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Effects of seeding date on grain and biomass yield of intermediate wheatgrass

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Abstract

Intermediate wheatgrass (*Thinopyrum intermedium*) (IWG) is a perennial grass being domesticated for grain production with potential to provide economic return and ecosystem services across a broad geographic range in North America, yet optimum seeding dates for grain and biomass yield are unknown. Our objective was to determine the effect of late-summer, fall, and spring seeding dates on grain and biomass yield of a grain-type IWG population. Trials were conducted at St. Paul and Roseau, MN, Kalispell, MT, and Salina, KS. Seeding dates ranged from August to June of the following year. Grain and biomass yields were highest when seeded at the earliest late-summer date for all environments except for Kansas, where a September 29 seeding date produced the greatest grain and biomass yields. Little to no grain was produced from spring seedings in the first production year, substantiating that photoperiod and vernalization requirements are needed for seed head induction. Grain and biomass yields were positively correlated to cumulative growing degree days (GDD) from seeding date to winter dormancy. A quadratic response was observed at Salina, KS, where seed yields maximized when GDD accumulation reached 912. Accumulation of vernalization units throughout fall, winter, and spring after seeding was also positively correlated with grain yield. The minimum vernalization units for grain production varied from 50 to 87 across sites. Results highlight important associations between thermal units and IWG grain yield when seeded in late summer; however, other variables affecting IWG seed head induction (e.g., photoperiod, snow cover) require further study.

Abbreviations: IWG, intermediate wheatgrass; GDD, growing degree day.

1 | INTRODUCTION

Intermediate wheatgrass [IWG; *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey] is a cool-season perennial grass introduced into the U.S. in the early 20th century as a forage grass (Hitchcock et al., 1951). Cultivars have been developed for forage production in regions throughout the Intermountain West and Great Plains (Ogle et al., 2011). Because of its large seed size, IWG was identified as a potential perennial grain crop to provide economic return as well as ecosystem services (DeHaan & Ismail, 2017; Wagoner, 1990). Plant breeding programs at The Land Institute and the University of Minnesota have been developing varieties with traits for improved grain yields (Bajgain et al., 2020; DeHaan et al., 2018). Grain harvested from improved, grain-type IWG populations is marketed as Kernza and yields can exceed 1,000 kg ha^{-1} in the first year of production (Jungers et al., 2017). Intermediate wheatgrass produces short rhizomes and a deep, fibrous root system that supports winterhardiness and year-round ground cover. Ecosystem services provided by IWG include reduced nutrient leaching, decreased soil erosion, and potential for reduced greenhouse gas emissions (Culman et al., 2013; de Oliveira et al., 2018; Jungers et al., 2019).

Effective stand establishment is critical for long-term productivity of all perennial crops. For IWG grain production systems in the Midwest, late-summer and fall are the most probable times for successful establishment. Intermediate wheatgrass requires a two-stage induction period with vernalization for flowering (Duchene et al., 2021; Locatelli et al., 2021), thus spring seedings will not produce grain during the first year (Jungers et al., 2017; Kilcher, 1961). Late-summer and fall seedings of IWG in the Midwest may also provide the opportunity for economic return from a spring seeded small grain crop harvested before early August. However, late-summer and fall planting dates can also affect stand establishment if plants are not developed enough to survive winter (Olugbenle et al., 2021). Delayed plantings of perennials in the fall can result in stand mortality and subsequent reductions in biomass yields the year following seeding (Hall, 1995). Previous work with perennial grasses and forage legumes adapted to the northern U.S. has shown that for survival and significant yield the following spring, seeding should occur about 6 wk before the average date of the first killing frost (Hall & Collins, 2018).

Many cool season grasses, including IWG, have fall–winter temperature and photoperiod requirements to induce flowering (Heide, 1994; McDonald et al., 1996). Ivancic et al. (2021) reported that flowering of three grain-type IWG populations were greatest with a 4 ˚C air temperature and 10-h photoperiod, whereas Locatelli et al. (2021) found that flowering reached 95% when IWG plants were exposed to 5 ˚C air temperature and 10-h photoperiod for up to 7 wk. Duchene et al. (2021) modeled IWG phenology and seed head induction requirements using empirical data from four countries on two continents and determined that optimum vernalization temperatures were between 4 and 5 ˚C. Thermal requirements are also important for fall planting dates because IWG needs sufficient morphological development beyond a juvenile stage with developed apical meristems to respond to temperature or photoperiod (Cooper & Calder, 1964). For example, Ketellapper (1960) determined that *Phalaris tuberosa* L., a perennial grass, could be successfully vernalized only when plants had at least three leaves. Like many other cool-season perennial grasses, evidence exists that IWG has dual induction requirements. Duchene et al. (2021) determined that a secondary induction phase based on a photoperiod between 13 and 14 h significantly influenced flowering, but the critical number of long day cycles is still unknown for IWG.

Core Ideas

- Late-summer seeding dates maximized IWG grain and biomass yield.
- IWG seeded in spring did not produce grain the summer immediately after seeding.
- IWG yields were positively correlated with cumulative GDDs between seeding and winter.
- IWG grain yield was positively correlated with cumulative vernalization units.

Intermediate wheatgrass has been successfully established using spring, summer, and fall seedings (Jungers et al., 2017), but the effect of a range of seeding dates on grain and biomass yields is unknown for a broad range of growing environments. Our objective was to determine the effect of late summer, fall, and spring seeding dates on seed and biomass yield of an IWG population developed for grain production and identify potential correlations with temperature on grain and biomass yields. We hypothesized that earlier seeding dates in late summer compared with fall would result in greater IWG grain yields the following year as a result of greater GDD accumulation and biomass production before winter dormancy, and that spring seeding IWG would not produce grain for lack of vernalization and seed head induction requirements.

