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# Productivity of intermediate wheatgrass responds more to local soil and climate factors than fertility treatments in the first establishment year

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The intensive cultivation practices of annual cereal crops have been causing unprecedented degradation of natural resources. Perennial crops such as intermediate wheatgrass (IWG) could provide numerous benefits to address these issues, but there is still little comprehensive information about the establishment, fertilization needs, or range of IWG productivity on a regional basis in the first production year, which can be the highest over the lifespan of IWG's grain production. The objective of this study was to evaluate how IWG establishment and first-year grain and forage yields varied across soil types, climate conditions, and in response to ten fertilization treatments at six locations in the Midwestern USA. The 10 treatments included N fertilizer application at 5 rates; N application with or without P or K; varied timing of N application, and varied N fertilizer source. We found that fertilization influenced summer and fall forage yields but not grain yields. We also found that grain and forage yields varied greatly between locations, ranging from 556–1343 kg ha<sup>-1</sup> for grain yields, 3732–8930 kg ha<sup>-1</sup> for summer forage, and 927–3561 kg ha<sup>-1</sup> for fall forage yields. Using a multiple linear regression approach, we found that a combination of local edaphic soil and climate factors explained 74%, 92%, and 69% of variance in grain, summer forage, and fall forage yields, respectively. Anomalies in expected and actual yields across locations led us to identify potential critical

periods for IWG grain and forage production. We found accumulated precipitation in the 60 days before anthesis explained the most variance in grain and summer forage yields while the accumulated precipitation from May through October explained the most variance in fall forage yields. These findings are a first step toward identifying the regional expectations for IWG yields and could inform grower management and decisions regarding grain and forage harvest.

#### KEYWORDS

perennial crop, Kernza®, soil characteristics, ecological intensification, nitrogen fertility, regional variance

## 1 Introduction

Present-day agricultural systems are degrading the global natural resource base necessary for sustained agricultural productivity and ecosystem functionality, at an unprecedented rate and scale (IPBES, 2019). Approximately 600 million hectares globally are cleared of vegetation each year to grow wheat, maize, and rice, which provide more than 50% of human calories (FAO 2022, FAO, 2023). These and other annual crops must be planted each year often after tillage, which causes ecosystem disservices such as soil degradation and greenhouse gas emissions (Pimentel et al., 2012; Lal, 2015). Current annual row crop agriculture can degrade the soil and increase the need for energy-intensive inputs which, in turn, generate environmental and economic costs such as increased farmer dependence on agrochemicals and fuel (Massobrio et al., 2023; Tsoraeva et al., 2020). Another challenge that farmers of annual grains have faced for millennia is the need for timely, favorable weather conditions to germinate and establish a crop. For example, more than \$13 billion were distributed to farmers in 2022 to compensate for lost revenues because of excess or lack of moisture which delayed planting of corn and soybean (USDA, 2024). Agricultural strategies to avoid the environmental and economic challenges associated with annual replanting could improve productivity and food security (Glover et al., 2010).

The development of perennial grain crops provides an opportunity to overcome disservices inherent to annual agriculture (Zhang et al., 2023). There is increasing evidence that perennial crops have the potential to improve agricultural sustainability because their deep root systems and perennial life strategy lead to reduced tillage and fossil fuel dependency, herbicide applications, soil erosion, nutrient leaching, and runoff (Culman et al., 2013; Crews et al., 2016; Jungers et al., 2019; Reilly et al., 2022a; Glover et al., 2010; Zimbric et al., 2020). Since perennial crops might only require replanting every few years (or longer), such systems can reduce the economic burdens related to seeding and establishment. After perennials are established, their extensive root systems can increase soil water infiltration, storage, and plant uptake throughout the year (de Oliveira et al., 2020;

Clément et al., 2022) thereby enhancing resilience to extreme drought or flood conditions relative to annual crops. Increased climate resiliency by perennials can ensure some harvestable product consistently where annuals may be more prone to crop failure (Smith, 2014; Schipanski et al., 2016).

One of the most advanced perennial grain crops being developed is derived from Intermediate wheatgrass (IWG) [*Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey]. IWG is a cool-season grass with good winter hardiness, relatively large seeds for a perennial grass, and high biomass and forage quality. Because of these qualities it emerged as a promising candidate for perennial grain breeding and crop development (Wagoner, 1990; Wagoner and Schauer, 1990; Crain et al., 2024; DeHaan et al., 2014). IWG seeds can be harvested as grain for direct human consumption, while vegetative biomass can be used simultaneously as livestock forage, thus providing multiple market opportunities while offering enhanced environmental quality (Crews et al., 2018; Natural Resources Conservation Service (NRCS), 2021; Pinto et al., 2022; Cureton et al., 2023). Over 40 years of breeding has resulted in modern IWG lines with improved yield, seed size, and disease resistance (Wagoner, 1994; Cox et al., 2002; DeHaan et al., 2005, 2014; Zhang et al., 2016; Cattani and Asselin, 2017; DeHaan et al., 2018; Hayes et al., 2018; Bajgain et al., 2022). In 2009, The Land Institute trademarked the grain harvested from improved IWG lines as “Kernza®” (Natural Resources Conservation Service (NRCS), 2009), and in 2019 the first commercial variety “MN-Clearwater” was released in the United States by the University of Minnesota (Bajgain et al., 2020). Since that time, IWG research in the Midwestern United States has been concentrated in Minnesota (Zhang et al., 2016; Jungers et al., 2019; Bajgain et al., 2020), Kansas (Culman et al., 2023; DeHaan et al., 2018; de Oliveira et al., 2018; McKenna et al., 2020; Barribal et al., 2022; Means et al., 2022), Wisconsin (Zimbric et al., 2020; Pinto et al., 2021, 2024), Ohio (Pugliese, 2017; Pugliese et al., 2019), and Michigan (Culman et al., 2013). Results of these and other studies have shown first year IWG grain yields to range from 500 to 1000 kg ha<sup>-1</sup>, and forage yields from 3800 to 10800 kg ha<sup>-1</sup> (Supplementary Table S1). Both geographic location and fertility optimization influence grain and biomass yields

(Jungers et al., 2017) but with rapid IWG expansion in the past decade, there is a strong need to better understand both IWG's fertility needs and the other management and environmental characteristics which influence IWG establishment, growth, and grain and biomass yields.

Research to determine best practices to establish IWG as a grain crop in the Upper Midwest has provided a baseline for this and future research (DeHaan et al., 2025). For example, sowing IWG in the fall has been a common practice because it has the advantage of lowering weed pressure during establishment and allowing seeds to vernalize and produce a grain harvest in the subsequent first full growing season (Locatelli et al., 2022). Within this planting period, researchers have quantified the influence of temperature on seedling success and subsequent yields when sown on various dates (Jungers et al., 2022). Temperature and precipitation in the first spring after planting can also significantly affect survival and first-year yields of IWG as it does for annual grain crops (Carrera et al., 2024). Within the general influence of weather on first year establishment, there is a 'critical period' defined for many crops but not yet defined for IWG, when weather conditions during flowering and grain-filling strongly influence yield or seed abortion in the first or subsequent growing seasons (Fischer, 1985; Slafer and Andrade, 1993; Andrade et al., 1999). Other edaphic factors such as soil aggregate structure, organic matter contents and temperature are also important for perennial species growth and productivity (Crews et al., 2018; Culman et al., 2023). Little is known how these variables affect establishment success and first-year yields, but because IWG often has the highest grain yields in the first production year (Zhen et al., 2024), understanding and predicting first year establishment and yields is of importance for improving producer success.

How IWG yields are influenced by the interaction between endogenous nutrient supplies of different soil types and fertilizer amendments is another important area of investigation. N addition rates of 90 kg N ha<sup>-1</sup> in Minnesota have been found to sustain harvests near yield potential (Tautges et al., 2023), but a wide range of rates (e.g. 67–112 kg N ha<sup>-1</sup>) have been found to be sufficient in other regions (Vogel et al., 1993; Fagnant et al., 2024). Grain yields have tended to decrease with higher N rates because of increased lodging (Jungers et al., 2017; Tautges et al., 2023) or tiller density resulting in a decrease in reproductive tillers (Fagnant et al., 2024). Fertilizer effects on IWG yield (grain or forage) vary strongly by location and stand age (Pugliese et al., 2019; Pinto et al., 2022; Reilly et al., 2022b; Bowden, 2023), and although less studied, growers are interested in organic sources of fertilizer for N or other nutrients. Although IWG often does not respond to N fertilizer in the first production year, (i.e. Reilly et al., 2022b; Crews et al., 2022), these studies are based on relatively few N rates or locations, and the optimal fertilization timing is also still unclear (Fernandez et al., 2020; Dobbratz et al., 2023; Tautges et al., 2023). Preliminary studies have also shown that macronutrients can limit productivity and that P and K concentrations in forage and grain affect their quality (Muhandiram, 2023; Tautges et al., 2018) but very few studies have explored the P and K limitation or requirements of IWG. Together, there is a need to better understand how the

establishment of Kernza varies across locations, and systematically how first year IWG grain and biomass yields respond to a range of fertilization strategies versus local climate conditions across a wider geographic range than has been previously explored.

In this analysis we addressed these research needs with the following objectives: 1) to determine the effect of N fertilizer application rate and timing along with the omission of P or K on first year IWG grain and biomass yields; and 2) to examine how a gradient of soil and climate conditions across multiple study locations in the Midwest influence IWG establishment, productivity and initial responses to fertilization treatments. These objectives were addressed using a multi-institutional, multi-site fertility experiment that was funded by the United States Department of Agriculture Sustainable Agricultural Systems Coordinated Agricultural Projects USDA SAS-CAP). Specifically, we focus on N fertilizer rates, timing of N application, interactions between N, P and K fertilizer applications. We expected that 1) IWG grain and biomass yields would increase in response to increasing N fertilization rates up to 135 kg ha<sup>-1</sup>, and then grain yield gains would diminish at higher N rates due to lodging or excess tillering; and 2) yield variation response to fertilization strategy within a site would be small relative to the variation across study locations due to climate and soil being primary drivers of plant establishment and growth. There has seldom been investigation about the interacting effects of soil, climate, and fertility management on IWG performance. This information is essential to develop management best practices across a range of suitable growing environments for IWG for grain, forage, and dual use.

## 2 Materials and methods

### 2.1 Location and characterization of the study area

The experiment was conducted in six locations: Salina, Kansas (KS-TLI; The Land Institute); Mead, Nebraska (NE; University of Nebraska-Lincoln); Rosemount, Minnesota (MN-ROS; University of Minnesota-Twin Cities); Arlington, Wisconsin (WI-UW; University of Wisconsin-Madison); Troy Center, Wisconsin (WI-MFAI; Michael Fields Agricultural Institute), and Wooster, Ohio (OH; The Ohio State University) (Figure 1; Table 1). The soil orders presented across these locations are Mollisols and Alfisols (Soil Survey Staff, 2023; Table 1). The climates are classified as follows (Kottek et al., 2007): NE and OH have hot and humid continental summers (Dfa); MN-ROS, WI-UW, and WI-MFAI have mild and humid continental summers (Dfb); KS-TLI is between a hot humid subtropical summer (Cfa) and a hot humid continental summer (Dfa).

