-furrow P fertilizer and N fertilizer increases tiller initiation (Spiertz, 1983; Rodríguez et al., 1999), and N fertilizer can reduce floret abortion (Ferrante et al., 2010;

González et al., 2011). Tiller production determines the potential heads m⁻² and floret development determines the potential kernels head⁻¹. Both yield components interact with environmental conditions to determine final kernels m⁻², which was highly positively related to yield (Fig. 4). Thus, N availability has to meet the requirements for both of these processes during the growing season as untimely N deficiency can result in floret abortion and reduce kernels m⁻², potentially reducing yield. Nitrogen rates offer an opportunity for increased yields (Lollato et al., 2021), especially in favorable seasons where the crop can capitalize on a greater yield potential (Cruppe et al., 2017; Lollato et al., 2019a). Expected N uptake based on yield potential can serve as a guide for managing N rates in the season (Leikam et al., 2003); and for wheat, a recent synthesis of global literature suggested that N uptake ranges from ~20 to 400 kg N ha⁻¹ (de Oliveira Silva et al., 2020a). Thus, matching N availability with the time when the potential kernels m⁻² are determined (i.e., early stem elongation) results in yield increases as grain number is the dominant driver of yield (Borrás et al., 2004; Slafer et al., 2014). We also note that this developmental stage coincides with the greatest N uptake rate by the crop, which increases under intensive management (de Oliveira Silva et al., 2021).

Kernels m⁻² and kernel weight are affected by complex interactions among many environmental factors in the late reproductive stages. Our results supports available literature that suggests that kernels m⁻² is a coarse regulator of wheat yield as compared to kernel weight (Borrás et al., 2004; Slafer et al., 2014); which is justified as each individual kernel has a narrow range in size (Sadras, 2007), thus greater increases in grain yield come from filling more kernels (Borrás et al., 2004)[.] We note, however, that increases in kernel weight through management associated positively with yield (inset, Fig. 4e), in particular through the application of foliar fungicides (Fig. 6). These findings agree with previous reports of highly managed wheat in the

US Great Plains (Lollato and Edwards, 2015; Jaenisch et al., 2019) and in higher yielding wheat growing regions (Lynch et al., 2017)[;] suggesting that kernel weight might, in some conditions, partially explain increases in yield.

Foliar diseases can occur prior to anthesis and last throughout the grain filling period, coinciding with a period of significant demand for photosynthesized resources by the developing grain (i.e., a very strong sink; Fischer, 1985). These foliar diseases decrease the green leaf area of the plant (Schierenbeck et al., 2019), reducing radiation interception and radiation useefficiency (Schierenbeck et al., 2016), and ultimately decreasing the source of assimilates to the developing sink. This mismatch between a reduced assimilate supply (i.e., source) during a period with large demand can cause kernel abortion and reduce yield (Ferrante et al., 2010; González et al., 2011). Foliar fungicides can also increase kernel weight under severe disease infestations which can reflect increases in grain yield (Cruppe et al., 2021), though this increase is environment-specific (Lynch et al., 2017). Wheat kernel weight is sensitive to environmental stresses (e.g., heat or drought) between booting to anthesis when carpel (which will turn into the external grain structures) growth increases rapidly (Calderini et al., 2001), and from anthesis to maturity during kernel weight determination (Bergkamp et al., 2018). Foliar diseases during these developmental stages can reduce kernel weight, which would result in yield reductions as compared to wheat yields that received a foliar fungicide (Fig. 4e, insert; Fig. 6). Similarly, increases in kernel weight have been associated with kernel-filling rate, and foliar diseases can reduce the rate of fill due to their competition for assimilates (Simmons et al., 1982).

Foliar fungicides increase grain yield by protecting the upper canopy and spikes, which supply a large portion of the carbohydrates that determine yield (Rawson et al., 1983) and can increase kernels m⁻² (Brinkman et al., 2014). The prolonged green leaf area maintained through

fungicides also allow for a longer duration of active photosynthesis, ultimately increasing grain yield (Joshi et al., 2019; Nehe et al., 2020), which was shown in the current research as a more negative slope of the green canopy cover dynamics after anthesis in the treatments not receiving foliar fungicides (Fig. 7). The positive relationship between the slope of canopy cover and grain yield also suggests that treatments not receiving foliar fungicides were, at least to some extent, source-limited, which was also evidenced by the greater grain protein concentration of treatments receiving foliar fungicides. Further evidence for this potential source limitation is shown in the inset of Fig. 4e, in which increases in kernel weight through management associated positively with yield increases. However, we note that large reductions in the green leaf area were needed to cause modest reductions in yield (Fig. 7), likely because wheat is mostly sink-limited and very efficient in translocating stem reserves to the developing kernels (Borrás et al., 2004). Even though foliar fungicides applied around anthesis have increased wheat yield and reduced yield gap in the region (Thompson et al., 2014; Jaenisch et al., 2019), producers may be reluctant to apply it consistently due to a high unpredictability in environment (Couedel et al., 2021) and inconsistencies in yield response (Cruppet al., 2021).

The evaluation of a reduced population under an otherwise highly managed system (IPP) suggested that yield responsiveness was negatively related to responsiveness in plants m⁻² (Fig. 6); reflected on the yield reduction of IPP as compared to Yw (4.82 vs 5.39 Mg ha⁻¹). Thus, it seems like the opportunity to reduce plant populations in dryland conditions for winter wheat might not be as evident as that for irrigated spring wheat in low latitudes (Fischer et al., 2019), likely due to the unpredictability of conditions for tillering in the fall. Nonetheless, we showed that there was a large genotypic component of tillering plasticity that might be further explored in this region. Tillering allows wheat plants to compensate for a low plant density, with greater

opportunities in higher yielding environments (Bastos et al., 2020), which was shown in this study with the IPP producing more tillers than other treatments. Tillering plasticity regulates the ability of a given genotype to tiller in different environments, which also interacts with seeding rate. Thus, a wheat variety with high tillering plasticity such as Zenda has the ability to produce more productive tillers at reduced seeding rates and modulate yield through harvest index and kernel weight (Fig. 6). Evidence for other cereals suggests that high phenotypic plasticity of tillering can result in increased panicle weight under low seeding rates (Kikuchi et al., 2017). Thus, selecting wheat genotypes for increased tillering capacity through conventional breeding could help reduced the risk associated with reduced seeding rates (Fischer et al., 2019), which aligns with the early concept (Fasoula, 1973) and more recent developments (Tokatlidis et al., 2006; Fasoula, 2013) of selecting per plant yield under nil competition.

Finally, grain protein concentration was largely unaffected by grain yield when evaluated by  $G \times E \times M$  (only 6 out of 96 yield-protein relationships were significant), which contradicts a plethora of literature suggesting that both variables are negatively related (e.g., Simmonds, 1995; Triboi et al., 2006; and citations therein). Our results showed that increases in protein at greater yield resulted from a greater supply of nutrients as compared to the baseline FP treatment (Fig. 6), as yield was unrelated to protein at the other individual steps in management intensification. The greater supply of nutrients would preclude protein dilution at greater yield levels (Barneix, 2007; Lollato et al., 2021).

## Genotypic characteristics to increase grain yield

Wheat genotypes responded to the environment differently but not to management practices or to the interaction of management and environment. Thus, our findings suggest that wheat genotypes have to be adapted to specific re-occurring environmental conditions or broadly

adaptable, and have other desirable agronomic traits such as high yield potential (Ferrante et al., 2017), disease resistance (Serrago et al., 2011), heat or drought stress tolerance (Bergkamp et al., 2018), to match those commonly experienced in the environment where the genotype is grown. While the lack of  $G \times E \times M$  in our data might result from the limited number of observations (i.e., four environments), previous research in the region also only found weak evidence for  $G \times E \times M$  (p = 0.14; de Oliveira Silva et al., 2020b).