2 | MATERIALS AND METHODS

2.1 | Seeding date research

Seeding date studies were conducted in 2015–2016 and 2016–2017 at St. Paul, MN (45.00˚ N, 93.09˚ W), in 2016–2017 at Salina, KS (38.84˚ N, 97.61˚ W), in 2017–2018 in Roseau,

TABLE 1 Monthly average temperature and accumulated precipitation for St. Paul, MN from 2015–2017, Salina, KS from 2016–2017, Roseau, MN from 2017–2018, and Kalispell, MT from 2019–2020

	Temperature												
	St. Paul, MN				**Salina, KS**			**Roseau, MN**			**Kalispell, MT**		
Month	**2015**	**2016**	**2017**	**20-yr avg.**	**2016**	**2017**	**20-yr avg.**	**2017**	**2018**	**20-yr avg.**	**2019**	**2020**	**20-yr avg.**
	˚C												
Jan.	−11	−12	−9	−11	0	2	−1	−21	−18	−18	−2	−3	−3
Feb.	−16	−7	2	−8	6	1	1	−12	−16	−14	−6	−1	−3
Mar.	0	3	−1	−1	11	10	8	−2	−6	−7	1	2	2
Apr.	8	7	8	−1	7	14	13	3	−2	3	6	6	7
May	14	7	14	15	19	20	20	10	14	10	14	11	12
June	21	21	22	21	29	28	27	17	18	17	15	14	15
July	23	21	23	23	31	32	29	20	21	20	19	18	19
Aug.	21	23	20	23	29	27	28	23	19	18	18	19	18
Sept.	20	18	18	18	23	24	23	13	12	13	12	14	13
Oct.	10	10	9	10	18	16	15	7	2	5	6	5	6
Nov.	4	6	−2	1	11	8	7	−2	−3	−4	1	2	1
Dec.	−9	−9	−10	−8	−1	1	−1	−18	−17	−14	−2	−2	−3
Avg.	8	8	7	8	14	17	14	2	2	2	7	7	7
	Precipitation												
	mm												
Jan.	8	8	23	15	18	51	20	30	15	20	30	5	30
Feb.	5	20	18	20	10	3	28	28	13	20	46	15	25
Mar.	18	28	15	41	18	91	43	15	3	28	23	8	28
Apr.	51	94	94	81	112	91	64	28	10	41	41	38	41
May	124	56	165	109	140	99	109	10	86	81	33	97	48
June	84	94	81	130	10	41	99	170	46	127	46	122	81
July	157	152	61	114	58	43	89	5	61	84	28	15	20
Aug.	71	249	226	117	198	28	86	41	56	89	13	10	18
Sept.	97	132	30	76	30	46	66	163	84	74	53	8	30
Oct.	74	84	122	69	58	147	46	58	81	64	23	64	33
Nov.	114	69	10	33	15	3	28	18	25	28	23	46	28
Dec.	53	51	15	28	20	3	813	36	38	23	13	23	33
Total	861	1,059	866	866	696	645	711	605	620	678	373	447	417

Note. Avg, average. Averaged data over 20 yr (1997–2017) are included as a comparison.

MN (48.84˚ N, 95.76˚ W), and 2019–2020 in Kalispell, MT (48.18˚ N, 114.13˚ W). The experiment was also established in San Angelo, TX and Booneville, AR in 2019, but drought and weed pressure prevented successful stand establishment. The four locations varied in monthly average temperature and monthly cumulative precipitation (Table 1). The experimental design at each location was a randomized complete block with four replications. Seeding date treatments varied the date of seeding by intervals of approximately 2–4 wk from August to December and April to June. The exact date of seeding varied by location and year, and these dates can be found in Table 2. Intermediate wheatgrass seed used for this study was from a single breeding population developed at The Land Institute in Salina, KS from four cycles of selection for yield per head, threshability, uniform maturity, and seed size (DeHaan et al., 2018). Seed from a single seed lot was used across all experiments, locations, and years of study. Intermediate wheatgrass was seeded at a rate of 50 pure live seeds m^{-1}. Treatments were randomly assigned to one-row plots, each 5.5 m long with 1 m between rows. Plots were fertilized with 67 kg ha^{-1} of N as pelletized urea in May of each year. Weeds were controlled with S-metolachlor 82.4% (Dual Magnum II, Syngenta) at 756 g a.i. ha^{-1} and 2, 4-dichlorphenoxyacetic acid at 385 g a.i. ha^{-1} at St. Paul and Roseau, MN, and controlled manually at Salina, KS and Kalispell, MT. Soil at St. Paul, MN is a Waukegan silt loam (fine-silty over sandy, mixed, superactive, mesic Typic Hapludoll) with a pH of 6.5, P of 25 mg kg^{-1}, and K of 219 mg kg^{-1}. Soil at Salina, KS is a Cozad

TABLE 2 Plant population, grain yield, biomass yield, and plant height of intermediate wheatgrass at harvest at St. Paul, MN, Salina, KS, Roseau, MN, and Kalispell, MT following different seeding dates