### 2.2 Experimental design

All locations were planted to oats (*Avena sativa*) in spring 2021 and harvested in July of that year before establishing experimental



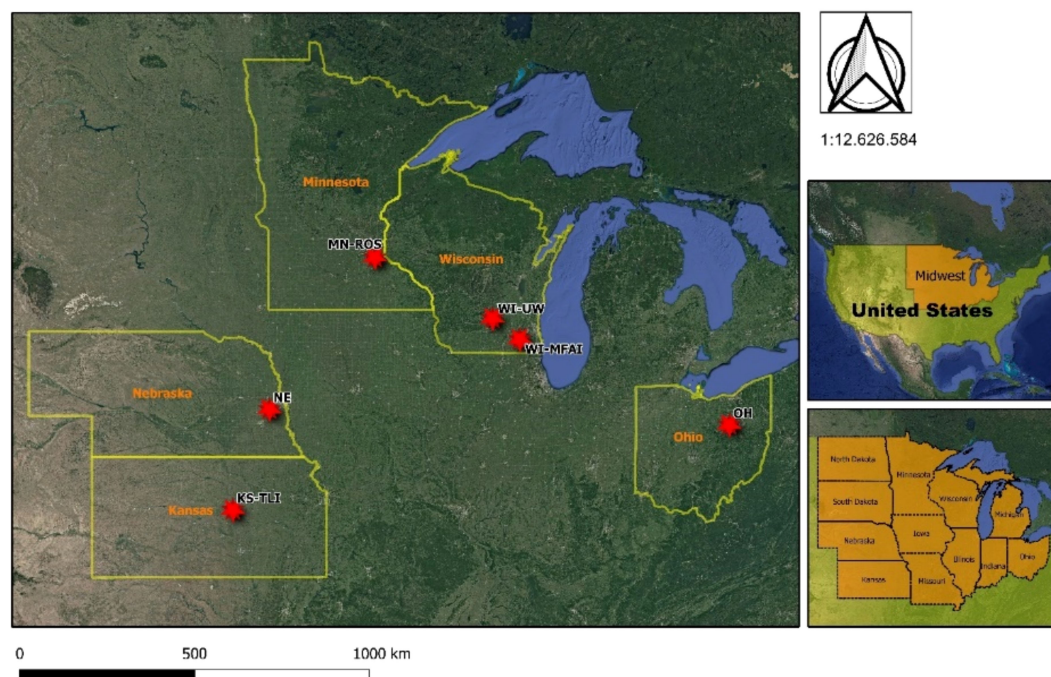


FIGURE 1

Visualization of the six study locations in the Midwestern United States, using a Modified satellite image of the Midwestern United States, based on imagery from Google Earth (Google, 2025).

treatments. Previous management at each location had been a continuous annual crop rotation typical of the region of each location (a corn-soybean rotation WI-UW, WI-MFAI, OH, MN-ROS, and NE, and a soybean-sorghum rotation at KS-TLI). We established the same random block design with twelve treatments (Table 2) replicated once per each of four blocks. We provide a detailed description of the site characteristics and agronomic management in Supplementary Tables S1 and S2. Plots were approximately 15.24 m x 6 m at each location. We collected baseline soil samples in a subset of the treatments referred to as the 'soil health treatments' with a hydraulic soil probe (5.08 cm diameter and 0–20, 20–50, and 50–90 cm deep) in the summer of 2021 following oat harvest as described below. There were 12 treatments total, including 10 IWG planted treatments with various fertilization strategies described below, and two "business as usual" (BAU) treatments that tested annual crops chosen to reflect typical crops of the given region. These BAU treatments were a soybean-corn rotation with both phases (labeled BAU1 and BAU2) included at most locations and a sorghum-soybean rotation at KS-TLI only (Table 2, Supplementary Table S2). Data from BAU treatments is not included in the analysis presented in this paper, but will be compared with IWG responses in the coming years. Prior to planting IWG, we applied fertilizer appropriate to each treatment (Table 2) and prepared the seedbed by tillage (Supplementary Table S2). Fertilizer rates were optimized so that at least one treatment could both meet the nutritional needs of IWG and to create a useful comparison between the IWG and BAU crops, as well as balance the amount of fertilizer all crops received over two-year periods (Jungers et al., 2017, Table 2). N application

rates in this study were selected to encompass the range of applications currently recommended as well as higher rates to assess potential N-limitation at current recommended rates with the newest released variety, MN Clearwater (Jungers et al., 2017; Bajgain et al., 2020). N rate treatments included 0, 45, 90, 135 and 180 kg N ha<sup>-1</sup> applied as urea in the spring. All N addition treatments also included 56 kg P ha<sup>-1</sup> and 168 kg K ha<sup>-1</sup>, and two additional fertility treatments tested the 90 kg N ha<sup>-1</sup> rate either without the added P or without the added K. P and K fertilizer rates were selected to approximate crop removal rates through harvest based on unpublished Kernza grain and forage data, as well as published corn and soybean removal data (e.g., Culman et al., 2020; Table 2). The K rate likely exceeded the BAU removal rates, but is within range of what would be considered typical farmer practice in Midwest corn and soybean cropping systems.

In addition to examining N rates, we examined IWG responses to N source and N timing. The N source treatment assigned 180 kg N ha<sup>-1</sup> added as chicken manure, with the same product used across all experimental sites. N timing treatments were implemented by applying N (at 90 kg N ha<sup>-1</sup>) in the fall or as a spring-fall split (45 kg N ha<sup>-1</sup> at each application). Tillage and seedbed preparation occurred as described in Supplementary Table S2 throughout the late summer of 2021 in all plots. In September 2021 the IWG variety 'MN-Clearwater' was planted at a density of approximately 7.8 (MN-ROS, TLI), 12 (NE, WI-UW), or 16 (MFAI, OH) pure live seeds ha<sup>-1</sup>, with either 30 (MN-ROS, KS-TLI) or 38 (OH, NE, WI-MFAI, WI-UW) cm between rows, depending on available equipment. We fertilized relevant IWG treatments in April-May 2022 as described in Table 2. Urea fertilizer was mixed with a urease inhibitor (ANVOL<sup>®</sup>) before application, at a

TABLE 1 Experimental site locations and characteristics including geographical coordinates, meters above sea level, and soil taxonomy (Soil Survey Staff, 2023).

| Location              | The Land Institute                               | University of Nebraska, Lincoln                   | University of Minnesota                                                              | University of Wisconsin-Madison                         | Michael Fields Agricultural Institute                                                | The Ohio State University                           |
|-----------------------|--------------------------------------------------|---------------------------------------------------|--------------------------------------------------------------------------------------|---------------------------------------------------------|--------------------------------------------------------------------------------------|-----------------------------------------------------|
| Abbreviation          | KS-TLI                                           | NE                                                | MN-ROS                                                                               | WI-UW                                                   | WI-MFAI                                                                              | OH                                                  |
| Coordinates           | 38°41'55.48"N 97°34'52.66"W                      | 41°09'24.68"N 96°25'30.41"W                       | 44°41'57.6"N 93°04'52.9"W                                                            | 43°18'07.3"N 89°20'57.6"W                               | 42°48'54.7"N 88°29'14.0"W                                                            | 40°46'52.3"N 81°50'36.7"W                           |
| Elevation             | 388 m                                            | 348 m                                             | 280 m                                                                                | 320 m                                                   | 280 m                                                                                | 365 m                                               |
| Soil family           | Fluventic Haplustoll, Coarse-silty, mixed, mesic | Mollic Hapludalfs, Fine-silty, mixed, superactive | Typic Hapludolls, Fine-silty over sandy or sandy-skeletal, mixed, superactive, mesic | Typic Argiudolls, Fine-silty, mixed, superactive, mesic | Typic Hapludalfs, Fine-loamy over sandy or sandy-skeletal, mixed, superactive, mesic | Aquic Fragiudalfs, Fine-loamy, mixed, active, mesic |
| Soil series           | McCook silt loam                                 | Yutan silty clay loam                             | Waukegan silt loam                                                                   | Plano silt loam                                         | Fox silt loam                                                                        | Canfield silt loam                                  |
| Prcp 1979-2022 (mm)   | 861                                              | 884                                               | 897                                                                                  | 911                                                     | 905                                                                                  | 1111                                                |
| Eta 1979-2022 (mm)    | 789                                              | 783                                               | 754                                                                                  | 726                                                     | 616                                                                                  | 617                                                 |
| Temp 1979-2022 (C°)   | 15                                               | 12.2                                              | 9.2                                                                                  | 9.4                                                     | 10                                                                                   | 11                                                  |
| Temp 2021 (C°)        | 14                                               | 11                                                | 8                                                                                    | 9                                                       | 9                                                                                    | 11                                                  |
| Temp 2022 (C°)        | 13                                               | 10                                                | 6                                                                                    | 7                                                       | 8                                                                                    | 11                                                  |
| Prcp 2021 (mm)        | 673                                              | 583                                               | 693                                                                                  | 570                                                     | 591                                                                                  | 837                                                 |
| Prcp 2022 (mm)        | 708                                              | 367                                               | 681                                                                                  | 892                                                     | 834                                                                                  | 1042                                                |
| PrcpCrop (mm)         | 538                                              | 274                                               | 404                                                                                  | 403                                                     | 330                                                                                  | 486                                                 |
| PrcpAnthesis (mm)     | 521                                              | 195                                               | 396                                                                                  | 452                                                     | 425                                                                                  | 587                                                 |
| Prcp60Anthesis (mm)   | 195                                              | 189                                               | 89                                                                                   | 190                                                     | 110                                                                                  | 252                                                 |
| Prcp20Anthesis10 (mm) | 66                                               | 88                                                | 31                                                                                   | 86                                                      | 77                                                                                   | 190                                                 |

Climate variables are presented in a number of ways: Mean annual precipitation (Mean prcp), actual evapotranspiration (Mean Eta), and temperature (temp) from 1979-2022. Total cumulative annual precipitation (prcp) and mean annual temperature (temp) in 2021 and 2022. Cumulative precipitation from May to October 2022 (PrcpCrop), accumulated precipitations from January to anthesis 2022 (Prcp anthesis), accumulated precipitations 60 days before anthesis 2022 (Prcp60Anthesis), accumulated precipitations 20 days before and 10 days after anthesis 2022 (Prcp20Anthesis10) in mm. Anthesis day varied according to location (Figure 2).

**TABLE 2** Description of study treatments in the study including the number, name, description, fertilizer rate (kg ha<sup>-1</sup>, - = no fertilizer), timing (spring or fall) and strategy [N fertilization timing, N fertilization rate, N fertilizer source, phosphorus (P) and potassium (K) fertilization].

| Treatment number | Treatment name    | Treatment description | Fertilization rate (kg ha <sup>-1</sup> ) |      |     |     | Fertilization strategy |
|------------------|-------------------|-----------------------|-------------------------------------------|------|-----|-----|------------------------|
|                  |                   |                       | Spring                                    | Fall |     |     |                        |
|                  |                   |                       | N                                         | N    | P   | K   |                        |
| 1                | BAU1*             | Corn or sorghum (+)   | 180                                       | –    | 112 | 168 | –                      |
| 2                | BAU2              | Soybean               | –                                         | –    | –   | –   | –                      |
| 3                | 0N_spring*        | No N fertilization    | –                                         | –    | 56  | 168 | N rate                 |
| 4                | 45N_spring        | Urea, TSP, KCl        | 45                                        | –    | 56  | 168 | N rate                 |
| 5                | 90N_spring*       | Urea, TSP, KCl        | 90                                        | –    | 56  | 168 | N rate, N timing, PK   |
| 6                | 135N_spring       | Urea, TSP, KCl        | 135                                       | –    | 56  | 168 | N rate                 |
| 7                | 180N_spring*      | Urea, TSP, KCl        | 180                                       | –    | 56  | 168 | N rate, N source       |
| 8                | 90N_fall*         | Urea, TSP, KCl        | –                                         | 90   | 56  | 168 | N timing               |
| 9                | 45-45N_split      | Urea, TSP, KCl        | 45                                        | 45   | 56  | 168 | N timing               |
| 10               | 180N_fall_manure* | Poultry manure        | 180                                       | –    | –   | –   | N source               |
| 11               | 90N_spring_noK    | Urea, TSP             | 90                                        | –    | 56  | –   | K                      |
| 12               | 90N_spring_noP    | Urea, KCl             | 90                                        | –    | –   | 168 | P                      |

(+) sorghum at KS-TLI only.

