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Investigating tradeoffs in perennial ryegrass turfgrass performance and seed yield capacity in the US Midwest

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Abstract

Understanding the trade-offs between improving turfgrass performance and seed production capacity would improve acceptance and accelerate the release of new perennial ryegrass (*Lolium perenne* L.) cultivars. An experiment was designed to measure the turfgrass quality, seed yield, and component traits among 20 perennial ryegrass entries grown in turfgrass and seed production swards at two locations in Minnesota, a seed production region of the United States. Turfgrass quality scores, when averaged across collection dates, were not strongly correlated with seed yield at either location. However, data from several individual turfgrass quality rating dates were moderately correlated with seed yield at both locations ($p < 0.100$). Within the dates that correlated with seed yield, turfgrass component traits were regressed against quality scores. Crown rust severity, color, and density were important in the first year, and winter injury and texture were important in the second year. Plots with more fertile tillers were associated with higher seed yield and lower turfgrass quality ($p < 0.050$), but there was no relationship between entries in the two growing environments for fertile tiller production ($p > 0.250$). Entries that exhibited a faster vertical growth rate in turfgrass swards tended to mature earlier in seed plots, a trait that was correlated with higher seed yield ($p < 0.001$). However, the vertical turfgrass growth rate was not directly correlated with seed yield ($p > 0.800$). Few tradeoffs between the growing environments were found under the growing conditions and germplasm employed.

1 | INTRODUCTION

Through plant breeding efforts, the turfgrass industry has seen tremendous gains in perennial ryegrass (*Lolium perenne* L.) performance for traits such as abiotic stress adaptation and disease resistance (Bonos & Huff, 2013; Sampoux et al., 2013). However, the adoption of new cultivars with superior turfgrass quality cannot be successful unless the seed production capacity meets acceptable standards to generate consistent profits for the seed producer while meeting consumer demand at a reasonable cost (McDonald & Copeland, 1997). Therefore, if an increase in turfgrass quality results in a drastic, or significant reduction in seed yield, seed producers may be unwilling to grow the cultivar. This in turn may not only reduce the efficiency of breeding programs but also result in serious losses in revenue due to the length of time to release a turfgrass cultivar (typically 4–8 years).

Abbreviation: GDD, growing degree day.

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Among cool-season amenity grasses, genetic gain in turfgrass quality is often assumed to be intrinsically and negatively correlated with seed yield (Bonos & Huff, 2013; van Wijk, 1985). Johnson et al. (2003) studied 45 lines of Kentucky bluegrass (*Poa pratensis* L.) in side-by-side seed production and turfgrass environments and found that seed yield had a moderate negative correlation with both color and average turfgrass quality over a 3-year span ($r = -0.40$ and -0.48, respectively, $p < 0.050$). The results suggested that for a single unit increase in turfgrass quality, a 21 g decrease in seed yield is expected (grand mean = 45 g m^{-2}) (Figure S1). Similar results were found in a later publication with 50 different Kentucky bluegrass lines (Johnston et al., 2011). Żurek et al. (2007) found no significant correlation between seed yield per plot and turfgrass quality ($r = 0.03$, $p > 0.050$) among 27 Kentucky bluegrass lines. However, strong negative correlations between turfgrass quality and culm height ($r = -0.50$, $p < 0.001$), panicle length ($r = -0.67$, $p < 0.001$), and yield per panicle ($r = -0.64$, $p < 0.001$) were revealed. The authors surmised that turfgrass quality was based on vegetative components remaining consistent throughout the year, whereas seed yield depends on generative components.

Little evidence directly links turfgrass performance and seed yield in perennial ryegrass; although Hazard et al. (2006) have been cited as providing mechanistic evidence for a potential tradeoff (Bonos & Huff, 2013). This previous study focused on the fitness implications and selection pressure imposed by repeated defoliation of perennial ryegrass. Parents selected from a heavily defoliated environment produced progeny with more tillers but displayed a slower vertical elongation rate and later heading date, leading to lower biomass accumulation. Progeny originating from parental sources lacking defoliation elongated faster, went into a reproductive phase sooner, and was hypothesized to yield more seed. Although seed yield was not measured, likely, selection for aesthetic traits such as slow vertical growth, heading date, and increased tillering would alter the initiation and length of time spent flowering in a seed production sward. These separate accounts (Hazard et al., 2006; Żurek et al., 2007) indicate that a general tradeoff between turfgrass quality and seed yield may occur due to the impact of changing the specific component traits of either factor.

Seed yield per unit area and turfgrass quality ratings can both be described mechanistically through the measurement of specific trait components. Seed yield in perennial ryegrass is determined by the establishment of seed potential (e.g., fertile tillers per unit area, spikelets per spike, and florets per spikelet) followed by the utilization of that potential (e.g., seeds per florets and yield per spike) combined with crop maturity and uniformity (Elgersma, 1985; Hebblethwaite et al., 1980). Turfgrass quality is composed of genetic- and stress-related trait components (Morris & Shearman, 2006).

Core Ideas

- Turfgrass quality and seed yield in perennial ryegrass need to be maintained for successful cultivar release.
- Twenty populations were grown in seed production and turfgrass environments to determine potential tradeoffs.
- Few tradeoffs between the environments were found under the growing conditions and germplasm employed.
- Future work is needed to determine genetic correlations between turfgrass performance and seed production.