Seeding date	Population	Grain yield	Dry biomass	Height	Vernalization units	Fall GDDs
	tillers m^{-1} row	——kg ha^{-1}——		mm		
St. Paul, MN (2015–2016)						
1 Sept. 2015	NA	840 b[a]	6,913 b[a]	155 c	91	1,052
1 Oct. 2015	NA	497 b	5,232 b	114 b	90	501
15 Dec. 2015	NA	4 a	1,068 a	58 a	50	4
21 Mar. 2016	NA	0 a	998 a	30 a	28	0
1 Apr. 2016	NA	0 a	909 a	33 a	19	0
1 May 2016	NA	0 a	688 a	25 a	5	0
St. Paul, MN (2016–2017)						
18 Aug. 2016	220 a	898 c[a]	10,370 d[b]	152 d	93	1,290
1 Sept. 2016	233 a	586 bc	5,699 c	127 cd	93	1,016
15 Sept. 2016	256 a	442 b	5,682 c	132 cd	93	754
1 Oct. 2016	279 a	459 b	4,816 c	127 cd	92	495
15 Oct. 2016	272 a	345 b	4,586 c	127 cd	87	335
1 Nov. 2016	154 ab	57 a	1,483 b	117 cd	78	184
17 Nov. 2016	118 ab	45 a	1,303 b	109 c	70	34
1 Dec. 2016	0 b	0 a	0 a	0 a	61	1
1 Apr. 2017	279 a	0 a	1,518 b	51 b	22	0
4 May 2017		0 a	289 ab	36 b	3	0
Salina, KS (2016–2017)						
6 Sep. 2016	66 c	1,109 bc	11,180 cd	137 cd	87	1,340
15 Sep. 2016	82 bc	1,257 c	13,759 de	140 cd	87	1,144
29 Sep. 2016	112 a	1,346 c	14,046 e	147 d	87	847
13 Oct. 2016	102 ab	1,193 bc	12,541 de	140 cd	85	636
1 Nov. 2016	66 c	925 b	8,958 c	132 c	85	315
17 Nov. 2016	66 c	288 a	5,087 b	114 b	81	114
15 Feb. 2017	89 abc	0 a	2,078 a	36 a	28	0
16 Mar. 2017	89 abc	0 a	2,508 ab	36 a	16	0
13 Apr. 2017	98 ab	0 a	1,074 a	25 a	5	0
Roseau, MN (2017–2018)						
15 Aug. 2017	630 a	779 d[b]	9,774 c[a]	145 c	52	927
30 Aug. 2017	722 a	506 cd	6,428 c	147 c	51	679
15 Sep. 2017	358 b	423 c	5,428 c	97 abc	51	426
1 Oct. 2017	190 c	103 b	1,763 b	119 bc	47	225
15 Oct. 2017	49 c	63 ab	936 ab	122 bc	38	108
2 May 2018	230 c	0 a	1,296 b	74 ab	5	0
1 June 2018	98 c	0 a	437 a	43 a	0	0
Kalispell, MT (2019–2020)						
20 Sep. 2019	276 a	1,152 a	9,229 a	140 a	148	404
27 Sep. 2019	161 b	532 b	4,796 b	127 b	148	319
4 Oct. 2019	190 ab	751 b	6,685 ab	130 ab	141	287

(Continues)

TABLE 2 (Continued)

Seeding date	Population	Grain yield	Dry biomass	Height	Vernalization units	Fall GDDs
17 Apr. 2020	59 c	59 c	4,830 b	38 c	41	0
1 May 2020	39 c	12 c	3,727 b	43 c	32	

Note. Cumulative vernalization units from the date of seeding to harvest and cumulative growing degree days (GDDs) from date of seeding to the onset of winter dormancy are reported for each seeding date. Values followed by similar letters are similar within columns for each year and location based on least-squares means procedure and $\alpha = .05$.

[a]Response was transformed using a logarithm of the response +1 to meet model assumptions.

[b]Response was square root transformed to meet model assumptions.

silt loam (coarse-silty, mixed, superactive, mesic Typic Haplustoll) with a pH of 7.3, P of 37 mg kg^{-1}, and K of 280 mg kg^{-1}. Soil at Roseau is a Zippel very fine sandy loam (coarse-silty, mixed, superactive, calcareous, frigid Typic Endoaquoll) with a pH of 8.0, P of 11 mg kg^{-1}, and K of 83 mg kg^{-1}. Soil at Kalispell is a Creston silt loam (coarse-loamy, mixed, superactive, frigid Typic Haplustolls) with a pH of 7.8, P of 16 mg kg^{-1}, and K of 260 mg kg^{-1}. Air temperature and precipitation for each location is shown in Table 1.

2.2 | Data collection and analysis

Prior to harvest, reproductive tillers were counted from a 1-m section of row. Plant height from ten plants within the same tiller count area was measured from the soil surface to the tip of the seed head. When seeds were determined to be close to physiological maturity based on endosperm texture (texture equivalent to hard dough staging for annual small grains; approximately equivalent to Zadoks stage = 91), plants were harvested to a 12-cm height from four 30-cm row length sections of each plot away from the ends of each row. Harvest occurred on 13 Aug. 2016 and 2017 at St. Paul, 20 July 2017 at Salina, and 20 Aug. 2018 at Roseau. At Kalispell, MT, plants were harvested by hand from a 1-m section row on September 14 for all seeding dates prior to 30 May, and 20 October for seeding date treatments of 30 May and later. Seed and biomass samples were dried at 35 ˚C and seed heads separated from biomass. Seed was threshed from seed heads using a laboratory thresher (Wintersteiger LD-50; Ried im Innkreis) to determine grain yields.