Urea was the source of mineral N, chicken manure was the source of organic N, triple superphosphate (TSP, P<sub>2</sub>O<sub>5</sub>) as the source of phosphorus, and potassium chloride (KCl) as the source of potassium. Asterisks after the treatment number indicate treatments chosen for detailed soil health analysis.

rate of 1.5 quarts per ton of urea, per product recommendations (Koch Agronomic Services, LLC). Grain and summer forage harvest took place in August 2022. Fall fertilizer for relevant IWG treatments took place in September 2022. Fall forage harvest for IWG took place after the first frost in October 2022.

## 2.3 Soil sampling and analysis

Baseline soil samples were collected from a subset of treatments including 1, 3, 5, 7, 8, and 10 (Table 2). This subset is hereafter referred to as the ‘soil health plots’. Multiple soil cores were randomly extracted from each plot to control for field heterogeneity and divided into the following depth increments: 0–20, 20–50, and 50–90 cm. Samples within each plot were combined by depth into one composite sample per plot (~450g), sieved to 8 mm, and stored appropriately for each subsequent analysis. All soil analysis followed standardized methods (Supplementary Table S3). Briefly, samples were refrigerated at 4° C until sieved to 2 mm and weighed and subsampled for gravimetric soil moisture (~10–20 g subsample dried to 105° C for 48 hrs). Bulk density was estimated by dividing the dry weight equivalent of each composite sample core by the volume of the core. Soil texture analysis was conducted on subsamples air dried (~100 g) using the hydrometer method (Carter and Gregorich, 2008). Subsamples were analyzed for soil organic matter (SOM), pH, cation exchange capacity, ammonium-N, nitrate-N, available P, exchangeable K, at A&L Great Lakes Laboratory (Ft. Wayne, IN) using standard procedures (Brown, 1998). Total soil carbon and total N were analyzed by combustion analysis using (varioPYRO cube, Elementer Inc., New

Jersey, US). For aggregate stability analysis, we collected three bulk soil samples with a 2.54 cm wide (0–20 cm deep) soil probe which were then combined into one composite ~100g sample per plot. Soil was then sieved to 8 mm and placed in a 4 mm sieve at the top of a stack containing 4 mm, 2 mm, 0.250 mm, and 0.053 mm sieves. The aggregates were first wetted with capillary action by setting the sieves just at water level, followed by oscillation for 10 min in a water tank using a mechanical sieving device ((Angers et al., 2008); with a modification that no sand correction was performed). After drying and weighing the soil remaining in each sieve, we calculated the mean weight diameter (MWD) of water stable aggregates (Rakkar et al., 2023). Soil subsamples were analyzed for nitrate and ammonium using extractions with 1M KCl and subsequent colorimetric analysis (Doane and Horwath, 2003; Sinsabaugh et al., 2000).

## 2.4 Measurement of crop establishment, growth staging, and grain, summer forage, and fall forage yields

To assess establishment, we conducted plant counts within three weeks after IWG planting by counting seedlings within a 50 cm section in two rows of each plot. We assessed IWG growth stages using Zadoks growth at stem elongation, anthesis, and harvest (Zadoks et al., 1974). Lodging was assessed following procedures described by Frahm et al. (2018) at harvest and was not a concern in 2022. We measured aboveground production (grain and summer forage yield) by harvesting 1 m sections from

three adjacent rows in two representative areas of each plot (see quadrats size for each location in ST2). IWG grain yield was measured by first clipping the seedheads from stems just below the bottom spikelet. Seedheads from both sampled areas were placed into the same bag and then all remaining vegetative biomass above 7.6 cm from both sampled areas was harvested, combined, and placed in a separate bag. The remaining vegetative biomass is referred to as summer forage. In all field sample collection and measurements, the outermost plot rows and 50 cm border of the plot edges were excluded from sampling to avoid edge effects. Both seedhead and summer forage biomass were weighed fresh before being dried for 7 days at 35°C and re-weighed again for determining moisture content and dry matter yield. Grain was threshed from seed heads using a laboratory thresher (Wintersteiger LD 350, Ried im Innkreis, Austria) followed by sieving and aspirating to fully separate the grain from the chaff. All plots were mechanically combine-harvested after the manual harvest such that both grain and remaining straw were cut and removed with only approximately 7.6 cm of residue remaining on the plots. Fall forage samples were collected from treatments 3, 5, and 7 and processed using the same methods described above for the summer forage harvest. Yields of all crops were expressed in kg ha<sup>-1</sup> by multiplying harvested kg per m<sup>-1</sup> by row spacing (m<sup>-1</sup>), then multiplying by 10000 (m<sup>2</sup> ha<sup>-1</sup>).

## 2.5 Climate data analysis

We compiled a suite of climate variables from 1979–2022 for each site so that we could characterize the 2022 data of this study within the context of historical trends. Actual evapotranspiration (Eta), precipitation (Prcp), net solar radiation, and temperature were derived by the European Centre for Medium-Range Weather Forecasts (ECMWF) and Reanalysis v5 (ERA5) (Hersbach et al., 2020; Supplementary Tables S4, S5, Supplementary Tables metadata). ECMWF consists of a dynamically consistent combination of numerical weather prediction forecasts, satellite, and *in-situ* observations of climatic variables. Data for 2021–2022, as the more recent trends for each location, were downloaded from National Centers for Environmental Information (National Oceanic and Atmospheric Administration (NOAA), 2023), the CFAES Weather System (Ohio State University, 2013), and Davis weather station at TLI (Supplementary Tables S6, S7).

To assess the correlation of climate factors with IWG grain and biomass yields, we selected a number of variables that would balance comprehensiveness and minimization of covariance. The selected variables included precipitation (Pp; mm, the sum of rainfall, snow and hail), actual evapotranspiration (Eta; mm), temperature (°C, annual, monthly and daily averages), frequency occurrence Prcp (25%, 50% and 75%; Irigoin, 2011) and evaporative fraction (Ef). Ef is defined as the ratio of latent heat flux to the available energy, *i.e.* how much of the radiation received can be used for Eta. Ef is controlled by water in the root zone (Bastiaanssen et al., 1997).

In addition, the cumulative actual evapotranspiration from May to October was calculated as an estimate of evapotranspiration over the crop growing season (EtaCrop). We also calculated cumulative Prcp over several different time intervals associated with various critical physiological periods to determine if any were correlated with yield. The cumulative growing season precipitation (PrcpCrop) was calculated as the sum Prcp from May to October 2022 (de Oliveira et al., 2018). Cumulative precipitation was also calculated for the 60 days before anthesis (Prcp60Anthesis, Figure 2), for the 20 days before + 10 days after anthesis (Prcp20Anthesis10; the critical period of the wheat based on Fischer, 1985), for the entire calendar year before anthesis (PrcpAnthesis) (beginning January 1<sup>st</sup> and ending on the date of observed anthesis at each location), and for the entire calendar year (PrcpAnnual). The mean temperature of crop establishment through harvest (TempCrop) was calculated as well (September 2021 to August 2022 for grain and summer forage; September 2021 to October 2022 for fall forage).

Additionally, growing degree days (GDD) were calculated according to Jungers et al. (2018) and Barribal et al. (2022) (Equation 1), where Tmax and Tmin are the maximum and minimum temperatures and Tbase (0 °C) is the minimum temperature threshold for IWG plant growth (Jungers et al., 2018; Barribal et al., 2022). Growing degree day accumulation began after the average daily temperature exceeded the base temperature for 5 consecutive days (Jungers et al., 2018) after January 1<sup>st</sup> 2022 (Barribal et al., 2022).

$$GDD = [(Tmax + Tmin)/2] - Tbase \quad (1)$$

## 2.6 Statistics

To assess how fertility treatment, climate and soil factors could be related to differences in IWG establishment and growth across locations, we used several data analysis approaches. We analyzed data using R Software (version 2023.06.1; R Core Team, 2021) and tools in the *dplyr* package to structure data frames appropriately (Wickham et al., 2021). For all analyses, we first assessed whether measured soil and IWG variables conformed to model assumptions of homogeneity of variance and normality, and applied a square root transformation as needed. We tested for the fixed effect of location on IWG plant counts and baseline soil parameters with blocks specified as random variables, since there were no fertility treatments implemented for these response variables. Linear mixed effects models were used to test the effects of the fertility treatments and locations for IWG grain and forage yield. We used both one-way ANOVA and mixed effects models using the following R packages: *stats* (R Core Team, 2021), *scales* (Wickham and Seidel, 2020), and *lme4* (Bates et al., 2015). For mixed effects models, we specified fixed effects for treatment, location, and the interaction of treatment and location and assigned block as a random effect. When fixed effects were deemed significant ( $\alpha \leq 0.05$ ), mean comparisons of levels within each fixed effect were conducted