The wheat genotype WB4303 was better adapted to higher yielding environments and responded to increased environmental index by producing more kernels m⁻², which was highly correlated to increases in grain yield (Fig. 4). These findings agree with those for other growing regions where modern genotypes were more adapted to higher yielding environments and led to the hypothesis that the growers use older genotypes in their lowest yielding soils and modern genotypes in their highest yielding soils (Ferrante et al., 2017). While we did not test this hypothesis in Kansas, our findings suggest that this could be a promising strategy as the older genotype WB4458 was more adapted to lower yielding environments, though further research is needed on this topic. For producers, selecting newer released genotypes might offer opportunities to capitalize on their ability to capture greater yields in higher yielding environments (Slafer and Andrade, 1993; Perronne et al., 2017; de Oliveira Silva et al., 2020b) despite the challenge of finding information on new genotypes coupled with their limited lifespan (Perronne et al., 2017).

## Conclusions

The results from this research confirmed a large yield gap that can be fulfilled through management, while highlighting the opportunity to modulate different yield components through specific management practices in a stepwise increase in management intensification. Overall, the results reinforced the need for an integrated wheat management based on crop scouting, as

environmental conditions determined which management practices resulted in the greatest grain yields: In higher yielding, wet environments, increased fertility and one application of foliar fungicide at anthesis maximized grain yields; while in lower yielding, dry environments, increased fertility alone was sufficient to maximize grain yields and the increased fertility was only warranted over farmer's practice when the soil did not have enough fertility at sowing.

This research also confirmed the important role of aboveground biomass and kernels m⁻² in maximizing grain yield at the expense of harvest index and kernel weight. Likewise, management of fertility led to yield modulation through improved biomass and kernels m⁻². We note, however, that independent steps in management intensification impacted different yield components, and a fungicide application around Zadoks GS55 had an important impact on grain yield partially through biomass, kernel weight, and maintenance of green canopy cover longer into the grain filling period. While the positive relation between green canopy cover during grain filling and yield suggests some potential for source-limitation, large changes in green canopy cover were needed to cause modest changes in yield.

The reduction of seeding rate in an otherwise highly managed system provided varying results and seems to limit yield through less green canopy cover at anthesis, harvest index, and kernel weight. Thus, future research could focus on optimizing seeding rates and identifying cultivars with increased phenotypic plasticity to maximize winter wheat yields within a highly managed system.

## Acknowledgements

This is research contribution no. 22-001-J from the Kansas Agricultural Experiment Station. We acknowledge Kavan Mark for the leadership with field operations and data

collection. Likewise, we would like to thank the visiting scholars from the Winter Wheat

Production team for all their hard work in data collection.

# **Conflict of interest**

The authors declare no conflict of interest.

## Funding

This research was partially sponsored by the Kansas Wheat Commission, Kansas

Agricultural Experiment Station, and the Kansas Cooperative Extension Service.

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# Chapter 4 - Nutrient use efficiency and co-limitation for nitrogen and sulfur in bread winter wheat

# Highlights

- We investigated the interactions of nitrogen, sulfur, genotypes, and environments and their effects on wheat grain yield.
- Significant environment  $\times$  N  $\times$  S and environment  $\times$  genotype  $\times$  N affected grain yield
- Nitrogen and sulfur limitation increased the wheat yield gap.

# Abstract

Quantifying the interactions of nutrients in wheat production are essential to reduce the yield gap. Nitrogen and S deficiencies (individually or in combination) reduce wheat yields and increase the yield gap. Our objectives were to quantify the colimitation of N and S in wheat in Kansas. We established an experiment with three N rates, four S rates and three genotypes in a split-split- plot design across eight site-years. Grain yields ranged from 0.9 to 5.9 Mg ha⁻¹ across all treatment combinations. Grain yield increased with increasing N rate at all locations; however, the application of S increased grain yield at two locations. Linear plateau models determined N and S uptake reached maximum uptake at 120 and 7 kg ha⁻¹, respectively and those uptake levels resulted in a yield value of 5.7 Mg ha⁻¹ (Yp). As expected, NUE decreased with increases in N rate and SUE decreased with increases in S rate. The colimitation (Cns) determined the optimal N:S ratios for stover and grain to be 16.4 and 17.3, respectively. The N and S rates had significant effects on the NSI and SSI.

# Introduction

Nitrogen (N) is an essential nutrient driving the growth and development of plants (Sinclair and Horie, 1989). At historical time scales, N has been the most limiting nutrient to crop yields (Sinclair and Rufty, 2012). Consequently, the management of N fertilizer and its role in yield determination has been extensively researched. In particular for wheat (*Triticum aestivum* L.), previous research attempted to determine optimal rates (Jaenisch et al., 2019; Lollato et al., 2019a, 2021), placement (Schlegel et al., 2003; Gardner and Drinkwater, 2009; Subbarao et al., 2013), timing (Mahler et al., 1994a; Gardner and Drinkwater, 2009; Smith et al., 2019; Lollato et al., 2021), and sources (Christensen and Meints, 1982; Mahler et al., 1994b; Grant et al., 2001). Nitrogen requirement for wheat is estimated as an approximately 40 kg ha⁻¹ of N to produce one Mg ha⁻¹ of wheat grain maintaining c.a. 12.5% protein concentration (Leikam et al., 2003).

Nitrogen use efficiency is defined as grain yield per unit of available N in the soil (Moll et al., 1982). Globally, NUE for cereals crops is c.a. 33% (Raun and Johnson, 1999), and for wheat it seems to range from 22-30 kg kg⁻¹ (Gaju et al., 2011; Dorsey, 2014). Nitrogen uptake efficiency (i.e., the ratio between N uptake and N available) and N utilization efficiency (i.e., the ratio between N uptake) determine NUE (Janssen, 1998). Nitrogen use efficiency is affected by agronomic management practices such as crop rotation (Timsina et al., 2001), genotype selection (Hawkesford, 2017), N management (de Oliveira Silva et al., 2020a), environmental conditions such as water availability (Lupini et al., 2021) and radiation (Salvagiotti and Miralles, 2008) and, of particular importance to the current study, the availability of other nutrients such as sulfur (S) (Duncan et al., 2018).

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Positive agronomic responses in commercial crops to the addition of S fertilizer seem to be more apparent in recent years (Girma et al., 2005; Camberato and Casteel, 2010). The two main reasons for the increased S response are the decline in organic matter in cultivated soils as compared to native vegetation (Lollato et al., 2012) and the decrease in S dioxide deposition in the rainfall, in particular in the U.S. due to the Clean Air Act which removed sulfate from coal fired plants, declining S emissions in as much as 30% (Ceccotti, 1996). Consequently, S deposition from rainfall decreased from 13.5-19 kg ha⁻¹ in 1980 (Barrie, 1984) to only 4 kg ha⁻¹ in 2014 (National Atmospheric Deposition, 2014).

Similarly to N, S is also an essential element to crops, playing variety of roles within the plant ranging from the synthesis of amino acids (Coleman, 1966) to the production of chlorophyll (Duke et al., 1986). Sulfur use efficiency (SUE) is defined as grain yield per unit of available S in the soil (Moll et al., 1982). For cereal crops, SUE was estimated as 18% worldwide (Aula et al., 2019) and the reported SUE range for wheat is ~11-13% (Singh et al., 2014). Wheat requirement for S are lower than for N, with ~10 kg S ha⁻¹ being required for one Mg ha⁻¹ grain (Leikam et al., 2003). Not only can S deficiency reduce yield (Withers et al., 2001; Salvagiotti and Miralles, 2008), it is also important in the end use quality of wheat (Zhao et al., 1999a; Wilson et al., 2020) as S application can increase the bread loaf volume (Jarvan et al., 2008), dough extensibility (Zhao et al., 1999b), and reduce asparagine concentration (Wilson et al., 2020).