Growing degree days (GDDs) were calculated using Equation 1:

$$\mathrm{GDD}_i = \left\{\left[T_{\max(i)} + T_{\min(i)}\right]/2\right\} - T_{\mathrm{base}} \quad (1)$$

where $T_{\max}$ and $T_{\min}$ are maximum and minimum temperatures for day i and T_{base} is the base temperature of 0 ˚C, which has been used for IWG in previous studies (Duchene et al., 2021; Frank, 1996; Jungers et al., 2018; Locatelli et al., 2021). The accumulation of GDDs was calculated by summing GDDs from the day after seeding and the last day of GDD accumulation prior to eight consecutive days of daily average temperatures below −2.2 ˚C. Intermediate wheatgrass can continue growth in the fall after experiencing individual days with average temperatures at or slightly below −2.2 ˚C; however, low temperatures and the duration of such temperatures that trigger winter dormancy are not known. We determined that an 8-d duration of daily average temperatures below −2.2 ˚C was a suitable benchmark for the beginning of winter dormancy because very few GDDs accumulated after such a term at each location. Vernalization units were calculated using Equation 2:

$$\mathrm{VV}_i = \max\left(1 - \left\{\left[T_{\mathrm{vern}} - T_{\min(i)}\right]/\mathrm{Ampli}_{\mathrm{vern}}\right\}^2, 0\right) \quad (2)$$

where VV_i is the vernalization units on day i, T_{vern} is the temperature to reach an optimal vernalization value, $T_{\min}$ is the minimum temperature on day i, and $\mathrm{Ampli}_{\mathrm{vern}}$ is added or subtracted from T_{vern} to define the upper and lower bounds of the vernalization temperature range. The coefficients T_{vern} and $\mathrm{Ampli}_{\mathrm{vern}}$ were estimated by Duchene et al. (2021) using a Bayesian Markov Chain Monte Carlo procedure based on empirical IWG phenology data and crop growth simulations using the STICS model (Brisson et al., 1998). Best estimates for the T_{vern} and $\mathrm{Ampli}_{\mathrm{vern}}$ parameters were 4.5 and 7.4 ˚C, respectively. The accumulation of vernalization units was calculated by summing VV_i from the day after seeding to grain harvest, thus vernalization units included days with temperatures suitable for vernalization in fall, winter, and spring prior to harvest. Daylengths of 13–14 h required to induce grain production occurred in the spring at all locations.

Statistical analyses were performed using the R software program and the nlme package to examine the effects of seeding date on seed and biomass yields, tiller number, and plant height response variables. Seeding date was treated as a fixed effect and replicate was considered a random effect. Because seeding dates varied by year, each location–year combination was analyzed independently. Least squared means were compared using Tukey's adjusted P value of .05 to examine the differences in response variables between seeding dates. Grain yield was log transformed and biomass yield was square root transformed to meet model assumptions. All responses were back transformed for presentation (Table 2). A regression analysis was then performed to examine the effect of GDD accumulation from the seeding date to the onset of winter dormancy on biomass and grain yield. Models tested the effect of GDDs as quadratic and linear fixed effects and replicate and seeding date as random effects. A maximum-likelihood ratio test was used for model selection ($\alpha = .05$). Regression analysis was used to determine the relationship between the accumulation of vernalization units from the seeding date to grain harvest on grain yield. Grain yield was log transformed to meet model assumptions for linear regression and back transformed for presentation. The conditional coefficient of determination was calculated from the mixed-effects regression models following Nakagawa and Schielzeth (2013). Pearson's product moment correlation coefficient was calculated to describe relationships between IWG biomass yield and plant height and deemed significant at $\alpha = .05$.

3 | RESULTS AND DISCUSSION

3.1 | Seeding date effects

Some planting dates resulted in emergence of IWG by November; this varied by location. Emergence of IWG occurred by November for plantings on 20 Sept. 2019 at Kalispell, on or before 1 Oct. 2015 and 15 Oct. 2016 at St. Paul, and before 15 Oct. 2017 at Roseau, MN. For planting dates that occurred after those dates at each location, no emergence was observed between November of the seeding year and the following spring. At harvest in the year following fall seeding, plants were present for all seeding dates except for the planting date of 1 Dec. 2016 at St. Paul (Table 2). At Roseau and Kalispell, the two most northern locations, delaying seeding to late fall and early spring resulted in lower tiller population at harvest (Table 2). A potential reason for the reduced tiller population with delayed seeding in the fall is that emerged seedlings at these locations were relatively smaller and immature going into winter and thus more vulnerable to winterkill. It is likely that some seed planted in October at Kalispell and Roseau and in November in St. Paul and Salina overwintered and germinated in the spring.

At all Minnesota sites and years and at Kalispell, grain yields were greatest when IWG was seeded at the earliest planting date in August or early September, whereas at Kansas, grain yields were greatest for September to mid-October plantings (Table 2). Despite adequate tiller density at harvest, seed yields were about an order of magnitude lower at St. Paul for planting dates in December 2015 and November 2016 than for August or September planting dates. Maximum grain yields in Minnesota and Kansas were similar to previously reported yields at these locations (Bajgain et al, 2020); however, this is the first report of IWG grain yields harvested from advanced, grain-type populations in Montana. Grain yields from the earliest fall planting date at Kalispell, MT exceeded yields from existing production-scale fields in Minnesota and are generally considered economically viable in a dual-use system (Hunter et al., 2020).

Biomass yields of IWG followed a similar trend as grain yields except that all seeding dates produced biomass. At both Minnesota locations and at Kalispell, biomass yields were greatest for the earliest seeding dates the previous year and declined with subsequent seeding dates. At Salina, planting September through October produced the most biomass with subsequent planting dates resulting in reduced yield. As occurred at St. Paul and Roseau, the trend of decreasing biomass from fall to spring occurred at Salina with less biomass produced from spring vs. late-summer plantings. At Kalispell, the reduction in biomass from spring plantings compared with fall plantings was not as pronounced as other locations. Spring planted biomass yields at Kalispell were 4,830 and 3,727 kg ha^{-1} for the April and May planting dates, respectively, which is considered adequate levels for forage harvest or grazing (Table 2; Hunter et al., 2020). Differences in biomass production across all locations and years resulting from diverse planting dates are likely partially due to the additional biomass being produced in stem structures of fall-seeded plants that flowered. Our results generally agree with other findings that have shown the negative effect of delayed fall planting date on fall forage grass production (Hall, 1995).