Genetic components relevant to perennial ryegrass include color, density, and texture. Because these can be confounded by stress-related components, genetic components should be reported under ideal growing conditions with respect to idealized turfgrass cultivars grown under an optimal environment and management regime (Krans & Morris, 2007). Stress-related components relevant to the turfgrass quality of perennial ryegrass grown in the US Midwest include susceptibility to crown rust (*Puccinia coronata* f. sp. *lolii*) and winter-related damage such as winter injury and spring greenup (Morris & Shearman, 2006). Although seed yield is usually measured once per season, turfgrass quality is repeatedly measured because individual turfgrass components vary in importance over time.

Measuring component traits may result in a more complete picture of potential tradeoffs between turfgrass quality and seed yield. For instance, cultivars that produce many fertile tillers often produce large amounts of seed but lack turfgrass merit because of poor texture (Bugge, 1987; Sampoux et al., 2013). In the Upper US Midwest, perennial ryegrass swards are limited by winter survival resulting in ephemeral turfgrass and seed production swards. Hulke et al. (2007) studied 300 perennial ryegrass accessions and found a negative correlation between darker green color and winter hardiness ($r = -0.10$ to -0.24, $p < 0.001$), possibly indicating a tradeoff between increasing seed production in cold climates and turfgrass quality. It is important to identify whether specific tradeoffs exist so breeding programs can weigh the risks of improving certain components, such as fertile tiller number or winter hardiness.

Cool-season turfgrass cultivars are often screened nationally, and selection for most biotic and abiotic stresses is primarily conducted in the northeast United States, whereas the majority of seed production occurs in Oregon, Washington, and Minnesota (Bonos & Huff, 2013). It is likely

that large genotype × environment interactions occur for both seed production capacity and turfgrass quality. For example, orchardgrass (*Dactylis glomerata* L.) for forage has been bred for low-frequency flowering in cold short-day climates, whereas in warmer short-day climates, such as western Oregon, higher frequencies of flowering occur (Casler et al., 2004). This exemplifies the need for assessment of germplasm in both turfgrass and seed production environments to adequately estimate tradeoffs.

The objective of this study was to compare turfgrass quality and seed yield of 20 perennial ryegrass entries grown in side-by-side turfgrass and seed production swards at two Minnesota locations. The experiment was designed to determine the general relationship between turfgrass quality and seed yield capacity and test several mechanistic hypotheses regarding the component traits.

2 | MATERIALS AND METHODS

2.1 | Plant material

Perennial ryegrass experimental entries consisted of 15 interrelated populations and five cultivars. Populations were bulked from several half-sib families originating from the same source. The maternal sources for each population were selected from advanced synthetic material in the DLF-USA breeding program that was collected from evaluation plots grown in Minnesota and Connecticut with pedigrees connected to the Rutgers University breeding program (Table S1). Each population was derived from bulking the half-sib seed from 10 to 15 individuals in a polycross containing each of the material sources. One forage-type and four turf-type cultivars were chosen based on a wide performance range for winter survival, turfgrass quality, and seed yield capacity (Table S1). Winter hardy check cultivars included NK200 and Arctic Green, which have poor and moderate turfgrass quality, respectively.

2.2 | Experimental design

Seed production and turfgrass experimental units (referred to as plots) were studied at two locations in 2017 (establishment year) and 2018 (seed production year). Plots were established in early June of 2017 at both the Minnesota Agricultural Experiment Station at the University of Minnesota in Saint Paul, MN, and at the University of Minnesota Magnusson Research Farm in Roseau, MN. The two locations are approximately 560 km apart and were chosen because Roseau is located within the major seed production region in Minnesota and the University of Minnesota turfgrass and seed production breeding programs are in Saint Paul. The soil at Roseau was a Borup silt loam with 2.7% organic matter and a pH of 7.7, while at Saint Paul the soil was a Waukegan silt loam soil with 4.8% organic matter and a pH of 6.4. Each of the 20 experimental entries were represented equally in seed production and turfgrass environments and were established at the same time at each location. The design was a randomized complete block with three replicates for each plot type at each location.

In both years, climate data for Roseau were collected from the North Dakota Agricultural Weather Network station (Fox, 48.685, −95.734) and the University of Minnesota Saint Paul weather station (44.995031, −93.185839). Growing degree days (GDD) were calculated using a base temperature of 0°C (Table 1). Soil temperature was recorded at each location at a depth of 10 cm.