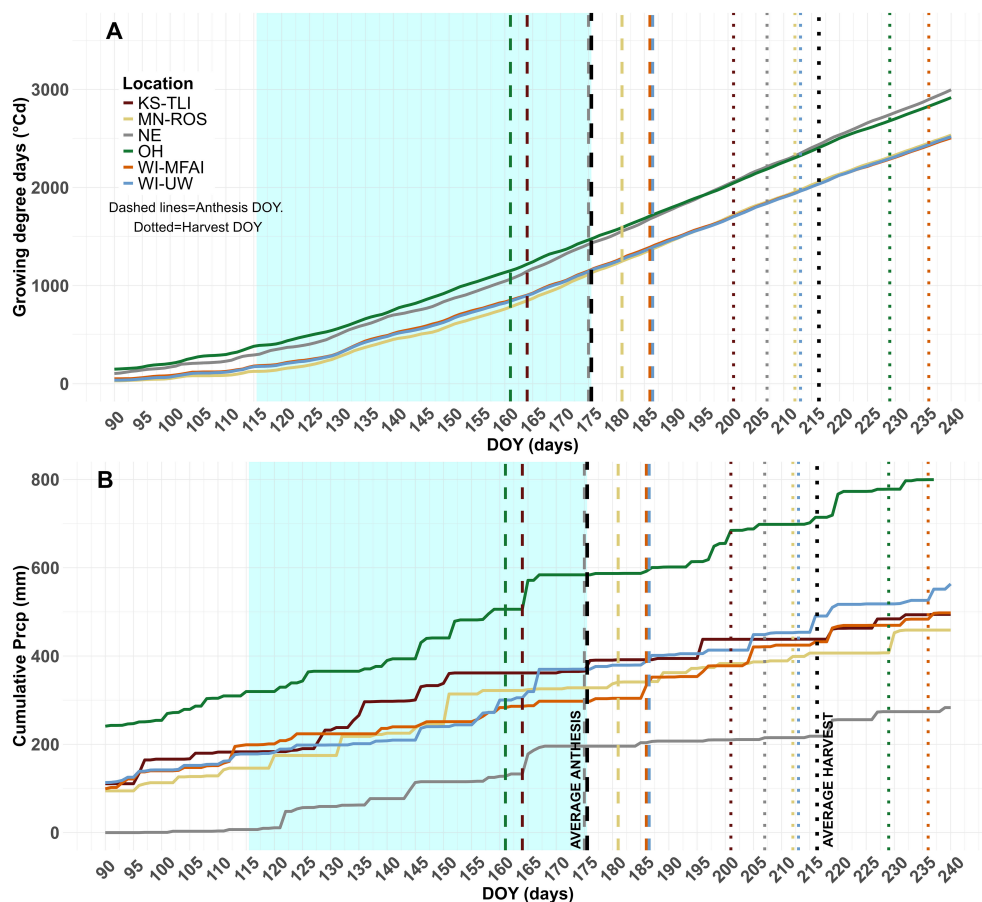


FIGURE 2

2022 cumulative growing degree days (GDD) ( $^{\circ}\text{Cd}$ ) (A) and cumulative precipitation (mm) (B) for each location. The x-axis shows day of the year (DOY) from day 90 to day 240. Dashed lines show the day of anthesis; dotted lines show the harvest day (DOY) where colors indicate different locations and black is the average day across sites. The light blue shadow shows 60 days before the average anthesis date.

using Tukey's HSD posthoc pairwise comparison with the *emmeans* package (Lenth, 2024).

To compare the potential productivity between locations, we estimated the crop productivity index (CPI) for each location using the National Commodity Crop Productivity Index (NCCPI) model developed by the NRCS-USDA. The CPI ranks soils according to their inherent capacity to produce dryland commodity crops. Ratings are based on soil properties and climate, and range from 0 to 100, with higher ratings indicating greater yield potential (Natural Resources Conservation Service (NRCS), 2022; Supplementary Figure S1).

## 2.7 Multiple linear regression modeling

Separate multiple linear regression models were developed to estimate the predictive value of soil baseline (0–90 cm depth average) and climate (2021–2022 series) data on grain, summer forage, or fall forage yields. Before constructing and fitting the models, Pearson correlation analysis (R Core Team, 2021) was

performed on all possible predictors, and variables with a correlation of 0.6 or greater were considered significantly correlated and thus excluded from consideration (Supplementary Table S8). Predictors were also centered by subtracting the mean. Based on this preliminary analysis, we used the following predictors in each model: SOM, CEC, P, K, Mg, Na, S, the MWD of water stable soil aggregates; sand; Prcp60Anthesis; PrcpAnthesis, and EtaCrop. For the fall forage model, we used PrcpCrop as the climate predictor instead of Prcp60Anthesis or PrcpAnthesis. We then used the dredge function of *MuMIn* package (Barton, 2013) for each of the three full models to explore all possible combinations of predictors and selected the model with the lowest AIC score. After a first run of the models, outliers were identified by calculating the standardized residuals for the models, identifying and deleting observations where the absolute value of the standardized residual was greater than 1.5. The variance inflation factor (VIF) analysis was performed to identify multicollinearity between predictors (Fox and Weisberg, 2019). Predictors with VIF values greater than 5 were deleted for fitting the models. Lastly, we performed an ANOVA, and tested the assumptions for linearity, independence,



homoscedasticity, normality and non-collinearity to each estimated model using the *lmtest* package (R Core Team, 2021).

Once the full models were finalized, we created bivariate linear regression models for each remaining predictor to better understand how each factor alone predicted variability in IWG grain yields, summer forage yields, and fall forage yields.

## 3 Results

### 3.1 Climate

Over the past 40 years (1979–2022), the month with the lowest average temperature (Feb) and highest average temperature (Aug) were consistent across locations; while the lowest mean temperatures ( $-0.16^{\circ}\text{C}$ ) occurred at MN-ROS and the highest ( $25.3^{\circ}\text{C}$ ) at KS-TLI (Table 1).

The 1979–2022 the minimum precipitation (Prcp) occurred in January or February at all locations. Maximum Prcp occurred in spring for KS-TLI, NE, and OH, and spring-summer for WI-MFAI, WI-UW and MN-ROS (Figure 3). The maximum actual evapotranspiration (Eta) occurred during late spring and summer in all locations. Precipitation varied seasonally for all locations, as was the case for Eta at KS-TLI, NE and MN-ROS (Supplementary Figures S2, S3). The evaporative fraction (Ef) was highest during late spring and summer months, and NE, MN and WI-UW had the highest values, while WI-MFAI and OH had the lowest (Supplementary Figure S4).

Temperature trends during our study period of 2021–2022 were similar to the long-term averages from 1979–2022, with the minimum occurring in February and maximum in August. MN-ROS was an exception with maximum temperatures in June (Figure 3). The years 2021 and 2022 had notably less precipitation than 1979–2022 means at all locations (by 188 and 153 mm in KS-TLI; 301 and 517 mm in NE, 186 and 198 mm in MN-ROS; 341 and 19 mm in WI-UW; 314 and 71 mm in WI-MFAI; 274 and 69 mm in OH, lower annual and accumulated Prcp, respectively; Figures 2, 3). Annual Prcp at NE was exceptionally low relative to its long-term average and was the lowest of all locations (367 mm). May and June 2022 were the only months at KS-TLI and NE that were not drier than average during our study. In this two-month window, Prcp in KS-TLI was higher (by 142 (May) and 79 (June) mm) than the 1979–2022 averages. Higher than average (by 73 mm) Prcp also occurred in MN-ROS in August 2022 (Figure 3; Table 1, Supplementary Table S7).

### 3.2 Soil characteristics

Soil parameters were statistically different across locations and with depth (Table 3, Supplementary Tables S9, S10). These location differences were reflected in the crop productivity index (Supplementary Figure S1). Soil texture analysis showed that all locations had relatively fine soil, ranging from loam to silty clay loam or silt loam 0–20 cm. At 50–90 cm, the texture was coarser,

sandy clay loam in WI-MFAI, and loam for MN-ROS and OH. Soil organic matter (SOM) percentage varied across depths and locations with SOM being lower at depth at a given location. The highest SOM was reported at MN-ROS at  $56\text{ g kg}^{-1}$ , at 0–20 cm, and the lowest values being reported at OH and WI-MFAI at  $11.5\text{ g kg}^{-1}$  at the 50–90 cm depth.

### 3.3 Establishment, growth, and yields across locations

Establishment success, measured by plant counts after germination, varied across locations ( $p < 0.001$ ). KS-TLI had the lowest plant count at an average of  $5 \pm 4\text{ plants m}^{-1}$  and OH had the highest, at an average of  $23 \pm 3.0\text{ plants m}^{-1}$  (Table 4, Supplementary Table S11).

IWG reached the anthesis growth stage at a similar timing at the MN-ROS, WI-MFAI, and WI-UW sites both when measured by DOY (day 181, 186 and 186 respectively) and by GDD ( $1249^{\circ}\text{Cd}$ ,  $1391^{\circ}\text{Cd}$ ,  $1378^{\circ}\text{Cd}$ ). KS-TLI and NE also reached anthesis at a similar DOY (164 and 174 respectively) and GDD ( $1536^{\circ}\text{Cd}$  and  $1422^{\circ}\text{Cd}$  respectively). OH had the earliest DOY of anthesis (day 161) and the least GDD  $1153^{\circ}\text{Cd}$  to anthesis across the locations (Figures 2A, B).

IWG yields varied significantly by location ( $p < 0.001$ ). MN-ROS had the lowest mean grain yields at  $556 \pm 34\text{ kg ha}^{-1}$  and WI-UW had the highest mean grain yields at  $1343 \pm 24\text{ kg ha}^{-1}$  for IWG (Figure 4, Table 4, Supplementary Table S11). Summer forage mean yields varied across locations with the lowest being at WI-MFAI at  $2054 \pm 124\text{ kg ha}^{-1}$  and the highest at WI-UW at  $8930 \pm 159\text{ kg ha}^{-1}$ .

### 3.4 Modeling the climate and soil predictors of grain and forage yields

Various combinations of soil nutrient concentrations, percent sand, aggregate stability, and climate variables including Prcp60Anthesis, EtaCrop, and PrcpCrop explained 74%, 92% and 69% of the variability in grain (Equation 2), summer forage (Equation 3) and fall forage (Equation 4) yields, respectively, across locations ( $p < 0.001$ ) (Tables 5, 6; Supplementary Table S12). Variables that best explained each harvest product varied, though all included some measure of precipitation (Table 6). The final models were as follows:

$$\begin{aligned} \text{IWG grain} = & 911.3 + (K \times (-0.57)) + \\ & (Mg \times 0.44) + (Na \times 16.1) + (P \times 14.6) + \\ & (Prcp60Anthesis \times 4.8) + (S \times -25.9) + (Sand \times -5.53) \end{aligned} \quad (2)$$

$$\begin{aligned} \text{IWG summer forage} = & 5221.3 + \\ & (Agg\text{ Stability} \times 2.5) + (EtaCrop \times 12.2) + (Mg \times 2.0) \\ & + (Na \times 83.4) + (SOM \times 623.3) + (P \times 40.1) + \\ & (Prcp60Anthesis \times 51.0) + (S \times -150.0) \end{aligned} \quad (3)$$