Plant height followed the same trend as biomass yield in response to planting date, as the earliest plantings with the highest biomass yield were consistently among those with the tallest IWG plants. Pearson correlation coefficients between biomass and height were very high for each experiment and year from the 2015–2016 and 2016–2017 experiments (St. Paul, MN 2015–2016, $r = .87$, $P < .001$; St. Paul, MN 2016–2017, $r = .75$, $P < .001$; Salina, KS 2016–2017, $r = .91$, $P < .001$; Kalispell, MT 2019–2020, $r = .66$; $P = .002$), indicating that plant height is a strong predictor of biomass yield for IWG. However, this relationship was not significant at Roseau, MN in 2017–2018 ($r = .45$, $P = .145$). At Roseau, biomass yields were surprisingly high for the May 2 planting date despite relatively low plant height compared with fall seedings, which deviated from the trends at other locations. Tiller number was also surprisingly high for the May 2 planting date at Roseau, thus the relatively higher tiller density may have compensated for the low plant height to support high biomass yields.

Very little information about the effects of seeding date on IWG seed production exists. Frischknecht (1951), working with a forage-type IWG in Utah, observed that only IWG planted in the fall produced seed the following year. In Wisconsin, Olugbenle et al. (2021) found that IWG grain yields from stands intercropped with red clover (*Trifolium pratense*

L.) were maximized when planted on August 26 and September 13 at Arlington and Lancaster, WI, respectively. The study also observed little to no grain yield from stands planted in spring. The lack of seed production in our study from winter and spring seeding dates across diverse latitudes confirms that grain-type IWG has a fall growth, temperature, and photoperiod requirement for seed production. It is likely that late-planted IWG had reduced crown growth, carbohydrate storage, and axillary bud sites for inducement to flowering (Cooper & Calder, 1964). To explore potential effects of temperature on IWG grain yields in the context of fall growth and vernalization, we calculated daily GDDs and vernalization units based on daily maximum and minimum temperature data collected at each site.

3.2 | Effects of fall GDDs on grain yields

Cumulative growing degree days (GDDs) between planting and the onset of winter dormancy was positively associated with IWG grain and biomass yield across all locations and years (Figure 1). The relationships between GDDs and grain and biomass yield were linear for all site-year combinations in Minnesota and Kalispell. At Kalispell, the positive effect of GDDs on grain yields was stronger than at Roseau and St. Paul, suggesting that fall thermal units may be more limiting at this location compared with the others. Biomass yield responses to GDDs were similar to grain yield responses within locations. At Salina, both grain and biomass yield responses to GDDs were quadratic, which suggests that diminishing returns on yield accrue with increasing GDDs prior to the onset of winter dormancy. Yield plateaus were observed at 912 and 914 GDDs for grain and biomass yield, respectively. For the Minnesota and Kalispell locations, it is unclear if additional accumulation of GDDs associated with earlier seeding dates would result in even greater first-year yields than those observed in this study.

Relationships between GDDs accumulated in the fall and forage crop yields have also been observed by Hall (1995) in Pennsylvania, who found that delaying planting until after early August decreased plant height and percent cover for multiple cool-season and legume forage species, resulting in reduced stands that could not compete well against weeds or produce adequate forage yields during the subsequent year of production. Similar effects of growing season GDDs (accumulated GDDs from the beginning of crop regrowth in spring to harvest) on individual seed and biomass yields were observed in IWG (Jungers et al., 2018) as well as other perennial, cool-season grassland systems, with perennial ryegrass ground cover increasing with increasing GDDs in turf and forage grasses (Reicher et al., 2000; Undersander & Greub, 2007). The accumulation of GDDs between the time of seeding and the onset of winter dormancy is a measure of the thermal energy available to emerging seedlings, which is