2.3 | Plot design and management: Seed production environment

Seed production plots were seeded with a Hege 1000 small-plot seeder in early May 2017 (Hege Equipment Inc.). Each plot was 3.6-m long consisting of 10 drilled rows 15 cm apart. Each plot was seeded with 6.5 kg ha^{-1} of pure live seed resulting in approximately 70 seeds per linear meter of row. Each block had seeded border plots. Upon establishment in the first week of June 2017, plots were fertilized using a Gandy drop spreader (Gandy Company) at a rate of 24.4 kg N ha^{-1}, 40.1 kg P ha^{-1}, and 24.4 kg K ha^{-1}. In late September 2017, plots were fertilized at a rate of 0.0 kg N ha^{-1}, 33.6 kg P ha^{-1}, and 33.6 kg K ha^{-1}. Broadleaf weeds were controlled in the establishment year with a single application of bromoxynil and MCPA (3,5-dibromo-4-hydroxybenzonitrile and 2-ethylhexyl ester of 2-methyl-chlorophenoxyacetic acid; BASF) at a rate of 0.28 kg a.i. ha^{-1} at both locations. Fall and early spring weed seedlings were controlled with a single application of pendimethalin (*N*-(1-ethylpropyl)−3,4-dimethyl-2,6-dinitrobenzenamine; BASF) at a rate of 2.12 kg a.i. ha^{-1} at both locations. Fall broadleaf weeds were controlled on September 25, 2017, in Saint Paul and October 5, 2017, in Roseau with an application of 2,4-D (2,4-dichlorophenoxyacetic acid; Winfield) at a rate of 0.40 kg a.i. ha^{-1}. In the seed production year, fertilizer was applied in early May 2018 at a rate of 123.1 kg N ha^{-1}. Broadleaf weeds were controlled in the last week of May 2018 with an application of 2,4-D (2,4-dichlorophenoxyacetic acid; Winfield) at a rate of 0.27 kg a.i. ha^{-1} and dicamba (3,6-dichloro-o-anisic acid; Winfield) at a rate of 0.27 kg a.i. ha^{-1} at both locations. Sampling for seed yield occurred in early July 2018 in Saint Paul and in early August 2018 in Roseau. Sampling was conducted twice at both locations to ensure that ripe seed at approximately 400 g kg^{-1} moisture content was harvested. Yield samples entailed harvesting two 1 m^2 swaths per

TABLE 1 Summary of growing conditions at Saint Paul and Roseau during the establishment (2017) and seed production (2018) years.

	Roseau		Saint Paul	
	Summer			
	GDD[a]	Rainfall (cm)	GDD	Rainfall (cm)
Establishment (2017)	2388	36	2819	57
Production (2018)	2514	25	3336	57
5-year average	2526	32	2943	55
	Winter			
	Min soil (˚C)[b]	Soil (days < 0˚C)[c]	Min soil (˚C)	Soil (days < 0˚C)
2017–2018	−4.7	161	−2.0	117
5-year average	−4.2	122	−4.1	89

Note: Average conditions were based on 5-year averages from 2012 to 2016.

Abbreviations: Min soil, minimum soil temperature; Soil (days < 0˚C), number of day soil was below 0˚C; sod, the surface of the ground, with the grass growing on it.

[a]Growing degree days (GDDs) calculated from May 1 to September 30 using a base temperature of 0˚C.

[b]Average daily temperatures from October 1 to April 30 taken 10 cm below soil covered with sod.

[c]Number of days soil was below 0˚C at 10 cm under sod from October 1 to April 30.

experiential unit. Biomass was dried for 5 days at 35˚C in a forced air dryer.

2.4 | Plot design and management: turfgrass environment

Each individual turfgrass plot was 0.91 m × 0.91 m. Plots were hand seeded in early May 2017 at a rate of 100 kg ha^{-1} pure live seed resulting in approximately 0.5 seeds cm^{-2}. The low seeding rate was used due to a lack of breeder's seed. Turfgrass plots received the same establishment fertilizer and chemical regime as the seed production plots. Turfgrass plots were fertilized in May 2018 at a rate of 24.4 kg N ha^{-1}, 40.1 kg P ha^{-1}, and 24.4 kg K ha^{-1} at both locations. Plots at Roseau received an additional application at the same rate in July 2018 to facilitate regrowth from severe winterkill and a lower soil organic matter. Turfgrass was maintained at a height of 7 cm by mowing every other week during the growing season.

2.5 | Data collection: Seed production environment

Response variables for seed production swards in the establishment year included stand counts and image data. Seedling emergence was estimated 3 weeks after seeding by counting the number of seedlings that emerged in two 0.5 m transects. Image data were collected every 2 weeks in the late summer and spring at both locations to quantify crown rust incidence and winter injury (image analysis technique described below).

Response variables in the seed production year included winter injury, growth stage, plant height, spike length, seed yield per spike, fertile tiller number m^{-2}, and seed yield m^{-2}. Winter survival was quantified using digital image analysis, with the proportion of living tiller area to dead tiller area within a row equal to survival. Growth stage assessments were conducted in the seed production year three times at Saint Paul and twice at Roseau. The plant maturity scale was adapted from the condensed forage development scheme by Gustavsson (2011). The median tiller growth stage was visually assessed for each plot, with nine spike samples recorded along a 2.0 m transect. Plant culm height was measured twice after anthesis by selecting culms at three random points in each plot and taking the average of the two measures. Fertile tillers per meter square were estimated by cutting four 15 cm transects (within a row) of culms in each plot. Each of these transects was cut twice so that 0.25 cm pieces of culm were isolated from the bottom of each transect and funneled into a coin envelope. Culm pieces were cleaned with a general seed blower to remove leaves and other debris and counted using a Seed Count S-JR seed counter (Wintersteiger Corp.). A 10-spike sample was collected from each 15 cm transect which was measured for spike length and seed yield per spike. Clean seed yield per meter square was measured after processing each sample in an LD350 thresher (Wintersteiger Corp.). Seed and chaff were separated by passing the seed through a 1.625 mm × 9.525-mm sieve. Light seed was removed by aspiration using a Superior Fractionating Aspirator (Carter-Day International, Inc.).