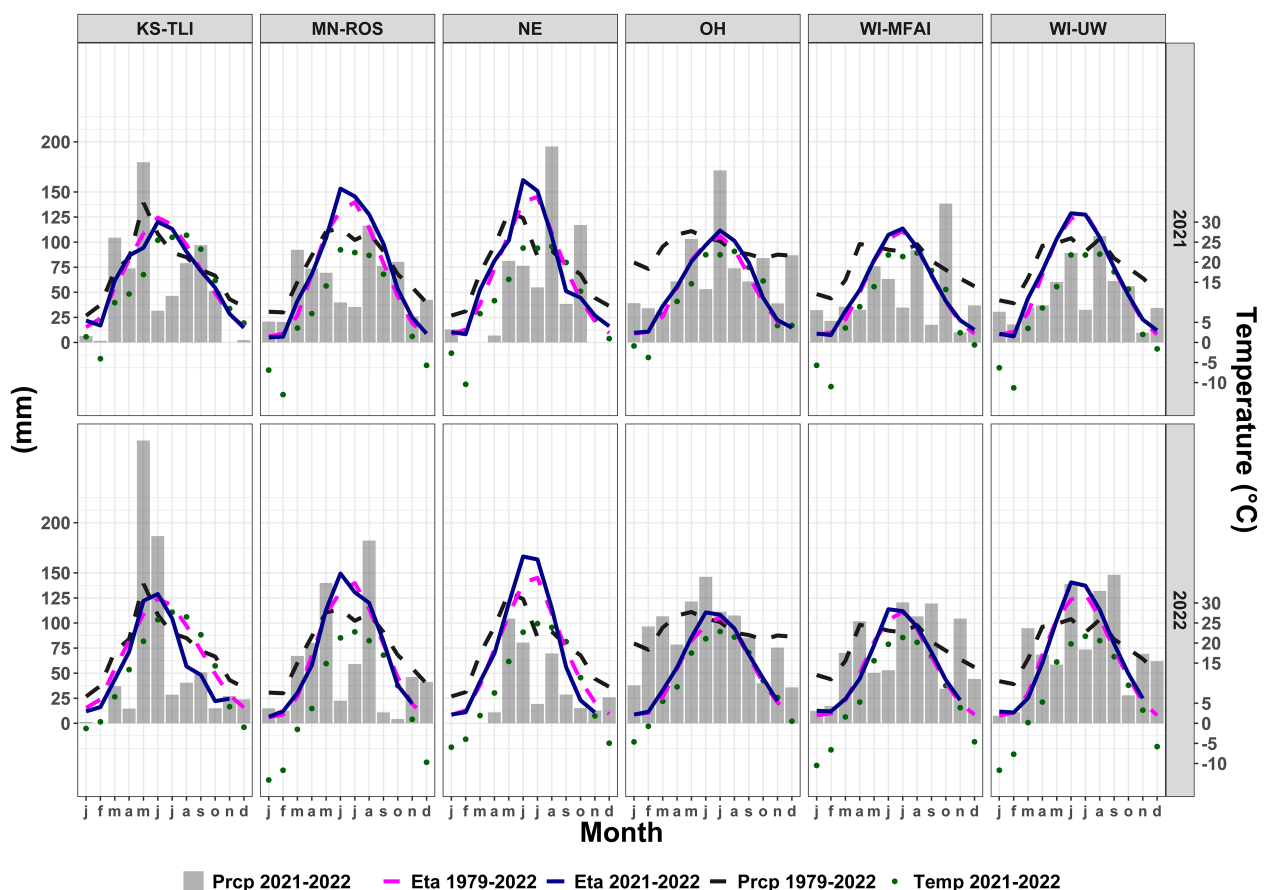


FIGURE 3

Mean monthly 2021–22 precipitation (Prpc, gray bars), 1979–2022 Prpc (black dashed lines), 2021–22 actual evapotranspiration (Eta; dark blue lines), 1979–2022 Eta (pink dashed lines), and 2021–22 temperature (green dotted lines) for each location. The left-hand y-axis shows mm of Prpc or Eta, and the right-hand y-axis shows the temperature (°C). The x-axis shows the month of the year for each location.

$$\begin{aligned}
 \text{IWG fall forage} = & 1988.2 + \\
 & (\text{Agg Stability} \times 1.4) + (K \times 11) + (Mg \times -6.1) \\
 & + (Na \times 68.7) + (SOM \times 410.9) + (P \times -93.4) + \\
 & (\text{PrpcCrop} \times -7.8)
 \end{aligned}
 \quad (4)$$

After model construction, we performed individual regressions for those variables included in the final models (Table 7). Based on this analysis, we found that Prpc60Anthesis (accumulated precipitation 60 days before anthesis) had the greatest influence on grain and summer forage yields and alone explained 21% and 45% of the yield variability in the individual regressions respectively (Table 7). By contrast, PrpcCrop (accumulated precipitation from May to October) alone explained 2% of the variability in fall forage (Table 7). Alone, EtaCrop (accumulated actual evapotranspiration from May to October) alone also had an important influence on summer forage and explained 20% of the variability based on individual regressions (Table 7).

Soil variables tended to explain less of the variation in yields in individual regressions than precipitation with the exception of fall forage. Mg, Na and P explained 28% in grain, 9% summer forage and 47% fall forage when individual regressions were summed (Table 7). K explained 7% in grain and 30% fall forage yields models (Table 7). Agg Stability (soil water stable aggregate stability) explained 15% and 5% in

summer and fall forage model in individual regressions (Table 7). Sand explained 32% of grain yields in individual regressions (Table 7). A difference between the individual regressions and the full multiple linear regression models was that although the full multiple linear regressions showed positive relationships with each response variable, some individual regressions demonstrated negative relationships with the response variables (Tables 6, 7).

### 3.5 Yield responses to fertility treatments

Neither fertility treatment alone nor the interaction of treatment by location influenced grain yields ( $p > 0.05$ ). Treatment and location both influenced IWG summer forage yield ( $p < 0.05$  and  $p < 0.001$  respectively; Figure 5, Table 4). Among treatments, only the addition of  $135 \text{ kg ha}^{-1}$  spring applied mineral N increased summer forage yields compared to the no N control ( $p < 0.05$ ; Figure 5, Table 4). Fall forage yields were affected by the interaction of treatment and location ( $p < 0.01$ ; Figure 6, Table 4), where treatments with 90 and  $180 \text{ kg N ha}^{-1}$  of spring mineral applied N had mean yields significantly greater than when no N was applied, only at the NE location or when fall forage was averaged across locations ( $p < 0.05$ ; Figure 6, Table 4, Supplementary Table S11).

TABLE 3 Means (SE) of soil parameters analyzed for each depth and location: clay (g kg<sup>-1</sup>), sand (g kg<sup>-1</sup>), silt (g kg<sup>-1</sup>), pH, cation exchange capacity (CEC), phosphorus (P), potassium (K), soil organic matter (SOM), mineral N (Min N), mean weight diameter (MWD) and bulk density (Bd). The 0–90 cm depth increment represents the parameter value averaged across the entire depth profile.

| Location                 | depth (cm) | Clay (g kg <sup>-1</sup> ) | Sand (g kg <sup>-1</sup> ) | Silt (g kg <sup>-1</sup> ) | pH         | CEC (cmolc kg-1) | P (mg kg-1) | K (mg kg-1) | SOM (g kg <sup>-1</sup> ) | Min N (mg kg-1) | MWD (mm)     | Bd (g cm-3)  |
|--------------------------|------------|----------------------------|----------------------------|----------------------------|------------|------------------|-------------|-------------|---------------------------|-----------------|--------------|--------------|
| KS-TLI                   | 0 – 20     | 29.2 (0.7)                 | 15.8 (1.3)                 | 54.9 (1.3)                 | 8.0 (0.01) | 37 (0.5)         | 21 (0.7)    | 322 (9.0)   | 3.33 (0.08)               | 4.43 (0.47)     | 1.442 (0.03) | 1.23 (0.006) |
|                          | 20 – 50    | 35.7 (2.4)                 | 14.4 (1.4)                 | 49.9 (1.9)                 | 8.1 (0.02) | 56 (2.3)         | 7 (0.3)     | 186 (11.1)  | 2.55 (0.16)               | NA              | NA           | 1.13 (0.004) |
|                          | 50 – 90    | 39.3 (3.0)                 | 12.9 (1.8)                 | 47.8 (2.6)                 | 8.2 (0.02) | 76 (2.7)         | 5 (0.13)    | 172 (10.0)  | 2.06 (0.15)               | NA              | NA           | 1.16 (0.008) |
|                          | 0 – 90     | 34.7 (1.4)                 | 14.4 (0.9)                 | 50.9 (1.2)                 | 8.1 (0.01) | 56 (2.2)         | 11 (0.92)   | 227 (9.9)   | 2.65 (0.10)               | NA              | NA           | 1.17 (0.006) |
| MN-ROS                   | 0 – 20     | 21.5 (0.5)                 | 21.5 (1.0)                 | 57.0 (0.7)                 | 6.0 (0.11) | 25 (0.7)         | 48 (2.5)    | 126 (4.0)   | 5.60 (0.15)               | 8.37 (1.98)     | 1.586 (0.03) | 1.30 (0.03)  |
|                          | 20 – 50    | 20.3 (0.7)                 | 22.1 (1.2)                 | 57.6 (1.2)                 | 6.1 (0.08) | 21 (1.0)         | 16 (1.4)    | 76 (2.7)    | 4.13 (0.27)               | NA              | NA           | 1.29 (0.02)  |
|                          | 50 – 90    | 18.5 (0.6)                 | 32.6 (3.0)                 | 48.9 (2.7)                 | 6.7 (0.13) | 16 (0.6)         | 11 (0.8)    | 74 (2.6)    | 1.89 (0.12)               | NA              | NA           | 1.32 (0.05)  |
|                          | 0 – 90     | 20.1 (0.4)                 | 25.3 (1.3)                 | 54.5 (1.1)                 | 6.3 (0.07) | 21 (0.6)         | 25 (2.16)   | 92 (3.4)    | 3.87 (0.21)               | NA              | NA           | 1.31 (0.021) |
| NE                       | 0 – 20     | 26.8 (0.7)                 | 13.4 (0.9)                 | 59.9 (1.0)                 | 5.8 (0.05) | 17 (0.2)         | 64 (4.6)    | 403 (24.0)  | 3.98 (0.12)               | 7.14 (1.65)     | 1.058 (0.04) | 1.40 (0.01)  |
|                          | 20 – 50    | 28.7 (0.6)                 | 12.3 (0.8)                 | 59.0 (0.7)                 | 5.8 (0.5)  | 16 (0.2)         | 32 (3.8)    | 246 (27.0)  | 3.56 (0.11)               | NA              | NA           | 1.35 (0.01)  |
|                          | 50 – 90    | 33.9 (0.5)                 | 9.6 (1.0)                  | 56.5 (0.9)                 | 6.3 (0.6)  | 18 (0.3)         | 25 (1.4)    | 307 (36.0)  | 2.88 (0.06)               | NA              | NA           | 1.81 (0.2)   |
|                          | 0 – 90     | 29.8 (0.5)                 | 11.7 (0.5)                 | 58.5 (0.5)                 | 5.9 (0.04) | 17 (0.2)         | 40 (2.82)   | 319 (18.5)  | 3.47 (0.08)               | NA              | NA           | 1.52 (0.03)  |
| OH                       | 0 – 20     | 15.4 (0.7)                 | 21.4 (1.0)                 | 63.2 (1.0)                 | 6.3 (0.09) | 9 (0.1)          | 23 (2.1)    | 102 (4.7)   | 2.25 (0.06)               | 9.17 (2.90)     | 1.231 (0.02) | 1.14 (0.03)  |
|                          | 20 – 50    | 20.5 (0.4)                 | 24.3 (1.2)                 | 55.2 (1.0)                 | 6.3 (0.1)  | 10 (0.3)         | 8 (0.5)     | 69 (2.2)    | 1.33 (0.03)               | NA              | NA           | 1.39 (0.04)  |
|                          | 50 – 90    | 20.2 (0.4)                 | 37.8 (1.0)                 | 42.0 (0.9)                 | 5.3 (0.05) | 14 (0.4)         | 4 (0.4)     | 69 (1.3)    | 1.16 (0.03)               | NA              | NA           | 1.47 (0.04)  |
|                          | 0 – 90     | 18.7 (0.4)                 | 27.9 (1.0)                 | 53.4 (1.2)                 | 5.9 (0.07) | 11 (0.3)         | 12 (1.2)    | 80 (2.5)    | 1.58 (0.06)               | NA              | NA           | 1.34 (0.03)  |
| WI-MFAI                  | 0 – 20     | 18.9 (0.8)                 | 34.7 (2.0)                 | 46.4 (2.4)                 | 6.1 (0.09) | 14 (0.3)         | 27 (2)      | 98 (5.9)    | 2.39 (0.08)               | 17.10 (5.32)    | 1.477 (0.02) | NA           |
|                          | 20 – 50    | 24.1 (0.8)                 | 34.9 (2.7)                 | 41.0 (2.6)                 | 6.7 (0.09) | 15 (0.5)         | 16 (1.1)    | 81 (3.9)    | 1.54 (0.04)               | NA              | NA           | NA           |
|                          | 50 – 90    | 21.4 (1.3)                 | 54.4 (4.4)                 | 24.2 (3.4)                 | 6.8 (0.13) | 13 (0.8)         | 26 (2.4)    | 82 (4.6)    | 1.15 (0.12)               | NA              | NA           | NA           |
|                          | 0 – 90     | 21.8 (0.6)                 | 40.6 (2.0)                 | 37.6 (1.9)                 | 6.5 (0.07) | 14 (0.3)         | 23 (1.18)   | 88 (2.8)    | 1.70 (0.08)               | NA              | NA           | NA           |
| WI-UW                    | 0 – 20     | 21.1 (0.2)                 | 14.2 (0.7)                 | 64.7 (0.7)                 | 6.2 (0.04) | 17 (0.3)         | 20 (0.7)    | 91 (3.0)    | 4.07 (0.09)               | 4.26 (1.0)      | 1.440 (0.02) | 1.24 (0.02)  |
|                          | 20 – 50    | 24.4 (0.4)                 | 11.5 (0.6)                 | 64.1 (0.5)                 | 6.5 (0.04) | 14 (0.2)         | 10 (0.4)    | 67 (1.0)    | 2.68 (0.06)               | NA              | NA           | 1.21 (0.02)  |
|                          | 50 – 90    | 27.1 (0.3)                 | 11.4 (0.7)                 | 61.6 (0.6)                 | 6.0 (0.04) | 18 (0.2)         | 31 (0.9)    | 96 (2.0)    | 2.09 (0.05)               | NA              | NA           | 1.29 (0.02)  |
|                          | 0 – 90     | 24.2 (0.3)                 | 12.3 (0.4)                 | 63.5 (0.4)                 | 6.2 (0.03) | 16 (0.23)        | 20 (1.08)   | 85 (2.0)    | 2.94 (0.11)               | NA              | NA           | 1.25 (0.01)  |
| Significance by location |            | ***                        | ***                        | ***                        | ***        | ***              | ***         | ***         | ***                       | ***             | ***          | ***          |