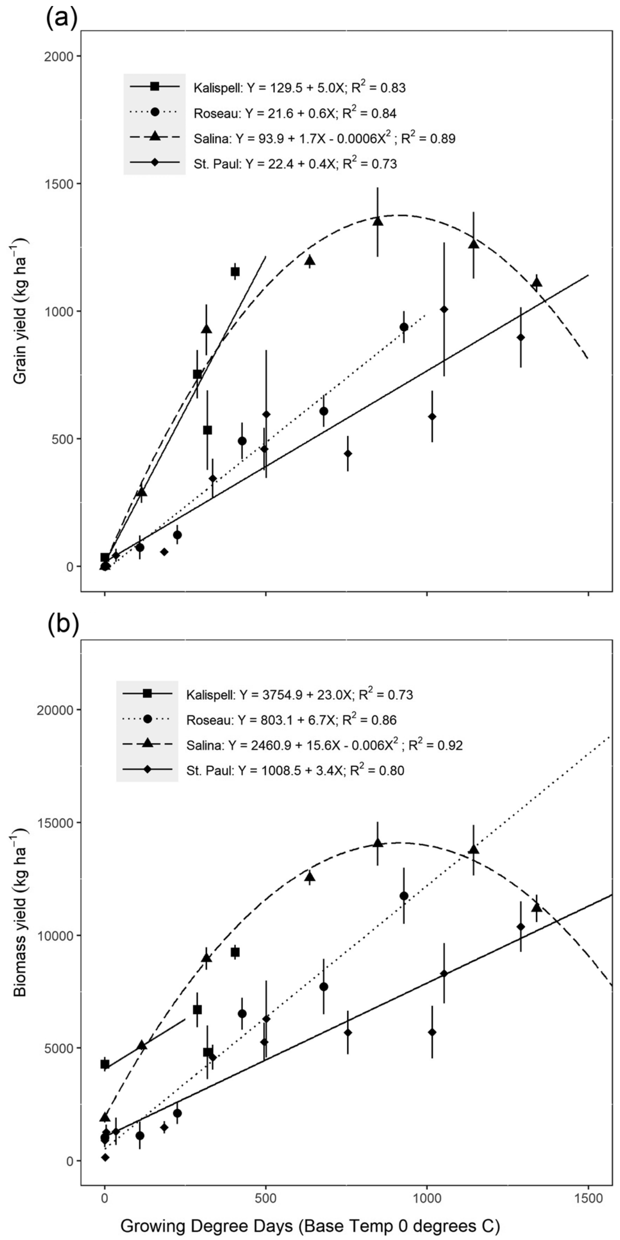

FIGURE 1 Effect of cumulative growing degree days from the seeding date to the onset of winter dormancy (determined as the last day of growing degree day accumulation before eight consecutive days with average daily temperatures below −2.2 ˚C) on intermediate wheatgrass grain and biomass yields when fall planted in 2015 and 2016 at St. Paul, MN, 2016 in Salina, KS, 2017 at Roseau, MN, and 2019 in Kalispell, MT

important for grain and biomass yields in subsequent years. This thermal energy, along with adequate soil nutrients and water, allows fall seeded perennial plants to build carbohydrate reserves for overwintering. In the spring, carbohydrate reserves are important for increasing relative growth rate and overall plant productivity, and thus grain and biomass yields.

Many perennial grass species also undergo juvenility, a growth stage after seed germination when plants cannot respond to seed head induction cues (Heide, 1994). Although the physiological definition of juvenility has not been reported for IWG as it has for other cool-season grasses, observations from growth chamber studies have indicated that IWG plants with fewer than three leaves may not initiate seed heads even under adequate vernalization conditions (Locatelli et al., 2021). Late seeding can result in insufficient GDDs for plants beyond the juvenile stage, which can then prevent those plants from entering reproductive induction phases. Such circumstances, where late-seeded plants had limited GDDs prior to winter but enough vernalization units prior to harvest, may have been observed in this study. For the November 17 seeding date at Salina, a lack of GDDs (114) between the seeding date and the onset of winter dormancy could have prevented plants from maturing beyond the juvenility stage, which could explain the low grain yields observed from these plants despite producing adequate biomass yields.

3.3 | Effects of vernalization units on grain yields

No grain was produced from spring plantings in Kansas or Minnesota, confirming that IWG requires certain conditions for seed head induction. Here, we show that some minimum thermal unit requirement is necessary for seed head induction, but this minimum can vary by location. Duchene et al. (2021) used more than 30 site-years of phenology data from advanced grain-type IWG populations grown across a broad range of environments to calibrate and validate the STICS crop growth model to estimate vernalization conditions for IWG. Their results found that the optimum vernalization temperature for IWG was 4.6 ˚C with a range of ±7.9 ˚C. Ivancic et al. (2021) and Locatelli et al. (2021) confirmed this vernalization temperature in greenhouse studies where photoperiod was also fixed for 10 h. Using Equation 2, Duchene et al. (2021) also found that the best estimate of minimum vernalization units for seed head induction was 71.9 with a 10–90% confidence interval range of 36.1 and 79.4 at an optimum daylength of between 13 and 14 h. Reducing daylength slows reproductive development, which explains why Locatelli et al. (2021) found that IWG flowering was maximized after 7 wk (49 vernalization units) at 10-h photoperiod. Our study is the first to apply this method of quantifying vernalization units to IWG flowering and grain yield in a field setting. We found that grain yields were strongly correlated to the accumulation of vernalization units prior to grain harvest (Figure 2), and that seeding dates that allowed for the accumulation of more than 78 vernalization units prior to harvest resulted in grain yield (Table 2). However, even the earliest seeding date at Roseau did not receive the expected minimum vernalization units, yet plants still produced grain. One potential reason for this anomaly could be related to differences between air temperature measurements gathered from the weather station used for calculating vernalization units and actual air temperatures at the soil surface. Snow cover can insulate the air at the soil surface and result in higher temperatures compared with air temperatures above the snow cover (Taras et al., 2002). Turf temperature sensors in Roseau showed an average temperature of 1.9 ˚C in November 2017, which is almost 4 ˚C warmer than the average air temperature at the station that month.

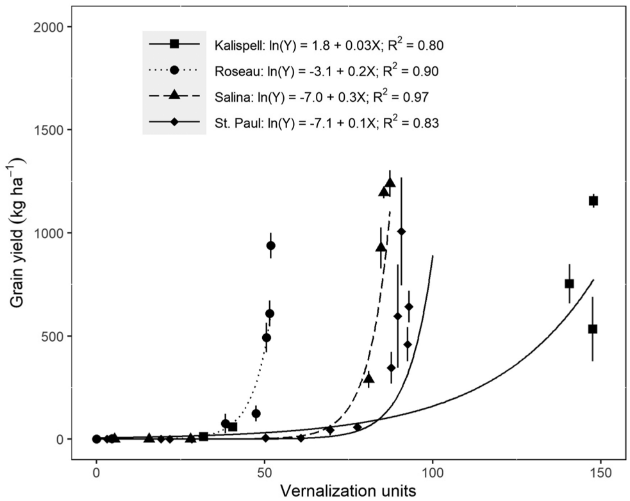

FIGURE 2 Effect of cumulative vernalization units from the seeding date to grain harvest on intermediate wheatgrass grain yield when fall planted in 2015 and 2016 at St. Paul, MN, 2016 in Salina, KS, 2017 at Roseau, MN, and 2019 in Kalispell, MT