2.6 | Data collection: Turfgrass environment

Turfgrass sward establishment was assessed on a 1–9 visual scale with a 5 equal to 50% of the seedlings filling in a 15 × 15 cm^2 grid (Figure S2). Other visual ratings started one month after establishment was assessed. Turfgrass plots were rated repeatedly and with respect to an idealized turfgrass standard grown under an optimal environment and

management regime (Krans & Morris, 2007). Turfgrass quality was visually assessed on a 1–9 (with a 9 being the most favorable score) scale based on genetic and stress-related components.

Major stress-related components important for perennial ryegrass in Minnesota include crown rust severity and winter-related stress. Crown rust was measured utilizing repeated analysis of digital images. Winter stress was broken down into winter injury and spring green-up (Morris & Shearman, 2006). Winter injury referred to the proportion of necrotic aboveground tissue that can be attributed to abiotic winter-time stress in the early spring and could occur in spatially uniform or non-uniform patterns. Spring green-up refers to the transition of dormant turfgrass from a winter-damaged state to actively growing (Morris & Shearman, 2006). The use of "transition" in this definition implies repeated measures of density during suboptimal growing conditions up until genetic traits (e.g., density) may be measured.

The genetic components of quality, defined as genetic color, density, and texture, were measured post-winter injury assessments, but prior to signs of rust (Morris & Shearman, 2006). Custom diagrammatic scales were used for density and genetic color to maintain consistent quantitative assessments across locations (Figure S2). Texture specifically refers to the width of the lamina or leaf, however, the presence of dried culms or stems in second-year swards also affects "texture." Therefore, leaf texture and stem texture can be genetic components used to describe the texture of perennial ryegrass turf. Leaf texture was measured on a 1–9 scale with 9 representing the finest texture (Islam et al., 2013). Stem texture was measured through stem counts and analysis of digital images. The use of the term stem texture does not conform to common measurements taken for the National Turfgrass Evaluation Program, but was important for this study. Image data were collected every 2 weeks at both locations to quantify stem texture, crown rust severity, and winter-related stress (see image analysis technique). Turfgrass height was quantified in both the establishment and production years before each mowing by measuring three points in each plot using a TurfChek II grass height gauge (Turf-Tec International).

2.7 | Image analysis technique

Images were taken with a Nikon D300 digital SLR camera and saved as high-quality JPEG files of 4288 × 2848 pixels. Imaging was conducted under ambient conditions in the establishment year between 1200 and 1400 h with a fixed monopod mounted 80 cm above the ground for turfgrass plots and 160 cm for seed plots, squarely above the plot. Camera settings were a shutter speed of 1/160 s, an aperture setting of F8, a white balance 5000K, and a focal length of 80 mm. In the production year, images were taken using the same camera but with a light box constructed of an aluminum frame (0.8 m wide × 0.6 m long × 0.9 m tall) with coroplast walls lined with mylar to eliminate light infiltration. The interior was lit by 200 cm of high color rendering index light emitting diode light strip with an output of 221 lumens 0.3 m^{-1} and a 4000K color value (SuperBrightLEDs.com). Camera settings for lightbox images were a shutter speed 1/80 s, an aperture setting F2.7, a white balance 5000K, and a focal length of 80 mm. Weeds did not need to be taken into account due to successful control using herbicides and hand weeding.

Quantification of crown rust, winter injury, spring green-up, and stem texture was conducted using an automated system described by Heineck et al. (2019) for both turfgrass and seed environments. Image analysis was done using ImageJ and R (Version 3.6.0; R Core Team, 2020; Schneider et al., 2012). Core packages in R were EBImage and randomForest (Liaw & Wiener, 2002; Pau et al., 2010). Separate training data sets were made for each year and environment using three images from each rating date with about 300 data points collected from each image to train the model. Crown rust severity was measured as the proportion of crown rust pustule-related pixels to vegetative pixels. Winter injury was estimated in early spring by first removing all soil-related pixels in each image and then measuring the proportion of green tillers to necrotic tillers. Spring green-up was the repeated measure of winter injury through May at Saint Paul and through June at Roseau. Stem texture was quantified by training on the color profile and shape of the dried stems.

2.8 | Statistical analysis

Analysis of all data was conducted in the R environment (R Core Team, 2020). Analysis of variance (ANOVA) for seed yield, yield components, and turfgrass quality components was conducted using a linear mixed effects model in the lme4 package (Bates et al., 2015). Entry was modeled as a fixed effect and block was considered random. Modeling winter injury effects on yield and turfgrass quality were fit by adding significant polynomial terms up to a cubic degree until lack of fit became non-significant ($\alpha = 0.050$). ANOVA was conducted using a sequential fit and Satterthwaite's degrees of freedom approximation (Piepho & Edmondson, 2018). Growth stage data were ordinal and needed to be analyzed using a Friedman's test for blocked nonparametric data (Witkowski & Song, 2012). Marginal means for turfgrass and seed yield components were estimated as needed using the "emmeans" package (Lenth, 2018). Bivariate relationships were explored through simple linear regression and Pearson product-moment calculations. Model assumptions were checked using residual plots, and heterogeneity was corrected using transformations of the response variable.