In wheat, S seems to interact with N to determine NUE. Previous research demonstrated that the application of S improved N use efficiency in wheat by increasing soil N recovery rather than increasing N utilization efficiency (Salvagiotti et al., 2009). Sulfur application allowed for the production of more shoot biomass which increased root biomass and allowed for greater soil exploration and uptake of N (Salvagiotti et al., 2009). Similarly, other research demonstrated that S application increased soil N recovery by ~40% (Tabak et al., 2020), high N rates increased and S concentration in the grain (Randall et al., 1981a). Further research demonstrated that N application increased both the N and S concentrations in the grain, but S application had no effect on the baking quality of wheat in S sufficiency environments (Randall et al., 1990). Nitrogen and S interactions occurred for wheat grain yield the first year wheat was planted but the interactions were not measured in later wheat crops due to the mineralization of S from organic matter and applications of fertilizer (Ramig et al., 1975). Despite these previous efforts to untangle N and S impacts on wheat performance, to our knowledge, to our knowledge, there have been no attempts to understand this interaction from a co-limitation perspective.

Sterner and Elser (2002) developed a co-limitation and stoichiometry theory to understand the interaction of plant and animals in an ecosystem. In their case, the limitation of plants within the ecosystem will result in an abundance of animals initially (co-limitation is equal to zero). However, as time passes, animals will be decreased by the reduction in plants, and the co-limitation value will increase until both plants and animals are equally limiting to the ecosystem's productivity. The same theory can be applied to agricultural experiments (Sadras, 2004). Cossani and Sadras (2018) used this co-limitation theory to disentangle the interactions of water and N on wheat grain yield. The stoichiometry theory has used to quantify the optimal N:S ratios in maize (Carciochi et al., 2020), N:P:S ratios in maize (Salvagiotti et al., 2017), N:P ratios in cereal, grain legume and oilseed crops (Sadras, 2006), and water and N for wheat (Sadras, 2005). Nutrient stoichiometry determined an optimal N:S level of 12.2 in the stem of soybeans (*Glycine max* (L.) Merr.), suggesting that the stem was a better indicator of S deficiency as compared to the leaves (Divito et al., 2016). In maize (*Zea mays*), shoot N:S ratios were optimal at 9.3-9.8 (Carciochi et al., 2020) though it seems to depend on the plant part evaluated [e.g., Pagani and Echeverría (2011) suggested an optimum N:S ratio of 14-16 in maize leaves]. In wheat, Maeoka et al. (2020) determined whole plant uptake of a N:S ratio of 15.4. Randall et al. (1981) and Byers et al. (1987) determined maximum wheat yield to be achieved at a N:S ratio of 15-17. The minimum requirement of N:S ratio has been reported at 12:1 and can be as high as 20:1, beyond which S becomes deficient (Camberato and Casteel, 2010).

In the current research, our overarching aim was to further the current understanding about the interaction of and co-limitation between N and S on wheat productivity, using winter wheat in Kansas as a case-study. To do this, we applied the co-limitation theory combined with a linear-plateau model of wheat yield potential as determined by N and S uptake to determine N and S limitation effects on the nutrient use efficiencies across a range of N and S rates, wheat genotypes, and environments.

#### **Materials and Methods**

#### **Experimental environments and agronomic management**

Field experiments were established in eight Kansas environments resulting from the combination of locations across three years, namely: Ashland Bottoms (39.14°N, -96.63 °W; 300 m) during the 2018-19 and 2019-20 winter wheat growing seasons (Belvue silt loam soil); Belleville (39.81°N, -97.67°W; 471 m) during the 2017-18 and 2019-20 winter wheat growing seasons (Crete silt loam soil); Manhattan (39.22°N, -96.59°W; 311 m) during the 2017-18 season (Kahola silt loam soil); Hutchinson (37.93°N, -98.03°W; 468 m) during the 2018-19 and 2019-20 seasons (Funmar-Taver loam soil); and Viola (37.34°N, -97.67°W; 418 m) during the 2019-20 season (Milan loam soil). All experiments were conducted under rainfed conditions. Winter wheat was sown using no-tillage practices following a previous soybean crop at all environments. Plots were established using a Great Plains 606 no-till drill (7 rows spaced at 19 cm) with plot dimensions of  $1.3 \times 9.1$  m. Seed was treated with 6.9 g a.i. ha⁻¹ thiamethoxam, 1.4 g a.i. ha⁻¹ mefenoxam, and 8.9 g a.i. ha⁻¹ difenoconazole, to avoid early-season disease and insect damage. Composite soil samples consisting of 15 individual soil cores were collected at sowing from the 0-15 and 15-60 cm depth to quantify initial soil nutrient status (Table 1). Weeds were controlled using pre- and post-emergence herbicides. Insect pressure was not observed in this study. Foliar fungicide (fluxapyroxad-26 g ha⁻¹, pyraclostrobin-171 g ha⁻¹, propiconazole-107 g ha⁻¹) was applied at anthesis (Zadoks GS55) at all locations so that variety-specific disease tolerance was not a confounding factor. Plots were trimmed prior to harvest to avoid edge effects, and wheat was harvested using a small-plot Massey Ferguson 8XP combine. Grain moisture was measured at harvest and grain yield was corrected for 135 g kg⁻¹ water content.

Each experiment was located within ~12 km of a weather station from the Kansas Mesonet (Patrignani et al., 2020), from which we collected daily values for precipitation, reference evapotranspiration (ETo), maximum (Tmax) and minimum (Tmin) temperatures, and solar radiation. The weather data was either averaged (Tmin and Tmax) or accumulated (precipitation, ETo, and solar radiation) for the growing season and for important periods within the growing season, including the fall, winter, critical period (20-d before to 10-d after anthesis) and grain filling (10-d after anthesis to harvest).

Table 4-1.Initial soil fertility at the studied environments. Soil test variables includes soil pH, Mehlich-3 extractable phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), ammonium-(NH4-N) and nitrate- (NO₃-N) nitrogen, chloride (Cl), sulfate-sulfur (SO₄-S), organic matter (O.M.) and cation exchange capacity (CEC). Sampling depths were 0-15 cm and 15-60 cm.

Environments	Depth	pН	Р	K	Ca	Mg	Na	NH ₄ -N	N0 ₃ -N	Cl	S0 ₄ -S	O.M.	CEC	Sand	Silt	Clay
Year	cm		(mg kg ⁻¹ )	) (mg kg ⁻¹	) (mg kg ⁻¹ )	%	Meq 100g ⁻¹	%	%	%						
2017-18																
Belleville	0-15	5.6	47	510	2032	295	15	6	8	6	2	2.9	26	16	56	28
	15-60	6.3	24	517	3372	498	40	5	5	6	2	2.5	31	10	50	40
Manhattan	0-15	7.1	21	233	5033	323	21	3	5	6	2	4.2	29	16	52	32
	15-60	7.7	11	239	6495	301	16	5	4	5	1.2	3.1	36	10	52	38
2018-19																
Ashland Bottoms	0-15	6.2	45	179	1129	138	9	3	3	4	3	1.5	10	34	52	14
	15-60	6.6	27	116	1284	144	8	3	1	3	1	1.5	8	37	48	15
Hutchinson	0-15	5.3	50	228	1018	185	8	3	10	4	4	1.8	17	14	60	26
	15-60	6.4	11	151	1920	330	17	3	3	5	2	1.8	16	10	54	36
2019-20																
Ashland Bottoms	0-15	5.9	46	263	1279	141	9	4	6	3	1	1.8	13	34	54.00	12
	15-60	6.8	22	181	1674	161	10	3	3	3	1	1.4	10	26	60.00	14
Belleville	0-15	5.5	73	603	1876	237	13	5	10	6	2	3.5	23	14	64.00	22
	15-60	5.9	48	616	2741	368	24	2	7	9	2	2.9	27			
Hutchinson	0-15	5.4	89	426	1959	348	9	4	8	4	4	2.8	24	28	44	28
	15-60	6.2	46	369	2779	506	15	5	6	4	5	2.2	26	26	40	34
Sumner	0-15	5.1	82	116	852	234	16	3	6	5	3	1.6	18	50	32	18
	15-60	5.7	40	146	1572	446	43	3	4	4	2	1.5	21	44	32	24