Unlike the other locations, some spring-seeded plants at Kalispell produced grain (Table 2). Cumulative vernalization units following spring seedings were highest at this location. Although the vernalization units did not reach the best estimate of 71 determined by Duchene et al. (2021) for seed head induction, values recorded here are within the 90% confidence interval of their estimate and may have been greater given the insulation properties of snow in the spring. It should also be noted that photoperiod is an important component of secondary induction, and the time of the year during which vernalization units accrue can influence induction.

4 | CONCLUSION

In northern cropping systems with temperature and precipitation conditions within those ranging from Minnesota to Montana, seeding IWG following a small grain harvest is recommended sometime between mid-August to early September to provide the greatest IWG grain yields. This recommended seeding date for IWG is similar or slightly earlier than recommended seeding dates for winter wheat in these regions, which ranges from September 1 to October 1. For growing conditions more similar to Kansas, a wider range of seeding dates (September to October) can result in maximized yields. Increased grain yields associated with early fall seeding dates is likely related to the greater morphological development of plants with multiple tillers that can vernalize and produce grain the following year. Late fall and spring plantings that result in little seed production can still result in biomass for soil conservation and grazing the following spring. Cumulative GDDs from fall seeding date to the onset of winter dormancy are positively associated with grain yields, but more research on temperature-dependent growth stages and primary seed head induction are needed before GDDs can be used to predict grain yields. Cumulative vernalization units were also positively correlated with grain yields and helped explain rare instances of grain production from spring seeded IWG. Our findings provide the first field-study validation of some greenhouse and model-based estimates of vernalization requirements for IWG, but variability introduced by snow cover and photoperiod require additional study. These results highlight the practical challenges of seeding IWG for grain production following soybean or other late-harvested grains where the crops are often not harvested until mid-October or later.

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AUTHOR CONTRIBUTIONS

Jacob Michael Jungers: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Supervision; Visualization; Writing-original draft; Writing-review & editing. Sydney Schiffner: Data curation; Methodology; Project administration; Visualization; Writing-original draft; Writing-review & editing. Craig Sheaffer: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Writing-original draft; Writing-review & editing. Nancy Jo Ehlke: Funding acquisition; Investigation; Project administration; Supervision; Writing-review & editing. Lee DeHaan: Investigation; Methodology; Project administration; Resources; Supervision; Writing-review & editing. Jessica Torrion: Investigation; Project administration; Resources; Supervision; Writing-review & editing. Reagan L. Noland: Investigation; Methodology; Resources; Writing-review & editing. Jose G. Franco: Investigation; Methodology; Resources; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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REFERENCES

Bajgain, P., Zhang, X., Jungers, J. M., DeHaan, L. R., Heim, B., Sheaffer, C. C., Wyse, D. L., & Anderson, J. A. (2020). 'MN-Clearwater', the first food-grade intermediate wheatgrass (Kernza perennial grain) cultivar. *Journal of Plant Registrations*, *14*(3), 288–297. https://doi.org/10.1002/plr2.20042

Brisson, N., Mary, B., Ripoche, D., Jeuffroy, M. H., Ruget, F., Nicoullaud, B., Gate, P., Devienne-Barret, F., Antonioletti, R., Durr, C., Richard, G., Beaudoin, N., Recous, S., Tayot, X., Plenet, D., Cellier, P., Machet, J.-M., Meynard, J. M., & Delécolle, R. (1998). STICS: A generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. *Agronomie*, *18*(5–6), 311–346. https://doi.org/10.1051/AGRO:19980501

Cooper, J. P., & Calder, D. M. (1964). The inductive requirements for flowering of some temperate grasses. *Grass and Forage Science*, *19*(1), 6–14. https://doi.org/10.1111/j.1365-2494.1964.tb01133.x

Culman, S. W., Snapp, S. S., Ollenburger, M., Basso, B., & DeHaan, L. R. (2013). Soil and water quality rapidly responds to the perennial grain Kernza wheatgrass. *Agronomy Journal*, *105*(3), 735–744. https://doi.org/10.2134/agronj2012.0273

DeHaan, L., Christians, M., Crain, J., & Poland, J. (2018). Development and evolution of an intermediate wheatgrass domestication program. *Sustainability*, *10*(5), 1–19. https://doi.org/10.3390/su10051499

DeHaan, L. R., & Ismail, B. P. (2017). Perennial cereals provide ecosystem benefits. *Cereal Foods World*, *62*(6), 278–281. https://doi.org/10.1094/CFW-62-6-0278

De Oliveira, G., Brunsell, N. A., Sutherlin, C. E., Crews, T. E., & DeHaan, L. R. (2018). Energy, water and carbon exchange over a perennial Kernza wheatgrass crop. *Agricultural and Forest Meteorology*, *249*, 120–137. https://doi.org/10.1016/j.agrformet.2017.11.022

Duchene, O., Dumont, B., Cattani, D. J., Fagnant, L., Schlautman, B., DeHaan, L. R., Barriball, S., Jungers, J. M., Picasso, V. D., David, C., & Celette, F. (2021). Process-based analysis of *Thinopyrum intermedium* phenological development highlights the importance of dual induction for reproductive growth and agronomic performance. *Agricultural and Forest Meteorology*, *301–302*, 108341. https://doi.org/10.1016/j.agrformet.2021.108341

Frank, A. B. (1996). Evaluating grass development for grazing management. *Rangelands*, *18*(3), 106–109.