Turfgrass quality and spring green-up were modeled as repeated measures using the R package "nlme." Autocorrelation structure classes from corClasses function in "nlme" were tested and the exponential spatial correlation with a nugget fit data best based on Akaike information criterion value (Pinheiro et al., 2020). Each location and year was modeled separately due to differences in rating duration and sampling dates. The rating date was modeled by fitting a full polynomial model up to a cubic degree until lack of fit became non-significant ($\alpha = 0.050$), then exploring interactions with entry. Spring green-up was considered the slope of the increase in green turfgrass over time (multiple winter-injury ratings). The model contained entry, rating date, block as fixed effects, and plot as random. The linear slope from each model was used as the measure of spring green-up and was calculated using "emtrends" (Lenth, 2018).

The relationship between turfgrass quality and seed yield was measured using grand means and individual rating dates ($\alpha = 0.100$). When regression was conducted between turfgrass and seed environments, entry means were used; however, when the regression was done within growing environments, data points from each plot were used. Turfgrass rating dates of interest were explored through backward stepwise regression with turfgrass component traits included as explanatory variables and insignificant terms were eliminated (Snedecor & Cochran, 1989). The importance of each variable in the optimal model was measured through multiple regression of scaled data to determine the relative importance of each explanatory variable in units of standard deviation (σ) (Siegel, 2016).

3 | RESULTS

3.1 | Turfgrass quality

Weather conditions at both locations during the establishment year were close to the 5-year average for GDD accumulation and rainfall (Table 1). No differences were found among entries for establishment at Roseau or Saint Paul. ANOVA for turfgrass quality showed that the rating date was best modeled with a cubic polynomial except in the establishment year at Saint Paul, which was best modeled with a quadratic polynomial (Table 2).

In the establishment year, ANOVA for turfgrass quality showed that entry interacted with the linear term for rating date at both locations (Table 2). Turfgrass quality at Roseau was generally at a maximum at the first rating date for most entries, followed by an entry-dependent decrease in turfgrass quality until early fall, when turfgrass quality among all cultivars began to increase (Figure 1A). At Saint Paul, the linear term for rating date interacted with entry so that several entries initially increased in quality whereas others maintained a consistent quality. After mid-August, turfgrass quality decreased among all entries at Saint Paul.

In the production year, entry did not interact with rating date (Table 2), and moderately significant differences were found among entries for turfgrass quality ($p < 0.100$). Turfgrass quality was much lower in the production year compared to the establishment year at both locations. Turfgrass quality at Roseau increased over rating dates before leveling off in mid-summer and began increasing again in late summer. At Saint Paul, turfgrass quality increased initially before decreasing in late June and increased again in early fall.

Components of turfgrass quality measured in the establishment year included color, density, texture, crown rust severity, and vertical growth. Differences among entries were found for each of these characters at both locations in the establishment year (Table 3). Crown rust severity was greater at Roseau compared to Saint Paul; however, genetic color, density, and texture were similar at both locations.

Substantial winter injury was observed at both locations, on average, only 29% and 52% of tillers survived at Roseau and Saint Paul, respectively, and entries did not differ for winter survival due to extremely high variability among plots (Table 3). On a per-plot basis, as winter injury decreased, turfgrass quality increased until about 70% tiller survival was exceeded (Figure 2A,B). This was much more evident at Saint Paul simply because Roseau plots never exceeded 60% survival, which resulted in mean turfgrass quality scores of <5 for all entries in the production year. This level of winter kill is common in Roseau due to the harsh winter conditions (Table 1). ANOVA for spring green-up took into account repeated measures of winter injury and showed significant linear and quadratic terms for rating date at both locations (Table 2). There was a positive linear trend for spring green-up over time at Roseau (.97% tiller survival per day) and Saint Paul (1.98% tiller survival per day). There was no main effect of entry at either location, entry interacted with the linear term for rating date at Roseau (Table 2) and entries ranged from 0.72% to 1.26% increase in tiller survival per day.

3.2 | Seed yield

Seed production plots at Saint Paul obtained a higher plant population than Roseau (49 vs. 32 plants m row^{-1} respectively); however, no differences were found among entries. Crown rust was present at both locations, and entries differed in severity estimates ($p < 0.001$). Differences were found among entries for winter survival at both locations (Table 4). Winter injury on an entry mean basis ranged from 1% to 16% and 29% to 74% tiller survival at Roseau and Saint Paul, respectively. Tiller survival showed a quadratic relationship with seed yield. Polynomial regression showed that seed yield was only moderately affected as tiller survival approached and

TABLE 2 Analysis of variance for turfgrass quality scores taken as a repeated measure.