#### **Treatment structure and experimental design**

The experiment was arranged in a  $3 \times 3 \times 4$  split-split-plot design with four replications. Three wheat genotypes were assigned to whole plots, three N rates were assigned to sub-plots, and four S rates were assigned to sub-sub plots. The three genotypes were selected based on being representative of producer's choices in the region [their seeded area in central Kansas during the 2019-20 season were 9.7% for SY Monument, 2.6% for LCS Mint, and 6.4% for Zenda (USDA-NASS, 2020)[]] and for their differences in N uptake levels while maintaining similar N utilization efficiency (de Oliveira Silva et al., 2020b). Nitrogen was applied as urea ammonium nitrate (28N-0-0) and rates consisted of 50%, 100%, and 150% of KSU recommendations for a 4.0 Mg ha⁻¹ yield goal. The actual amount of N applied depended on the initial soil NO₃-N in the 0-60 cm profile (Table 2). Sulfur was applied as ammonium thiosulfate (12-0-0-26S) at 0, 11, 22, or 45 kg S ha⁻¹. The combination of available N at sowing plus N fertilizer rate, and available S at sowing plus S fertilizer rate, resulted in available N:S ratios to vary across locations and treatments. A pressurized  $CO_2$  back sprayer with a three-nozzle spray boom was used to apply all fertilizer treatments. The specific streamer nozzles (SJ3-02-VP - SJ3-05-VP) varied due to the change in N and S rates. The N and S were applied in combination for specific treatments and application occurred at Zadoks 30 (Zadoks et al., 1974).

Table 4-2. Sowing, harvest, and treatment application dates at the nine studied environments. Nitrogen was applied at rates consisted of 50%, 100%, and 150% of KSU recommendations for a  $4.0 \text{ Mg ha}^{-1}$  yield goal (YG). The actual amount of N applied depended on the initial soil NO₃-N in the 0-60 cm profile

Year	Location	Sowing date	N rate for	N rate for	N rate for	Top-dress	Fungicide	Harvest
			50% YG	100% YG	150% YG	N and S at	application	
			(kg N ha ⁻¹ )	(kg N ha ⁻¹ )	(kg N ha ⁻¹ )	Zadoks 30	Zadoks 55	
2017-18	Belleville	10/17/2017	59	107	156	03/08/2018	05/24/2018	06/24/2018
	Manhattan	10/16/2017	56	104	152	03/01/2018	05/21/2018	06/22/2018
2018-19	Ashland Bottoms	11/01/2018	82	152	222	03/22/2019	05/22/2019	06/28/2019
	Hutchinson	11/02/2018	68	125	181	03/18/2019	05/22/2019	07/04/2019

2019-20	Ashland Bottoms	10/25/2019	72	131	200	03/06/2020	05/19/2020	06/26/2020
	Belleville	10/16/2019	48	85	123	03/25/2020	05/29/2020	07/05/2020
	Hutchinson	10/29/2019	56	102	147	03/11/2020	05/14/2020	06/17/2020
	Sumner	10/24/2019	74	138	203	03/12/2020	05/04/2020	06/15/2020

# **Biomass sampling**

Shoot biomass was sampled from a one linear row-meter area (~0.19 m²) from one of the center-rows of each experimental unit in the same day of wheat harvest. Samples were dried at 65°C until constant weight before shoot biomass was weighted. Shoot biomass was partitioned into heads and stover. The heads were threshed to separate the grain from the chaff, and grain and stover were ground to pass a 2-mm sieve, and sent separately to the laboratory for nutrient concentration analysis. Nitrogen and S concentration in plant tissue were determined by combustion using the inductively coupled plasma (ICP) (Tabatabai, 2018).

#### Calculations

First, we divided the range of N uptake in nine different intervals and selected the highest value within each division. Next, we fit independent linear plateau models for shoot N and S uptake (independent variables) versus grain yield (dependent variables) on the nine values and forced the intercept to zero. The linear plateau model was built using the R package "nlsLM" (Padfield and Matheson, 2020). The linear plateau model consisted of: y =b*x if x < c and y = b*c for  $x \ge c$ . In this equation, "b" is the slope during the linear phase, and "c" is the value of x at which the linear model reaches a plateau, equivalent to the yield potential (Yp). The Yp is the maximum yield per unit of N or S uptake. Next, the boundary function was used to estimate the Yp for each level N and S uptake until the linear plateau model reached a maximum. At the break point of the linear plateau model, a default yield value was used for the Yp to calculate the yield gap, as yield did not increase with further increases in N or S uptake. This approach was

adapted from French and Schultz (1984) and similar to Carciochi et al. (2020) and (Riar et al., 2016).

Afterwards, the yield gap was calculated as:

```
Yield gap (Mg ha^{-1}) = Ya-Yp
```

(1)

where Ya is actual grain yield and Yp is potential grain yield.

Stress indices for N (NSI) and S (SSI) were calculated as Sadras (2004):

RSI = (1-Ra/Ryp) if Ra < Ryp

(2)

RSI=0 if Ra>Ryp

(3)

where RSI refers to either NSI or SSI with Ya and resource uptake Ra and Ryp is the resource uptake for Yp. Nitrogen stress index (NSI) and SSI range from 0 (no stress) to 1 (maximum stress).

Multiple indices were calculated to quantify the co-limitation and intensity of N and S stresses in wheat. Co-limitation (Cns) tends to be 1 when both stresses are of similar magnitude. First, we calculated the N and S Cns as the absolute vale of the difference between NSI and SSI:

Cns = 1 - |NSI-SSI|

(4)

Second, we calculated two indices of stress intensity: Tns= NSI + SSI (5)

```
Mns=Max(NSI, SSI)
```

(6)

Where Tns is the total N and S stress index (stress intensity) and Mns is the maximum N or S stress index (i.e., the largest stress value between NSI and SSI). Third, co-limitation and total stress were combined:

CTns= Cns/Tns (7)

CMns=Cns/Mns

(8)

Where CTns and CMns are the effects of co-limitation and total stress intensity. It is expected that grain yield is proportionally related to degree of Cns and CTns, and inversely related to Tns.

The N and S use efficiencies were calculated using the definitions provided by Gastal et al. (2015) and Weih et al. (2018), which takes into account the soil nutrient available at sowing plus the nutrient from applied fertilizer.

NUE (kg kg⁻¹) = Grain yield (Mg ha⁻¹) / N available (soil + fertilizer) (kg ha⁻¹)

(9)

SUE (kg kg⁻¹) = Grain yield (Mg ha⁻¹) / S available (soil + fertilizer) (kg ha⁻¹)

(10)

A limitation in this nutrient use efficiency calculation is that it does not account for the contribution of N and S from the mineralization of soil organic matter during the growing season, potentially overestimating nutrient use efficiency.

The N:S ratio were calculated for the N and S concentration in the wheat stover or grain, respectively.

N:S ratio = N concentration / S concentration

(11)

#### **Statistical Analyses**

Analysis of variance was performed using "ImerTest" in R software version 3.4.0 (Kuznetsova et al., 2017). Genotype, N rate, S rate, environment, and their interactions were considered fixed effects, while block nested within environment, and genotype nested within block, N rate nested within genotype, S rate nested within N rate were random effects (the latter accounted for the split-split-plot design). The co-limitation indices were regressed against the yield gap, NUE, NUpE, NUtE, SUE, SUpE, or SUtE. A linear or exponential rise to maximum models were built using the packages of "Im" (Bates et al., 2015) and "nls" (Fox and Weisberg, 2011), respectively to determine the regression coefficients (slope and intercept) and coefficients of determination (R²) among the co-limitation and agronomic indices. For the N:S stoichiometry, a linear-linear model was built using the "segmented" (Muggeo, 2008) package to determine when either N or S were limiting in the wheat shoot or grain.