NA, data not available.  
\*\*\*Significant at the.001 probability level.

TABLE 4 Results of mixed model analysis of variance (ANOVA) F-statistic and statistical significance values of IWG grain, summer and fall forage.

| ANOVA results | F - statistic |     |             |     |                     |     |                    |
|---------------|---------------|-----|-------------|-----|---------------------|-----|--------------------|
|               | Plant counts† |     | Grain yield |     | Summer forage yield |     | Fall forage yield† |
| treatment (T) | –             |     | 0.5646      | NS  | 2.372               | *   | 15.78 ***          |
| location (L)  | 300.8         | *** | 54.66       | *** | 234.4               | *** | 40.25 ***          |
| T*L           | –             |     | 0.8036      | NS  | 0.7810              | NS  | 2.838 **           |

\*Significant at the.05 probability level; \*\*Significant at the.01 probability level; \*\*\*Significant at the.001 probability level. NS, not significant.† square root transformed.

4 Discussion

Research and commercial production of IWG has been focused within a few states and regions but is now rapidly expanding to new

regions. This is the most comprehensive study to date to examine the climate, soil, establishment, and fertilizer management effects on both grain and forage yields of the IWG MN-Clearwater variety in regions with increasing grower presence. At these multiple locations, we used a multiple regression analysis to determine which local factors most explain first year yields in order to generalize or guide future research to regions even beyond those studied here. Our specific objective was to understand how the first year of IWG establishment and yields (grain, summer and fall forage) were related to fertilization strategies and environmental conditions across six locations in the Midwestern United States. While other factors such as weed pressure and seeding date have been explored as factors influencing IWG establishment in the first year, the intersection of climate and fertility has been less explored. We expected that grain and forage yields would be mainly determined by soil and climate characteristics and would be further modified by fertilization treatments. These expectations were only partially confirmed.

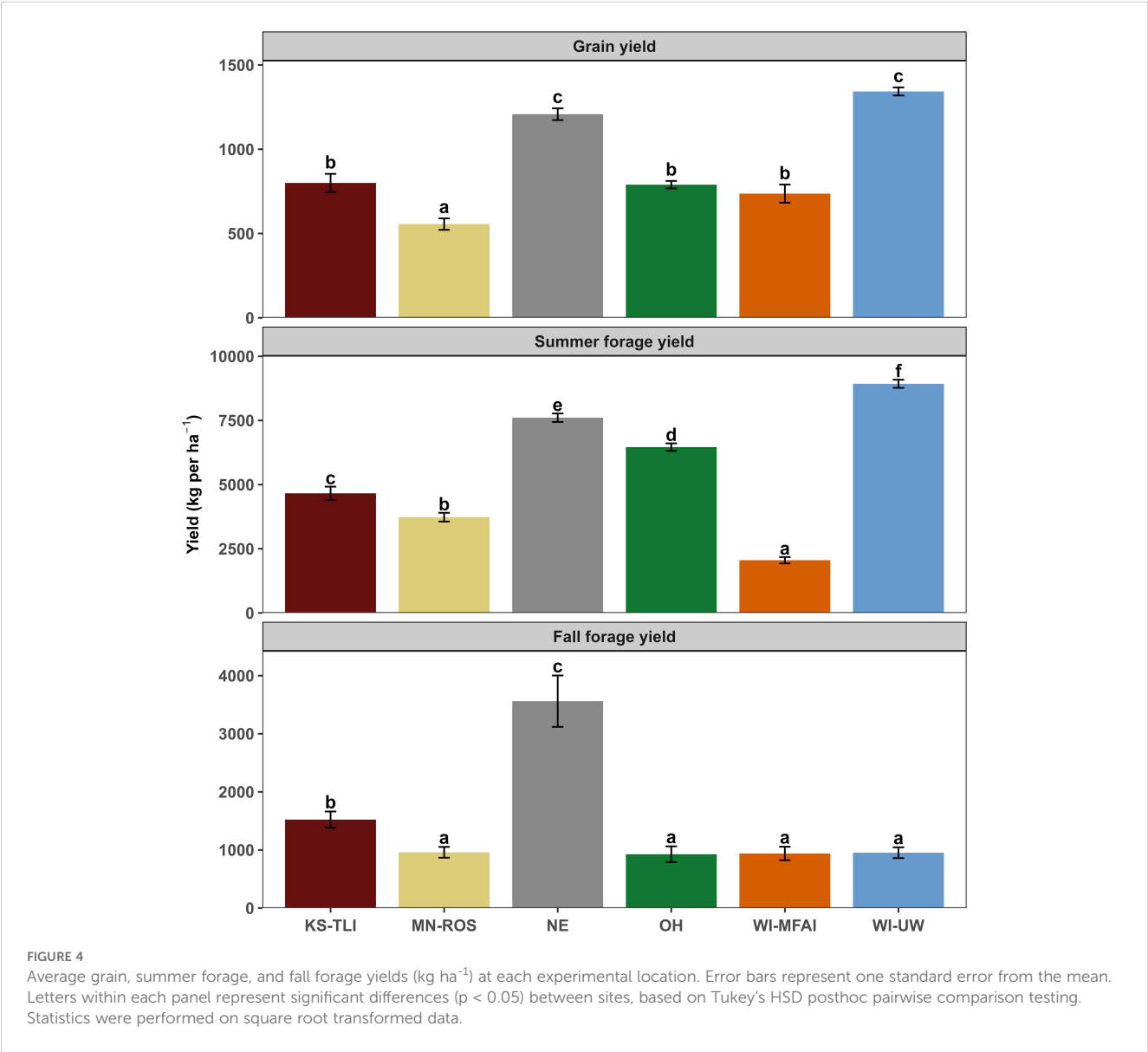




TABLE 5 Multiple Linear Regression model output statistics for IWG grain, summer and fall forage yields for soil parameters and climate data that were significant in final models

| Multiple Linear RegressionFull Model Statistics |                |           |
|-------------------------------------------------|----------------|-----------|
|                                                 | R <sup>2</sup> | F-value   |
| Grain                                           | 0.74           | 38.060*** |
| Summer forage                                   | 0.92           | 119.6***  |
| Fall forage                                     | 0.69           | 20.6***   |

Asterisks indicate significance levels as follows:  
. Significant at the 0.1 probability level.  
\* Significant at the .05 probability level.  
\*\* Significant at the .01 probability level.  
\*\*\* Significant at the .001 probability level.

#### 4.1 IWG establishment

Establishment of IWG varied significantly across locations with OH having more than double, and KS-TLI with less than half the number of plants per length of planted row than the other locations (MN-ROS, WI-UW, WI-MFAI, and NE (Table 4). The low establishment observed at KS-TLI could have been associated with low precipitation at that location during the months around seeding (Figure 3). Despite variability across locations, plant counts did not predict grain or biomass yields. IWG spreads via tillers and rhizomes that can take up space between plants within sown rows. This ability to vegetatively propagate is an establishment strategy in the first year of growth (Woeltjen et al., 2024; Shoenberger, 2022). Because of this, initial plant counts in the range we observed (5.3–23 plants per m<sup>1</sup>) are expected to be able to produce a robust stand in the first year given other growth conditions and agronomic variables such as weed pressure. Research is needed to determine threshold plant populations for IWG after establishment and the first winter period to inform growers on when stands should be terminated as a result of poor establishment. Such information is available for overwintering crops like winter wheat and canola, for example (Paulsen, 1987; Assefa et al., 2018).

#### 4.2 Variability of IWG grain and forage yields across locations

First year IWG grain yields (ranging from 586–1343 kg ha<sup>-1</sup>) were similar to and sometimes higher than year 1 yields reported in other studies (ranging from 494–1074 kg ha<sup>-1</sup>; see Supplementary Table S1 for a summary of publications reporting grain yields). WI-UW and KS-TLI yields were ~30% and ~20 – 30% higher than those described in the literature for Wisconsin and Kansas respectively (Bowden, 2023; Culman et al., 2023; Pinto et al., 2022).