		Roseau			Saint Paul		
		Establishment year (2017)					
Source	Numerator *df*	Denominator *df*[a]	*F*-value[b]	*p*-value	Denominator *df*	*F*-value	*p*-value
Block	2	38	0.9	0.429	38	8.6	<0.001
Entry (E)	19	38	3.2	0.001	38	10.1	<0.001
Day	1	116	19.4	<0.001	116	40.3	<0.001
Quad. day	1	116	89.9	<0.001	116	61.5	<0.001
Cubic day	1	116	29.7	<0.001	116	2.0	0.164
E × linear day	19	116	5.7	<0.001	116	2.4	0.002
E × quad. day	19	116	0.8	0.661	116	1.6	0.065
E × cubic day	19	116	1.0	0.472	116	1.9	0.019
		Production year (2018)					
Block	2	38	4.9	0.012	38	7.5	0.002
Entry (E)	19	38	1.7	0.083	38	2.5	0.008
Day	1	176	98.5	<0.001	176	1.8	0.178
Quad. day	1	176	26.3	<0.001	176	5.7	0.018
Cubic day	1	176	5.8	0.017	176	25.5	<0.001
E × linear day	19	176	1.0	0.515	176	0.7	0.798
E × quad. day	19	176	0.7	0.805	176	1.4	0.159
E × cubic day	19	176	0.9	0.648	176	1.7	0.050

Note: Separate models were fit for each location and year due to differences in rating frequency and duration.

Abbreviation: Quad, quadratic.

[a]Degrees of freedom obtained using Satterthwaite's method.

[b]*F*-values obtained using sequential type-1 *F*-tests.

TABLE 3 Turfgrass quality and quality components measured in the production year.

		Roseau			Saint Paul		
Trait	Year	*F*-value[a]	Mean	CV	*F*-value	Mean	CV
Color (1–9)	Establishment	3.3***	5.5	11.9	7.8***	7.4	6.2
	Production	1.5	4.4	11.1	6.8***	5.1	9.4
Density (1–9)	Establishment	2.4*	8.3	4.9	4.8***	7.4	4.9
	Production	1.3	4.7	33.0	2.5**	6.9	8.7
Height (cm)	Establishment	5.2***	9.6	31.5	3.2**	13.7	19.4
	Production	2.6**	16.8	29.4	2.0*	22.7	21.5
Texture (1–9)	Establishment	1.5	6.8	5.2	2.4**	6.0	6.5
Texture (stems 0.5 m^2)[b]	Production	2.1*	80	23.8	2.7**	223	8.1
Texture (% stems)[c]	Production	2.4**	3.3	15.1	1.8•	9.5	16.0
Crown rust (%)[d]	Establishment	10.1***	0.78	51	21.0***	0.08	23.7
Winter injury (%)[e]	Production	1.3	29.1	24.6	0.5	51.6	23.0

Note: Analysis of variance was conducted for each trait to determine the effect of entry, estimated marginal mean, and coefficient of variation (CV) for each trait.

[a]Numerator degree of freedom = 19, denominator degrees of freedom = 38.

[b]Texture as measured by the number of dried seed culms in 0.5 m^2 of a plot.

[c]Texture as measured by the proportion of pixels in an image that were related to dried seed culms.

[d]Severity of crown rust as measured by the ratio of pustule related pixels to total leaf related pixels.

[e]Winter injury was measured in early spring as the ratio of healthy tiller to necrotic tiller related pixels.

•, *, **, and *** denote significance at the 0.1, 0.05, 0.01, and 0.001 probability levels, respectively.