# Results

# Weather conditions

The 2017-18 wheat growing season (environments: Bell18 and Man18) had a cold and dry winter, a cold and dry early spring, and a hot and dry late spring/early summer (Fig. 1). The drought and cool temperatures maintained the wheat crop dormant until late April, and the reduced rainfall in the season (49-60% of the annual rainfall) combined with above normal May and June temperatures, accelerated late-season crop development and decreased the grain-filling

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period. The 2018-19 wheat growing season (environments: AB19 and Hut19) had a cold and wet winter, a cold and wet early spring, and a cool and wet late spring/early summer (Fig. 1). The wet and cool temperatures maintained the wheat crop dormant until late April. The cool and moist spring reduced spring increased grain fill duration and delayed grain harvest. Overall, the environments established in 2019-20 had a cold and wet winter, a cold and wet early spring, and a cool and wet late spring/early summer (Fig. 1). These conditions resulted in later than average sowing date and the wheat had very limited time to tiller in the fall.

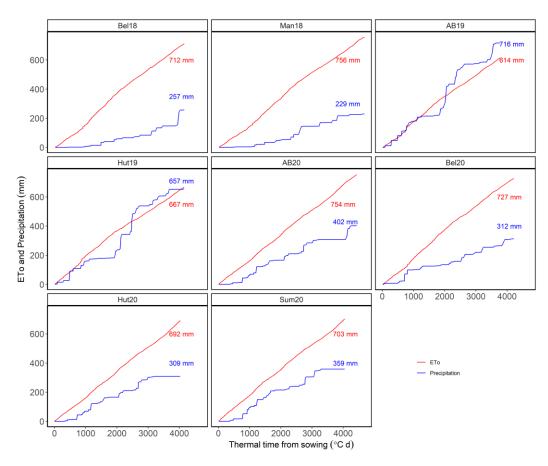


Figure 4-1. Precipitation and evapotranspiration (ETo) experienced during the winter wheat growing season at the eight Kansas environments (Bel8, Man18, AB19, Hut19, AB20, Bel20, Hut20, and Sum20). Cumulative reference evapotranspiration (ETo) and precipitation are shown as red and blue lines, respectively. Inset values show cumulative ETo and precipitation that occurred between sowing and harvest.

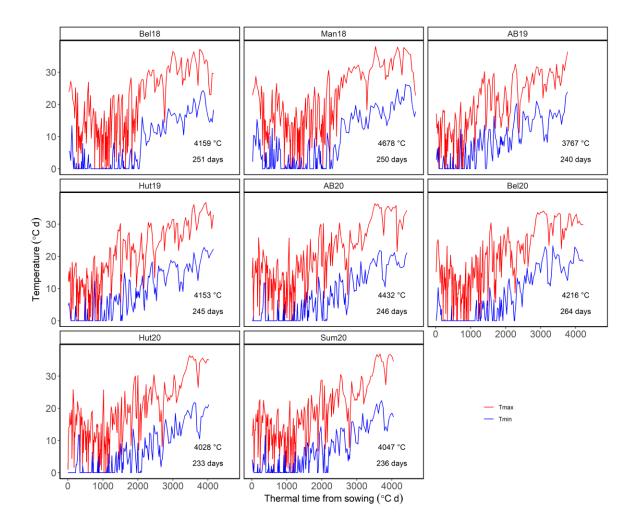


Figure 4-2. Minimum and maximum temperature experienced during the winter wheat growing season at the eight Kansas environments (Bel18, Man18, AB19, Hut19, AB20, Bel20, Hut20, and Sum20). Maximum and minimum temperatures are shown as red and blue lines, respectively. Inset values show cumulative thermal time between sowing and harvest and season duration in days.

# Grain yield

Across all environments, genotypes, and N and S rates, grain yield averaged 3.7 Mg ha⁻¹ and ranged from 0.9 to 5.9 Mg ha⁻¹. Grain yield variability resulting from the studied factors (i.e., averaged across all other factors) was 3.3 to 4.3 Mg ha⁻¹ depending on environment, 3.4 to 4.0 depending on N rates, 3.4 to 3.9 depending on S rates, and from 3.5 to 3.9 Mg ha⁻¹ depending on genotype.

Significant three-way interactions for environment (E)  $\times$  N  $\times$  S, E  $\times$  genotype (G)  $\times$  N rate, and  $E \times G \times S$  rate, impacted grain yield. Increased N rate increased grain yields in all eight environments, with yield gains ranging from 0.1 to 0.9 Mg ha⁻¹. This benefit of N rate to yield depended on S rate in three environments (AB19, AB20, Sum20). In these environments, the presence of S increased grain yield in 2.7 to 3.8 Mg ha⁻¹ at the lowest N rate, and allowed the crop to more efficiently respond to increases in N rate, increasing grain yield in 2.9 to 4.5 Mg ha⁻ ¹ in the higher N rates (Fig. 3). The  $E \times G \times N$  rate interaction was mostly portrayed due to the genotype Zenda vielding the least in six of the environments at the lowest N rate and, as N rate increased, yielding the highest in three environments. At the highest N rate, SY Monument had the highest yield in six environment (range: 3.9 - 4.5 Mg ha⁻¹) and at the lowest N rate, yield losses ranged from 0.4 -1.1 Mg ha⁻¹. The  $E \times G \times S$  rate interaction on grain yield occurred mostly because genotypes responded similarly to S rates in five environments, with grain yields ranging from 2.0 - 3.4 Mg ha⁻¹. However, in two environments (AB19 and AB20), Zenda yield less than Monument at the 0 kg S ha⁻¹ (difference: 0.51 Mg ha⁻¹) and, as the S rate increased, Zenda seemed to recover from those yield losses and all genotypes yielded similarly. We also note that in one environment (Hut19), Zenda was the only genotype to respond to S rate with increases in grain yield of 0.27 Mg ha⁻¹ from the 0 to 11 kg S ha⁻¹.

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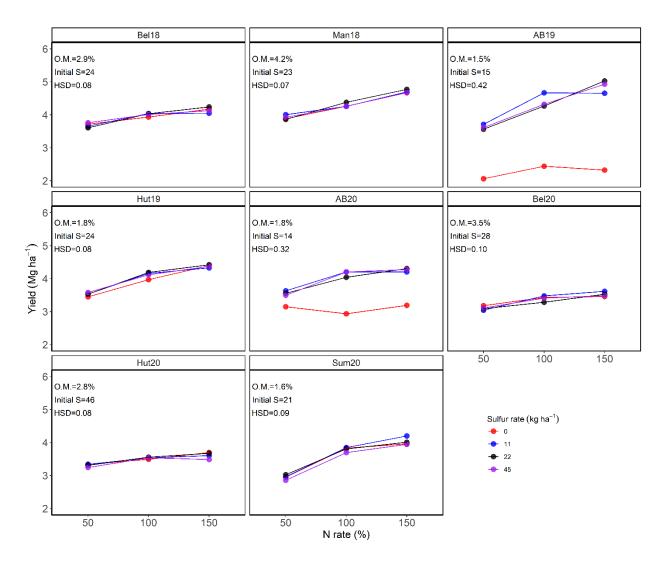


Figure 4-3. Average winter wheat gain yield affected by N rate (50, 100, and 150%), S rate (0, 11, 22, and 45 kg S ha⁻¹), and environments (Bel18, Man18, AB19, Hut19, AB20, Bel20, Hut19, and Sum20). The Honest Significant Difference was calculated within each environment. Soil samples were taken before sowing to determine organic matter (%) and initial plant available S at sowing (kg ha⁻¹).