Frischknecht, N. C. (1951). Seedling emergence and survival of range grasses in central Utah. *Agronomy Journal*, *43*(4), 177–182. https://doi.org/10.2134/agronj1951.00021962004300040004x

Hall, M. H. (1995). Plant vigor and yield of perennial cool-season forage crops when summer planting is delayed. *Journal Of Production Agriculture*, *8*(2), 233–238. https://doi.org/10.2134/jpa1995.0233

Hall, M. H., & Collins, M. (2018). Forage establishment. In M. Collins, C. J. Nelson, K. J. Moore, & R. F. Barnes (Eds.), *Forages, volume 1: An introduction to grassland agriculture* (7th ed., pp. 221–233). Wiley-Blackwell.

Heide, O. M. (1994). Control of flowering and reproduction in temperate grasses. *New Phytologist*, *128*(2), 347–362. https://doi.org/10.1111/j.1469-8137.1994.tb04019.x

Hitchcock, A. S., & Chase, A. (1951). *Manual of the grasses of the United States*. USDA. https://doi.org/10.5962/bhl.title.65332

Hunter, M. C., Sheaffer, C. C., Culman, S. W., Lazarus, W. F., & Jungers, J. M. (2020). Effects of defoliation and row spacing on intermediate wheatgrass II: Forage yield and economics. *Agronomy Journal*, *112*, 1862–1880. https://doi.org/10.1002/agj2.20124

Ivancic, K., Locatelli, A., Tracy, W. F., & Picasso, V. (2021). Kernza intermediate wheatgrass (*Thinopyrum intermedium*) response to a range of vernalization conditions. *Canadian Journal of Plant Science*, 1–4. https://doi.org/10.1139/cjps-2020-0251

Jungers, J. M., DeHaan, L. R., Betts, K. J., Sheaffer, C. C., & Wyse, D. L. (2017). Intermediate wheatgrass grain and forage yield responses to nitrogen fertilization. *Agronomy Journal*, *109*(2), 462–472. https://doi.org/10.2134/agronj2016.07.0438

Jungers, J. M., DeHaan, L. H., Mulla, D. J., Sheaffer, C. C., & Wyse, D. L. (2019). Reduced nitrate leaching in a perennial grain crop compared to maize in the Upper Midwest, USA. *Agriculture, Ecosystems and Environment*, *272*, 63–73. https://doi.org/10.1016/j.agee.2018.11.007

Jungers, J. M., Frahm, C. S., Tautges, N. E., Ehlke, N. J., Wells, M. S., Wyse, D. L., & Sheaffer, C. C. (2018). Growth, development, and biomass partitioning of the perennial grain crop *Thinopyrum intermedium*. *Annals of Applied Biology*, *172*(3), 346–354. https://doi.org/10.1111/aab.12425

Ketellapper, H. J. (1960). Growth and development in *phalaris*. I. Vernalization response in geographic strains of *P. tuberosa* L. *Ecology*, *41*(2), 298–305. https://doi.org/10.2307/1930219

Kilcher, M. R. (1961). Fall seeding versus spring seeding in the establishment of five grasses and one alfalfa in southern Saskatchewan. *Journal of Range Management*, *14*(6), 320. https://doi.org/10.2307/3895078

Locatelli, A., Gutierrez, L., & Picasso Risso, V. D. (2021). Vernalization requirements of Kernza™ intermediate wheatgrass (*Thinopyrum intermedium*). *Crop Science*, *62*(1), 524–535. https://doi.org/10.1002/csc2.20667

McDonald, M. B. J., Copeland, L. O., Knapp, A. D., & Grabe, D. F. (1996). Seed development, germination & quality. In L. E. Moser, D. R. Buxton, M. D. Casler, J. M. Bartels, G. A. Peterson, P. S. Baenziger, & J. M. Bigham (Eds.), *Cool-season forage grasses* (34th ed., pp. 15–70). ASA, CSSA, and SSSA.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Ogle, D., St John, L., Tober, D., & Jensen, K. (2011). *Plant guide for intermediate wheatgrass (Thinopyrum intermedium)*. USDA-NRCS. https://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/idpmspg10369.pdf

Olugbenle, O., Pinto, P., & Picasso, V. D. (2021). Optimal planting date of Kernza intermediate wheatgrass intercropped with red clover. *Agronomy*, *11*(11), 2227. https://doi.org/10.3390/agronomy11112227

Reicher, Z. J., Throssell, C. S., & Weisenberger, D. V. (2000). Date of seeding affects establishment of cool-season turfgrasses. *Hortscience*, *35*(6), 1166–1169. https://doi.org/10.21273/HORTSCI.35.6.1166

Taras, B., Sturm, M., & Liston, G. E. (2002). Snow-ground interface temperatures in the Kuparuk River Basin, Arctic Alaska: Measurements and model. *Journal of Hydrometeorology*, *3*, 377–394. https://doi.org/10.1175/1525-7541(2002)003%3c0377:SGITIT%3e2.0.CO;2

Undersander, D. J., & Greub, L. J. (2007). Summer-fall seeding dates for six cool-season grasses in the Midwest United States. *Agronomy Journal*, *99*(6), 1579–1586. https://doi.org/10.2134/agronj2006.0194

Wagoner, P. (1990). Perennial grain: New use for intermediate wheatgrass. *Journal of Soil and Water Conservation*, *45*, 81–82.

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