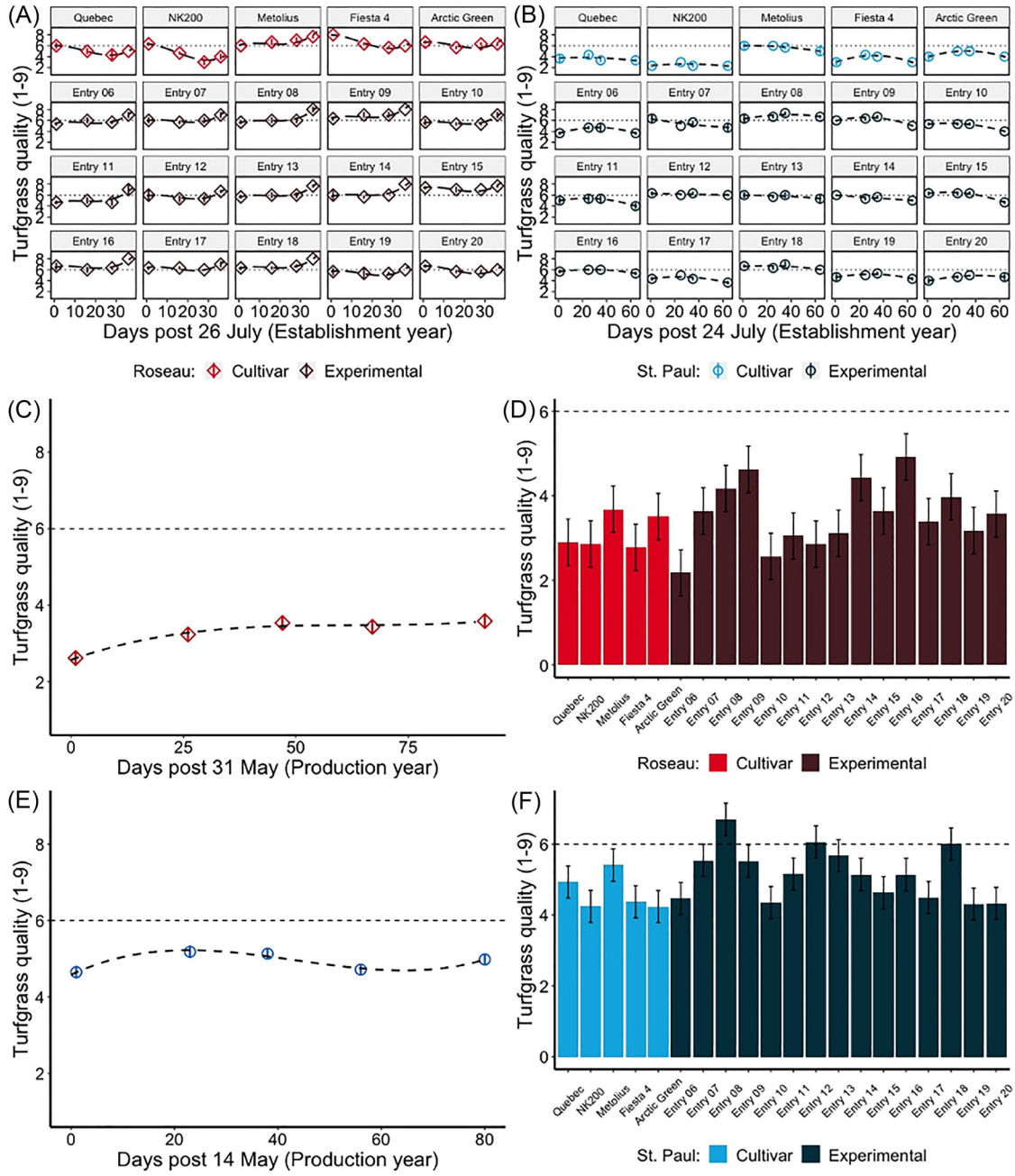

FIGURE 1 Turfgrass performance for each year and location. Rating in the establishment year began on July 26, 2017, in Roseau (A) and on July 24, 2017, in Saint Paul (B). Rating date interacted with entry at both Roseau and Saint Paul in the establishing year. Rating in the production year began on May 31, 2018, in Roseau (C and D) and May 14, 2018, in Saint Paul (E and F). The rating date did not interact with entry at both Roseau and Saint Paul in the production year. (D) and (F) are estimated means among rating dates. Points with error bars are the estimated marginal mean ±1 standard error. The dotted black line is a turfgrass quality score of 6, which is equal to acceptable quality.

exceeded 20% (Figure 2B,D). Few plots at Saint Paul were below 20% winter injury, and the slope of the model was insignificant ($p = 0.320$).

Variation among entries was found for seed yield at both locations (Table 4), but a far lower coefficient of variation was observed at Saint Paul (coefficient of variation (CV) = 10.6%) compared to Roseau (CV = 49.0%). Significant differences among entries were found for growth stage, culm height, and spike length at both locations (Table 4). There was no effect of entry on fertile tiller number in Saint Paul ($p = 0.410$), but differences did exist in Roseau ($p = 0.040$). Seed yield per plot at Roseau and Saint Paul was positively correlated with fertile tiller number ($r = 0.76$ and 0.35, respectively; $p < 0.050$) and growth stage ($r = 0.61$ and 0.44, respectively; $p < 0.01$). Seed yield per plot at Saint Paul was not correlated with spike length, seed yield per spike, or culm height.