# Nutrient use efficiency

Nitrogen use efficiency (range: 4 to 39 kg kg⁻¹) and SUE (range: 27 to 315 kg kg⁻¹) varied across environments and treatments (Fig. 4). Three way interactions occurred for NUE among E  $\times$  N rate  $\times$  S rate and among E  $\times$  G  $\times$  S rate. The average NUE for each N rate across all S rates

and environments was 25, 21, 17 kg kg⁻¹ for the 50, 100, 150% N rate, respectively. Increasing N rate decreased NUE at all environments. In six environments, NUE decreased from 24 to 17 kg kg⁻¹ as N rate increased from 50% to 150%. In two environments, (AB19 and AB20), the zero kg S ha⁻¹ rate had significantly lower NUE (range: 9-25) as compared to treatments receiving a S application (range: 16X-31). In three environments (Bel18, Bel20, and Sum20), Monument and Mint resulted in a higher NUE than Zenda. In one location, Monument had a higher NUE than Zenda. In two locations, all three genotypes had the lowest NUE in the absence of S application, but at the zero kg S ha⁻¹ rate, LCS Mint and SY Monument still had greater NUE than Zenda (mean: 17 vs. 14 kg kg⁻¹).

Similarly to NUE, three-way interactions among  $E \times N$  rate  $\times S$  rate and  $E \times G \times S$  rate occurred for SUE (Fig. 9). Across environments, the zero kg S ha⁻¹ rate resulted in the greatest SUE which ranged from 73-228 kg kg⁻¹, while the 45 kg S ha⁻¹ resulted in the lowest SUE (range: 36-82 kg kg⁻¹). The only exception was ASB19, where the addition of 11 kg S ha⁻¹ increased SUE as compared to the zero S rate by 18 and 24 kg kg⁻¹ for the 100 and 150% N rates. In five environments, the addition of N increased SUE anywhere from 27 to 153 kg kg⁻¹ within the same S rate.

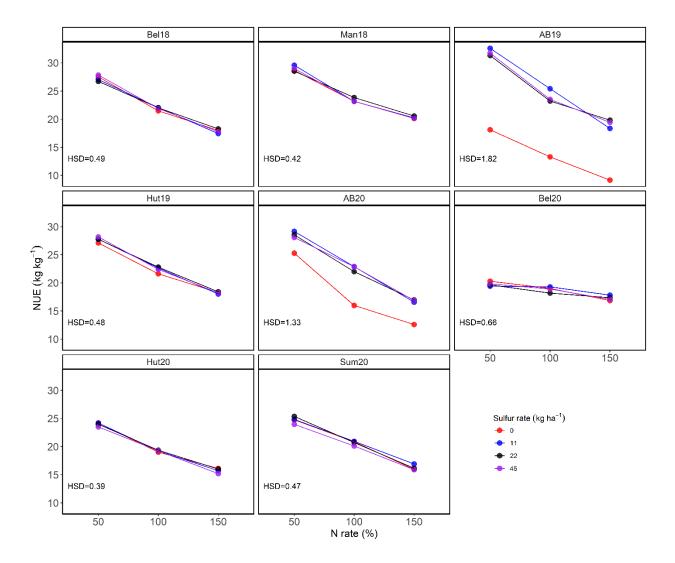


Figure 4-4. Mean nitrogen use efficiency (NUE) as affected by N rate (50, 100, and 150%), S rate (0, 11, 22, and 45 kg S ha⁻¹), and environment (Bel18, Man18, AB19, Hut19, AB20, Bel20, Hut20, and Sum20). The Honest Significant Difference was calculated within each environment.

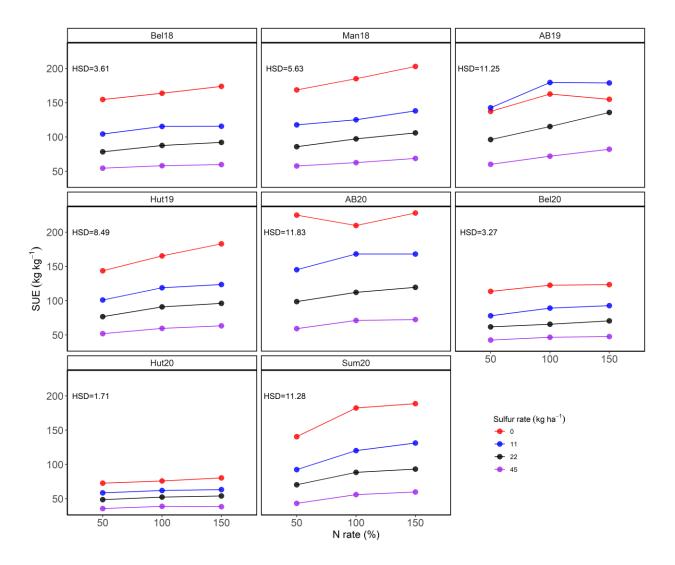


Figure 4-5. Mean sulfur use efficiency (SUE) as affected by N rate (50, 100, and 150%), S rate (0, 11, 22, and 45 kg S ha⁻¹), and environment (Bel18, Man18, AB19, Hut19, AB20, Bel20, Hut20, and Sum20). The Honest Significant Difference was calculated within each environment.

# Potential grain yield as dependent on N and S uptake

Both boundary functions for N and S uptake determined a Yp of 5.7 Mg ha⁻¹ (Fig. 1) with a minimum nutrient uptake of 120 kg N ha⁻¹ (Fig. 6a) and 7 kg S ha⁻¹ (Fig. 6b). The slope of the N and S uptake graphs were used to calculate the nutrient requirement to produce maximum yield, and it resulted in 40 kg grain kg N⁻¹ and 810 kg grain kg S⁻¹.

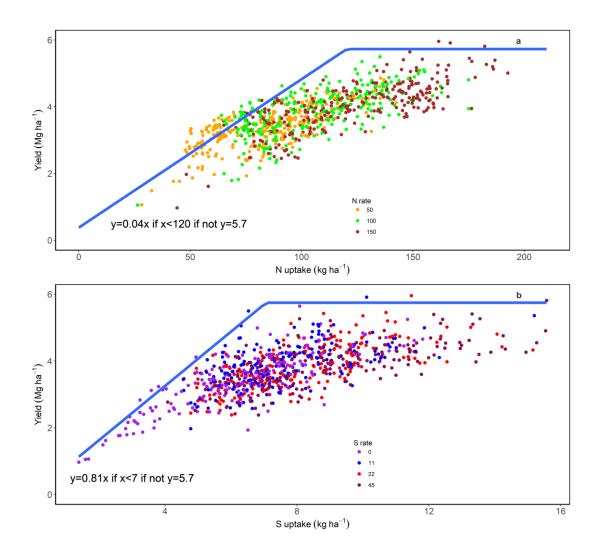


Figure 4-6. Scatter plots and boundary functions to determine nutrient-limited yield potential. The fitted linear plateau models are (a) nitrogen-limited yield potential and (b) sulfur-limited yield potential. Data from a complete factorial containing wheat genotypes (LCS Mint, SY Monument, and Zenda), N rates (50, 100, 150% of yield goal), and S rates (0, 11, 22, and 45 kg S ha⁻¹). Color points represent (a) N rates and (b) S rates.

# Yield gaps and co-limitation effects on grain yield, yield gap, and nutrient useefficiency

A three way interaction among  $E \times N$  rate  $\times S$  rate impacted yield gap. Averaged across all N and S rates, range of yield gaps were -1.5 to -2.5 Mg ha⁻¹. The yield gap decreased from - 2.3 Mg ha⁻¹ to -1.7 Mg ha⁻¹ with increases in N rate from 50% to 150%.