At the same time, MN-ROS yields were ~20 – 25% lower than those reported in other literature from Minnesota, WI-MFAI yields were 35% lower than other reports from Wisconsin, and OH yields

TABLE 6 Multiple linear regression detailed results for those soil parameters and climate data included in final models for IWG grain, summer forage, and fall forage yields.

| Multiple Linear RegressionVariables included in the full model |          |
|----------------------------------------------------------------|----------|
|                                                                | t-value  |
| Grain                                                          |          |
| (Intercept)                                                    | 48.95*** |
| K                                                              | -1.77    |
| Mg                                                             | 2.49*    |
| Na                                                             | 2.43*    |
| P                                                              | 5.61***  |
| Prpc60Anthesis                                                 | 9.87***  |
| S                                                              | -4.11*** |
| Sand                                                           | -2.52*   |
| Summer forage                                                  |          |
| (Intercept)                                                    | 62.87*** |
| Agg Stability                                                  | 4.08**   |
| EtaCrop                                                        | 4.15***  |
| Mg                                                             | 2.41*    |
| Na                                                             | 3.07***  |
| SOM                                                            | 4.04***  |
| P                                                              | 3.18**   |
| Prpc60Anthesis                                                 | 19.6***  |
| S                                                              | -5.22*** |
| Fall forage                                                    |          |
| (Intercept)                                                    | 16.58*** |
| Agg Stability                                                  | 1.82     |
| K                                                              | 6.33***  |
| Mg                                                             | -5.5***  |
| Na                                                             | 1.77     |
| SOM                                                            | 2.75**   |
| P                                                              | -4.82*** |
| PrpcCrop                                                       | -2.72**  |

Variables included are listed as follows: potassium (K, mg kg<sup>-1</sup>), magnesium (Mg, mg kg<sup>-1</sup>), sodium (Na, mg kg<sup>-1</sup>), phosphorus (P, mg kg<sup>-1</sup>), accumulated precipitation 60 days before anthesis 2022 (Prpc60Anthesis), Sulfur (S, mg kg<sup>-1</sup>), Sand (%), Stability of water stable soil aggregates (Agg Stability), cumulative actual evapotranspiration from May-October (EtaCrop), organic matter (SOM, g kg<sup>-1</sup>), and accumulated precipitation from May-October (PrpcCrop). P-values and associated t-values indicate the significance and relative contribution of the included variables.  
Significance levels  
. Significant at the 0.1 probability level.  
\* Significant at the .05 probability level.  
\*\* Significant at the .01 probability level.  
\*\*\* Significant at the .001 probability level.

**TABLE 7** Individual linear regression for IWG grain, summer and fall forage yields for soil parameters and climate data that were significant in final multiple linear regression models.

| Statistic            | Estimate        | R <sup>2</sup> |
|----------------------|-----------------|----------------|
| <b>Grain</b>         |                 |                |
| K                    | 0.81 (0.30)     | 0.07**         |
| Mg                   | 0.37 (0.21)     | 0.03           |
| Na                   | 38.79 (8.88)    | 0.16***        |
| P                    | 9.31 (3.01)     | 0.09**         |
| Prpc60Anthesis       | 2.96 (0.58)     | 0.21***        |
| S                    | -32.90 (8.43)   | 0.13***        |
| Sand                 | -16.65 (2.45)   | 0.32***        |
| <b>Summer forage</b> |                 |                |
| Agg Stability        | -4.56 (1.16)    | 0.15***        |
| EtaCrop              | 18.52 (3.96)    | 0.20***        |
| Mg                   | 0.052 (1.69)    | 0.00001        |
| Na                   | 212.26 (75.00)  | 0.08**         |
| SOM                  | 856.0 (280.9)   | 0.1**          |
| P                    | 25.16 (26.37)   | 0.01           |
| Prpc60Anthesis       | 33.03 (3.89)    | 0.45***        |
| S                    | -248.91 (85.96) | 0.09**         |
| <b>Fall forage</b>   |                 |                |
| Agg Stability        | -1.47 (0.79)    | 0.05           |
| K                    | 7.60 (1.39)     | 0.30***        |
| Mg                   | -6.31 (0.94)    | 0.39***        |
| Na                   | -136.88 (53.80) | 0.08*          |
| SOM                  | 121.4 (211.1)   | 0.01           |
| P                    | -3.99 (15.95)   | 0.0008         |
| PrpcCrop             | 30.08 (2.34)    | 0.02           |

Variables included are as follows: potassium (K, mg kg<sup>-1</sup>), magnesium (Mg, mg kg<sup>-1</sup>), sodium (Na, mg kg<sup>-1</sup>), phosphorus (P, mg kg<sup>-1</sup>), accumulated precipitation 60 days before anthesis 2022 (Prpc60Anthesis), Sulfur (S, mg kg<sup>-1</sup>), Sand (%), Stability of water stable soil aggregates (Agg Stability), cumulative actual evapotranspiration from May-October (EtaCrop), organic matter (SOM, g kg<sup>-1</sup>), and accumulated precipitation from May-October (PrpcCrop).

Significance

.Significant at the 0.1 probability level.

\*Significant at the 0.05 probability level.

\*\*Significant at the 0.01 probability level.

\*\*\*Significant at the 0.001 probability level.

were similar to previous findings from Ohio (Bowden, 2023; Culman et al., 2023; Pinto et al., 2022; Bajgain et al., 2020; Fernandez et al., 2020). The highest IWG grain yields are typically observed during the first production year. Although some studies have reported comparable or higher yields in second-year stands (Culman et al., 2013; Bowden, 2023), a decline over time is more commonly observed when IWG is well established in the first year (Culman et al., 2023; Pinto et al., 2024; Bajgain et al., 2020; Mårtensson et al., 2022; Tautges et al.,

2018; Zhen et al., 2024). Also, as discussed below, precipitation in the 60 day period before anthesis and local soil characteristics could be related to variance in grain yields across locations. Based on these results, expectations of yields should be established on a regional basis with the knowledge there is likely significant local variation in IWG performance depending on precipitation and establishment in the first growing year.

IWG summer forage yields also differed across locations. Similar to the trend with grain yields, WI-UW summer forage (8930 kg ha<sup>-1</sup>) was ~30–50% higher than that previously reported for Wisconsin (Pinto et al., 2024; Culman et al., 2023) (see [Supplementary Table S1](#) for a summary of publications reporting summer forage yields), and summer forage values at MN-ROS were ~20–75% lower than those previously reported for Minnesota (Bowden, 2023; Culman et al., 2023). KS-TLI summer forage yields were roughly the same as those previously reported in Kansas for the MN-Clearwater variety (Bowden, 2023) but ~20% higher than those previously reported for C4 TLI variety (Culman et al., 2023). This makes sense in that higher productivity is a major breeding goal (Bajgain et al., 2020). Although fall forage yields were lower than summer forage yields (Table S11), they were not as variable as summer forage yield by location, with the exception of NE, which had ~50–75% higher yield than the other sites. Together, the variance we and others have observed in grain and summer forage yields indicates a need to better understand what could give rise to this large range in growth from one year or location to the next. Fall forage has not been as extensively studied across our study locations, but our range of fall forage biomass, when averaged across locations, were similar to that reported previously (Pinto et al., 2024; Culman et al., 2023), with the average at NE approximately two-three times higher. Below, we discuss how climate and soil variables were also related to this variance in biomass yields across locations.

### 4.3 Modeled influence of climate and soil variables

One objective of our study was to determine the extent to which local climate and soil conditions explained variance of first year grain and forage yields. The context within which we performed this analysis with a first growing year of 2022 was that at our experimental locations, the temperature and precipitation in 2021 and 2022 were respectively colder and drier than the 1979–2022 means for all locations except OH, which had temperature similar to the historic average (Table 1). The drier conditions observed over this region are in line with the climate change patterns observed since 1900 across the Midwest (Yu et al., 2018). Although precipitation levels in the eastern Midwest were below average, they were still higher than the western Midwest region in 2022 as is typical (Marvel et al., 2023). Actual evapotranspiration (Eta) also varied across locations (Table 1, Figure 3). The relationship between Eta and precipitation determines the level of agricultural drought (Wilhite and Glantz, 1985). KS-TLI and NE are often at risk of drought because they have higher probability of seasonal crop

moisture deficit (Wilhelmi and Wilhite, 2002; Logan et al., 2010), more so than the other locations in our study (Yu et al., 2018) (Supplementary Table S5, Supplementary Figure S3).

Of the climate variables identified after model selection, cumulative precipitation 60 days before anthesis (Prpc60Anthesis) was the strongest predictor of grain and summer forage yields (Table 6). According to our multiple linear regression models, for every 1 mm increase in Prpc60Anthesis, we would expect  $4.7 \pm 0.5$  and  $50.9 \pm 2.6$  kg ha<sup>-1</sup> grain and forage increase respectively when other environmental conditions are held constant (Equations 2, 3).

In previous studies, temperature was more strongly related to grain and summer forage yields than precipitation (Culman et al., 2023), with precipitation explaining 16% and 6% of variability in grain and summer forage yields respectively. In this study, narrowing the window of precipitation to relate to yield may have strengthened this relationship as the 60 days before anthesis explained 21% to 45% of the variability of grain and summer forage yields (Table 7). The importance of this period of precipitation before anthesis is demonstrated by some of the observed trends. For example, while the MN-ROS location had a similar amount of annual cumulative precipitation as several other locations in 2021 and 2022, it had the lowest yields in the study perhaps because it also had 47% lower precipitation in this window compared to the average across locations. This may also explain why the WI-MFAI had significantly lower yields than the WI-UW location despite similar historical climate; the WI-MFAI precipitation before anthesis was 35% below average across locations while WI-UW was 12% above. Locations with 189–195 mm precipitation in the 60 days before anthesis had typical or higher than expected yields for the region, whereas locations with lower (MN-ROS, WI-MFAI) and higher (OH) precipitation in this period had significantly lower yields than expected for the region (Supplementary Table S1). We also observed anomalies in these trends. For example, despite having the lowest annual precipitation in 2021 and 2022 and high Eta (Table 1), grain yields from the NE location were among the highest in this study.

Narrowing the window of precipitation analyzed with grain yield resulted in greater correlation with grain yields and may be a meaningful starting point for identifying a ‘critical period’ for IWG. Common annual crops have established critical periods around anthesis when any water, temperature, or light stress influences the number and size of grain (Slafer and Andrade, 1993; Andrade et al., 1999). For example, the critical period for wheat is 20 days before and 10 days after anthesis (Fischer, 1985), while for corn, it is 15 days before and after anthesis (Andrade et al., 1999). Our results point to the potential need to investigate a much longer precipitation window (189–195 mm in the 60 days before anthesis) than for annual crops to infer potential weather impacts to grain and summer forage yields.

The analyses in this study on climate impacts are limited by having a single data point for precipitation and temperature within each location despite wide variation in yield both within and among locations. This could have resulted in the nonsignificant or negative relationships between some climate factors and grain and fall forage yield that seem contradictory to our ecological understanding of

plant growth during moisture limitation (Table 7). Thus, these results are not conclusive about the relationship between precipitation and IWG yield or the critical period for IWG. They do however provide preliminary data from which future determination of the critical period for IWG could be determined. Our results also demonstrate that many factors together influence yield across and within a given climate and that multi-site modeling efforts, with multidisciplinary datasets, are needed to synthesize and elucidate these patterns.

Soil characteristics explained as much or more variance in IWG grain and forage yield data than climate variables in multiple regression models (Tables 5, 6). Soil texture was the most influential variable in explaining grain yields, where each increase in percent sand resulted in a decline of  $16.7 \pm 2.5$  kg grain ha<sup>-1</sup>. Soil texture strongly influences soil water holding capacity, water retention, and provision of nutrients important to plant growth, and the ability of the soil to retain or form soil organic matter (Crews and Rumsey, 2018; Crews et al., 2018; Sprunger et al., 2018). Aggregate stability had a surprisingly negative but consistent relationship with forage yield. NE had lowest aggregate stability but nearly the highest yields, where MN-ROS was the opposite with the highest aggregate stability and lower yields. This could be an inadvertent correlation with baseline soil characteristics. We expect soil aggregate stability to increase with increasing IWG stand age (Rakkar et al., 2023; Chamberlain et al., 2022; Wuest et al., 2006), just as we expect improvements in SOM and infiltration (Culman et al., 2013). Potassium (K), sodium (Na) and magnesium (Mg) also consistently explained variance in our yield data (Tables 5, 6). Very few studies have investigated the IWG requirements of macro or micro-nutrients other than nitrogen but there is evidence that IWG total biomass, grain yield, or yield components can be explained by soil elemental composition (up to 35% of variance for grain yield, 39% for total biomass, 79% for the number of grain producing stems; Muhandiram, 2023). This suggests that although we did not find that other macro or micronutrients explained variance in grain or biomass yields in this study, they could be important for IWG fertility at certain locations.