Similarly, NSI and SSI decreased from 0.3 to 0.1 and 0.2 to 0.0, respectively as the N rate was increased from 50 to 150%. The NSI and SSI both correlated with yield gap at  $R^2$ = 0.55 and 0.46, respectively (Fig. 7). Sulfur limitation resulted in a more severe yield gap as compared to N stress due to having a more negative slope (3.49 ± 0.15 SSI vs 2.76 ± 0.10 NSI; Fig. 7). The yield gap also correlated with Tns, Mns CTns, and CMns (Fig. 7). The yield gap increased at a faster rate with increases in Mns as compared to Tns (slope values -2.82 ± 0.09 vs -1.93 ± 0.06).

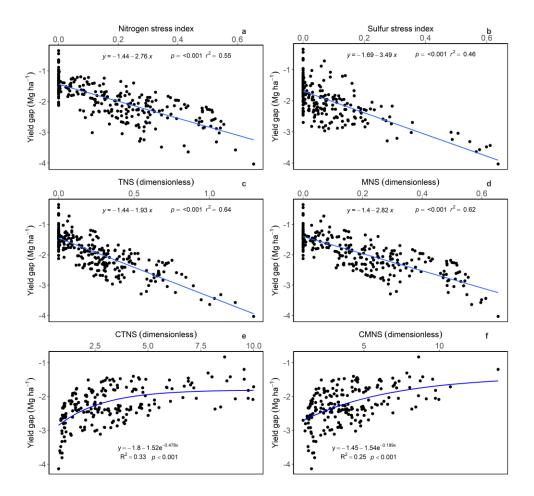


Figure 4-7. Relationship between yield gap and (a) nitrogen stress index, (b) sulfur stress index, (c) total N-S stress index (TNS), (d) maximum N-S stress index (MNS), (e) degree of colimitation (CTNS), and (f) degree of co-limitation (CMNS) in a complete factorial in split-splitplot design containing wheat genotypes (LCS Mint, SY Monument, and Zenda), N rates (50, 100, 150% of yield goal), and S rate (0, 11, 22, and 45 kg S ha⁻¹).

The 50, 100, and 150% N rates resulted in average NSI values of 0.3, 0.2, and 0.1.

Nitrogen use efficiency decreased linearly with increases in SSI, but the rate of decline was different among N rates (Fig. 8). As N rate increased from 50% to 150%, the slopes of NUE increased from 14.8 to 17.1 kg kg⁻¹, respectively. The highest N rate resulted in the greatest decline of 1.7 kg grain kg⁻¹ per 0.1 SSI growth. The Cns increased with increasing N rate (slope values of 9.9 vs 13.7 kg kg⁻¹), but the correlation was weak with  $R^2$ =0.08 for the 50% N rate as compared to  $R^2$ =0.35 for the 150% N rate (Fig. 8). The indices of CTns plateaued at NUE values of 26, 19, and 14 for the 50, 100, and 150% N rates, respectively. However, CMns followed a

different trend as 50% N rate increased linearly with increases in CMns values but the 100 and 150% N rates measured a plateau response.

The average SSI values ranged from 0.0 to 0.2 across the S rates. As NSI increased, the rate of decline for SUE decreased dramatically for the 0 and 45 kg S ha⁻¹ (slope values of 144 vs 57 kg kg⁻¹). Likewise, the correlations between NSI and SUE increased from  $R^2$ =0.28 to 0.56 with increases in S rate (Fig. 9). The slope increased from the low of 69 kg kg⁻¹ for the 45 kg S ha⁻¹ to 241 kg kg⁻¹ for the 0 kg S ha⁻¹ as Cns approached ~1. No relationship was measured at the zero kg S ha⁻¹ rate for SUE and CTns and CMns. For CTns, SUE plateaued at values of 100, 72, and 45 kg kg⁻¹ for the 11, 22, 45 kg S ha⁻¹, respectively.

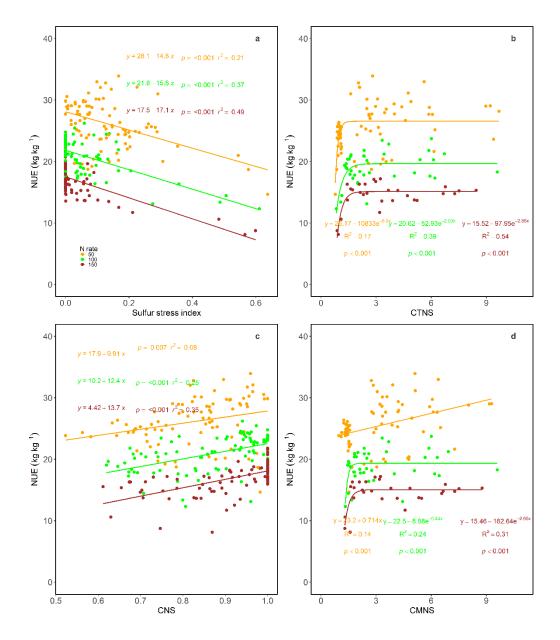


Figure 4-8. Relationship between nitrogen use efficiency (NUE) and sulfur stress index (a), N-S co-limitation (CNS) (c), co-limitation (CTNS) (b), and degree of co-limitation (CMNS) (d) in a complete factorial in split-split-plot design containing wheat genotypes (LCS Mint, SY Monument, and Zenda), N rates (50, 100, 150% of yield goal), and S rate (0, 11, 22, and 45 kg S ha⁻¹).

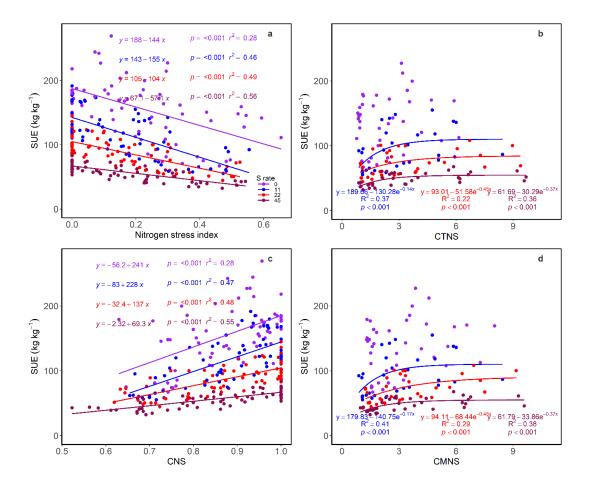


Figure 4-9. Relationship between sulfur use efficiency (SUE) and nitrogen stress index (a), N-S co-limitation (CNS) (c), co-limitation (CTNS) (b), and degree of co-limitation (CMNS) (d) in a complete factorial in split-split-plot design containing wheat genotypes (LCS Mint, SY Monument, and Zenda), N rates (50, 100, 150% of yield goal), and S rate (0, 11, 22, and 45 kg S ha⁻¹).

# N and S stoichiometry and colimitation

For N and S limited conditions, the N:S ratios varied was different between plant organs and increased linearly until reaching the 95% maximum value for Cns at 16.4 (confidence interval [CI]: 16.1-16.7) and 17.3 (CI: 17.1-17.5) for the stover and grain, respectively. The relationships were strong and significant for the stover (p < 0.001; R²=0.63) and grain (p < 0.001; R²=0.65; Fig. 10). We note that in situations when CNS was equal to one, N:S ratio in the stover ranged from 10.9-17.5 and in the grain from 15.0-21.3 (Fig. 10).

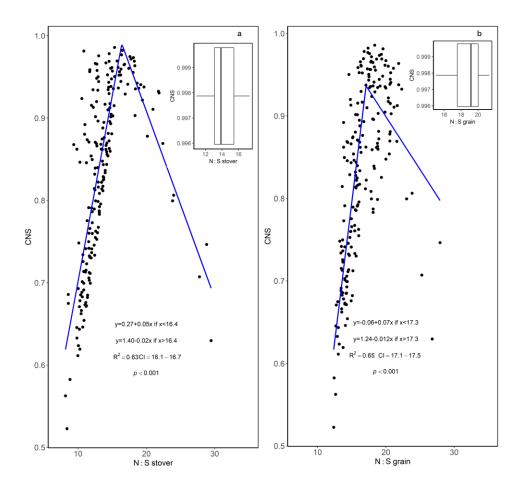


Figure 4-10. Relationship between N-S co-limitation (CNS) and nitrogen and sulfur ratio (N:S) in (a) stover and (b) grain of wheat measured at physiological maturity.

# Discussion

# Grain yield and crop response to N and S

This study aimed at quantify the  $E \times G \times N$  rate  $\times S$  rate interactions modulating wheat yield across a range of environmental conditions. Quantifying these interactions and determining the physiological components driving the crop's responses to nutrient rate and uptake can inform management practices to help increase grain yield. Wheat grain yield ranged 0.9 to 5.9 Mg ha⁻¹ under the experimental conditions evaluated, which is similar to the range in grain yield reported in this region from other experiments (Jaenisch et al., 2019; Maeoka et al., 2020).

Wheat grain yield increased linearly with increases in N rate at all locations (Fig. 3); however, the presence of S had a more modest impact on yield as only two environments responded to S fertilizer. The soil in these two environments were inherently low in plant available S at sowing and had low organic matter (<1.8%) and applications of 11-22 kg S ha⁻¹ were sufficient to maximize yields. We note that the environment requiring 22 kg S ha⁻¹ was also a higher rainfall environment (AB19). Similarly, Ramig et al. (1975) suggested that plant available S at sowing was sufficient at 17 kg S ha⁻¹, and Girma et al. (2005) and Dhillon et al. (2019) suggested that yield responses to S fertilizer application are more likely to occur on low organic matter (<2%), coarse textured soils (AB19 and AB20), or the combination of both. In the remaining environments with greater soil S available at sowing and/or organic matter content, yield response to S fertilization was not expected (Lamond, 1997; Leikam et al., 2003; Kaiser et al., 2019). We note that determining the amount of organic S that becomes available during the growing season is difficult as is it dependent on temperature and moisture regimes (Camberato and Casteel, 2010).

# Wheat yield gap limited by N and S

Wheat Yp of 5.7 Mg ha⁻¹ as determined by fitted boundary functions on N or S uptake was remarkably similar to previous estimates of wheat yield potential in this region, which ranged from 5.0 to 6.7 Mg ha⁻¹ (Patrignani et al., 2014; Lollato and Edwards, 2015; Lollato et al., 2017, 2019b; Jaenisch et al., 2019). However, a novel aspect of this research is that, to our knowledge, this is the first estimation of wheat Yp as function of N and S uptake in this region, similar to the approach adopted for maize (Carciochi et al., 2020).

The range in N uptake in the current study (26 to 193 kg N ha⁻¹) is within in the range reported in field experiments in this (de Oliveira Silva et al., 2020b, 2021; Lollato et al., 2021)

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and other regions (Salvagiotti et al., 2009; Savin et al., 2019), as well as within the range reported for a global literature synthesis on wheat N uptake and utilization efficiency of c.a. 20 to 400 kg ha⁻¹ (de Oliveira Silva et al., 2020a). We notice, however, that the maximum N uptake in the current study was 193 kg N ha⁻¹, which global (de Oliveira Silva et al., 2020a) and more localized (Savin et al., 2019) literature syntheses suggested maximum wheat N uptake in the 300-400 kg N ha⁻¹ range. This discrepancy is likely due to a relatively late sowing date in the current experiment due to all experiments following a previous soybean crop, which delayed sowing as compared to the optimal timing (Paulsen et al., 1997; Munaro et al., 2020). These later sowing dates can reduce the wheat plants' ability to uptake N especially early in the season (i.e., in the fall for winter wheat crops) (Lollato et al., 2021) and lead to a greater leaching potential for N and S around sowing (Arata et al., 2017), which may have been experienced in the AB19 environment. Still, these results are still locally relevant as this is the predominant system in the study region (Staggenborg et al., 2003).

The maximum yield per unit of nutrient uptake for N was 40 kg kg⁻¹ which is the same value Kansas uses to make fertility recommendations for wheat (Leikam et al., 2003). Sulfur uptake ranged from 2.9 -12.4 kg S ha⁻¹ which is within the range of what is reported in Kansas (Lamond, 1997; Maeoka et al., 2020; de Oliveira Silva et al., 2021). However, maximum yield per unit of nutrient uptake for S ranged from 350-750 kg kg⁻¹, which is higher than 255-268 kg kg⁻¹ and was reported by de Oliveira Silva et al. (2021).

# N:S ratios in stover and grain

Our findings of a N:S ratio of 16.4 and 17.3 in the stover and grain, respectively are similar to what has been reported in the literature (Randall et al., 1981b; Byers et al., 1987; Maeoka et al., 2020). In S deficient soils, the N:S ratios can be as high as 20:1 or as low as 12:1

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which is the minimum N requirement (Camberato and Casteel, 2010). The N:S ratio was higher in the grain as compared to the stover, perhaps because N can be remobilized to the grain more efficiently than S (Haneklaus et al., 2007; Carciochi et al., 2020). This is an important finding as rescue applications N can increase the protein concentration in wheat (Woolfolk et al., 2002) but it is unlikely that rescue S applications can be made to correct S deficiencies (Dhillon et al., 2019). Similarly, wheat will have "luxury accumulation" of N (de Oliveira Silva et al., 2021) and not of S (Randall et al., 1981a), which could have significant effects on the baking quality (Zhao et al., 1999a). Nitrogen and S ratios in the grain offer a great opportunity to check for nutrient deficiencies at the end of a growing season for producers (Randall et al., 1981a).

# Conclusions

We reported the first determination of the maximum attainable wheat grain yield as limited by N and S uptake. The co-limitation theory determined that yield gap increased as NSI and SSI increased. Similarly, NUE and SUE decreased as NSI and SSI increased but the rate of decreased was dependent on N or S rate. However, NUE and SUE improved as each as N and S became equally limiting or not-limiting (i.e., as Cns approached one), suggesting that the limitation of a both nutrients (N and S) was more detrimental to NUE and SUE than the limitation of a single nutrients. Our results suggested that soils with high clay and silt content and/or organic matter content greater than 1.8% were not responsive to S fertilizer and sufficient to maximize yield in multiple environments. Still, further research could focus on better quantifying the rate of mineralization of S from organic matter as it is affected by temperature and moisture and incorporate these findings into N:S co-limitation studies for wheat and other crops.

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# **Chapter 5 - Conclusions and future research**

This dissertation highlighted the need for future research to focus on improving N and fungicide management decisions in this region; on understanding wheat yield components and their determination; as well as the interaction of N and S rates for improving wheat grain quality. Optimizing the application of N either through rates, timing, placement, or source, has been researched for years. In the current research, N application increased wheat yields but the optimal rate differed significantly across the regions in Kansas both in the on-farm survey as well as in the field experiments. Determining the optimal N rate across the different growing regions of Kansas will allow producers to be more profitable. Foliar fungicides increased wheat yields; however, only ~50% of the fields in this survey received a fungicide. Thus, it will be important to determine why producers are reluctant to apply a fungicide during the winter wheat growing season. Informing producers on the genotype response to foliar fungicide application will allow producers to improve wheat yield at the commercial level and potentially increase their profitability. In dry years of our experiment two, the enhanced fertility treatment maximized grain yield and the economical intensification maximized grain yields in wet years due to the increased disease pressure, supporting for the need for future research on both topics. Kernels m⁻¹ increased grain yields by increases in kernels head⁻¹. This research also suggested the potential for increased intensity of management practices to increase kernels head ⁻¹. Thus, additional research is warranted to fully understand the role of this yield component in maximizing wheat yields. The interaction of N and S rates increased wheat grain yields on sandy and low organic matter soils. More research locations are needed to fully determine the optimal rate of S is on sandy and low organic matter soils. Similarly, determining the supply of S from organic matter mineralization during the growing season warrants additional research.