#### 4.4 IWG grain and summer forage yield responses to fertility treatments

Among all fertilization treatments, the only significant responses we observed were with summer forage when averaged across locations, and fall forage yields when averaged across locations or at NE, with no response from grain yields (Table 4). The lack of grain yield response to fertilizer is common in first year IWG production (Jungers et al., 2018; Reilly et al., 2022b; Pinto et al., 2022), but because these studies all used older varieties of IWG with lower yield potential than MN Clearwater, we had anticipated that we might see stronger year 1 responses. At the same time, a meta-analysis on IWG grain and biomass yields in response to N fertilizer rates showed that grain yields were not affected by increasing N rates in the first year, but a positive effect of N rates on grain yields increased as stands aged (Bianchin

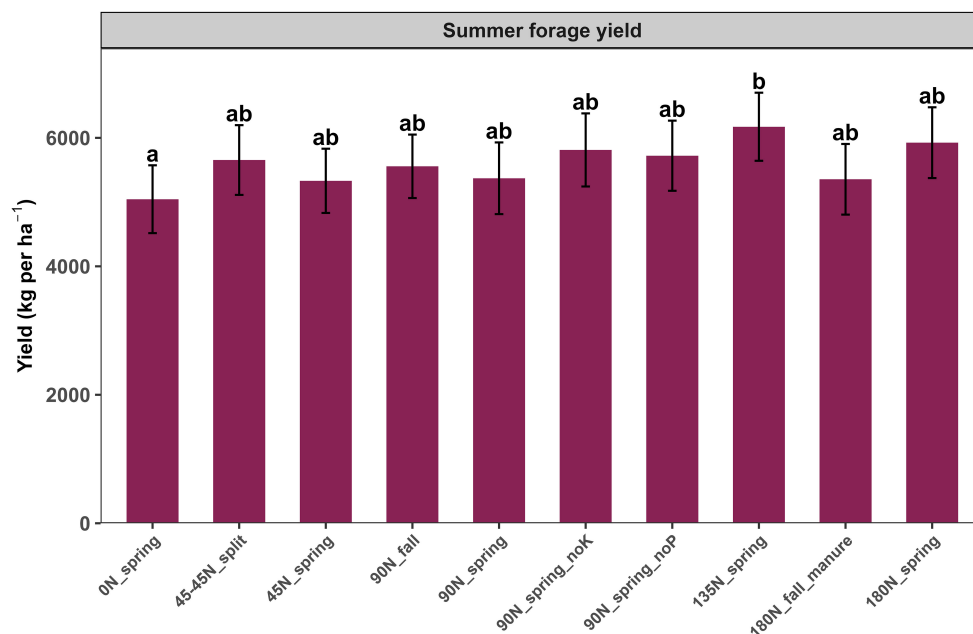


FIGURE 5

Summer forage yields by treatment, averaged across study locations. Error bars represent one standard error from the mean. Letters represent significant differences ( $p < 0.05$ ) between sites, based on Tukey's HSD posthoc pairwise comparison testing.

Rebesquini, 2023). IWG's large and deep root system that can access nutrients deep in the soil profile (Ryan et al., 2018) could be related to the lack of fertilizer response. Endogenous N mineralization from SOM induced by tillage before planting may help explain the lack of N limitation in year one. Between 0.9 and  $\sim 10$  mg N kg<sup>-1</sup> soil has been adequate for fulfilling IWG (Dobbratz et al., 2023) and, more generally, perennial grass demand (Vogel et al., 2002). Locations in this study (except KS-TLI) fell within the low end of that range (Table 3). Thus, it appears that for MN Clearwater, the range of sufficient soil N to meet IWG grain needs in the first year of growth remains the same. Also, since the number of grain producing spikes is highly correlated to grain yields, it could be that domestication traits and environmental factors that control tiller production are as important as fertility management for determining grain yields (Fagnant et al., 2024). With annual removal of N in grain and forage biomass, we expect there will be a grain yield response to treatment in future years as has been observed in other studies (Bianchin Rebesquini, 2023; Pugliese et al., 2019; Pinto et al., 2022; Bowden, 2023).

Although endogenous soil N may be adequate for IWG grain production, we found evidence that IWG may have a higher first year N demand for both summer and fall forage production. We observed summer forage yield responses to N fertilizer when averaged across locations, and fall forage yield responses when averaged across locations and at the NE location (Table S11). Specifically, we found that 135 kg ha<sup>-1</sup> of spring applied N produced  $\sim 19\%$  more summer biomass than the unfertilized control. We also found that both 90 and 180 kg ha<sup>-1</sup> of spring applied N produced  $\sim 55\%$  more fall forage biomass than the unfertilized control at the NE location, and  $\sim 60\%$  more fall forage biomass when averaged across locations (Table S11).

Although N absorption early in the season until the point of spike and grain development may be critical for grain yields, N can continue to be taken up or reallocated in fall for vegetative forage biomass production. There have been inconsistent results in terms of summer forage yield response to fertilizer (Bowden, 2023; Pinto et al., 2022; Reilly et al., 2022b). In the case of fall forage biomass, few studies have reported yield responses to variable N rates (Bowden, 2023; Pinto et al., 2024). In summary, the fertilization strategy of IWG could depend on specific management goals of grain, forage, or dual use Kernza production given that grain versus biomass production may require different N rates or timings in the first year.

## 5 Conclusions

This is the first study to inform a potential critical period for IWG and comprehensively assess soil, climate, and management conditions on both grain and forage production across the U.S. Midwest. We found that in the first harvest year IWG only responds to N fertilization vegetatively (summer and fall forage) and not with grain production. Our study also demonstrates that environmental factors such as precipitation, actual evapotranspiration, and soil characteristics influence IWG grain yields more than fertility management in the first harvest year. Specifically, the cumulative precipitation 60 days before anthesis may be critical for determining grain and summer forage yields, where the cumulative precipitation from May through October may be more important for fall forage yield production. Soil characteristics such as sand content, aggregate stability, magnesium, sodium, and potassium help predict first-year IWG yields as well.

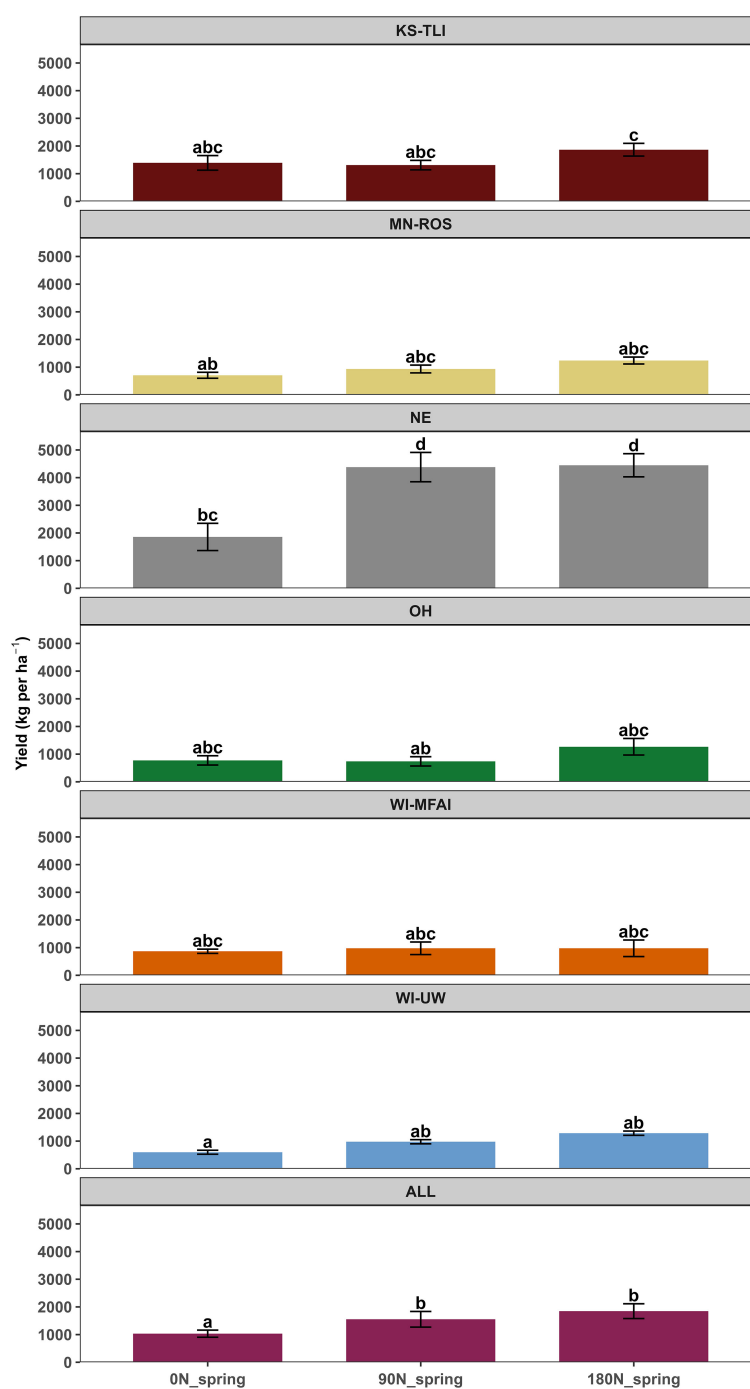


FIGURE 6

Fall forage yields averaged by treatment and location. Error bars represent one standard error from the mean. Statistics were performed on square root transformed data. Letters within each panel represent significant differences ( $p < 0.05$ ) between sites, based on Tukey's HSD posthoc pairwise comparison testing.

The role of precipitation may have been overemphasized in our models compared to edaphic soil characteristics due to the historic drought conditions at several locations during the study period. Despite this, our results could help explain how IWG performs across a range of environmental conditions, even beyond the 6 study sites presented here, which will contribute to a more nuanced decision-making tool for farmers and inform suitable regions for IWG as a viable grain crop.

Models such as those tested here can only provide correlative, not causal, relationships, but will still aid in developing accurate predictions for IWG establishment, first year performance, and refining the critical period for IWG as well. For example, once a more specific critical period is established for IWG in the first year, it can inform producers about whether to invest in a grain harvest in year one or simply harvest IWG for forage, saving resources, if precipitation during the critical



period is below a given threshold. In summary, the relationships described here will be informative to future best practices and outreach to producers establishing new IWG stands.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

MTC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. JG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. AB: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing, Resources. NB: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. TC: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. SC: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. LD: Investigation, Project administration, Resources, Writing – review & editing. CL: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Writing – review & editing. VP: Methodology, Project administration, Resources, Writing – review & editing, Conceptualization, Funding acquisition, Investigation. PP: Conceptualization, Data curation, Investigation, Methodology, Writing – review & editing. RR: Data curation, Investigation, Methodology, Writing – review & editing. NT: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. LP: Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. JJ: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

## Correction note

This article has been corrected with minor changes. These changes do not impact the scientific content of the article.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2025.1528534/full#supplementary-material>

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