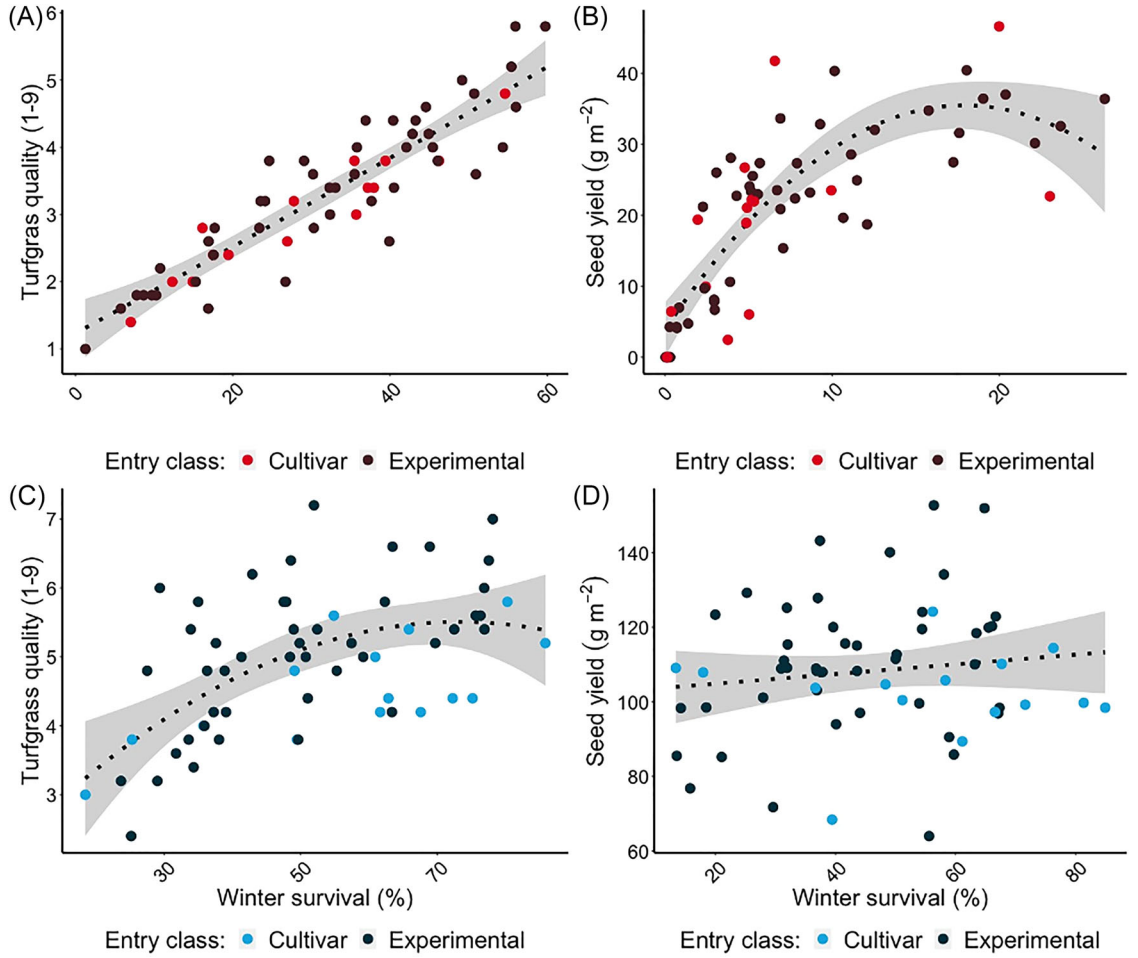

FIGURE 2 Linear and polynomial regression for winter survival against turfgrass quality and seed yield on a per-plot basis with the shaded region equal to ±1 standard error. (A) Linear relationship between survival and turfgrass quality at Roseau (fitted model $\beta_1 = 13.7^{**}$, $\beta_2 = -27.4^{\bullet}$, $R^2 = 0.84$). (B) Polynomial relationship between survival and seed yield at Roseau (fitted model $\beta_1 = 0.72^{**}$, $\beta_2 = 0.75^{**}$, $R^2 = 0.60$). (C) Polynomial relationship between survival and turfgrass quality at Saint Paul (fitted model $\beta_1 = 11.1^{**}$, $\beta_2 = -7.6^{*}$, $R^2 = 0.32$). (D) Insignificant relationship between survival and seed yield at Saint Paul (fitted model $\beta_1 = \text{NS}$, $R^2 = 0.02$). Symbols for model fit are as follows: "•", "*", "**", significant at the 0.1, 0.05, and 0.01 probability levels, respectively. NS, not significant.

TABLE 4 Seed yield and yield components measured in the production year.

	Roseau			Saint Paul		
Trait	***F*-value[a]**	**Mean**	**CV**	***F*-value[a]**	**Mean**	**CV**
Yield plot^{-1} (g m^{-2})	2.1*	20.8	49.0	5.3***	108	10.6
Yield spike^{-1} (g spike^{-1})	1.58	0.03	24.9	2.1*	0.19	8.9
Spike length (cm)	4.6***	12.2	3.5	10.3***	12.9	2.8
Fertile tillers (ct. m^2)	1.91*	1400	45.4	1.1	6400	16.9
Culm height (cm)	4.1***	37.2	9.6	16.6***	50.4	5.1
Growth stage[b]	30.9***	11	–	64.7***	11	–
Winter injury (%)	2.0*	7.8	21.8	2.3*	46.2	30.5

Note: Analysis of variance was conducted for each trait to determine the effect of entry, estimated marginal mean, and coefficient of variation (CV) for each seed production trait.

Abbreviation: ct. m^2, count per meter square.

[a]Numerator degree of freedom = 19, denominator degrees of freedom = 38.

[b]Growth staging data based on Gustavsson (2011) and were analyzed with a Friedman's test on a chi-square test distribution. Median instead of mean was reported.

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

At Roseau, seed yield per plot was correlated with seed yield per spike ($r = 0.35$, $p = 0.006$) and culm height ($r = 0.47$, $p < 0.001$).

3.3 | Relationship between turfgrass quality and seed yield

There was no significant correlation between seed yield and overall average turfgrass quality at either location (Roseau: β_1 = not significant (NS), $R^2 = 0.12$) and Saint Paul: β_1 = NS, $R^2 = 0.13$). In addition to regression analysis using the grand mean, quality scores for each rating date in the establishment and production year were regressed against seed yield. At Roseau, the third rating date (August 23) in the establishment year and the first and second dates in the production year (May 31 and June 26) were moderately correlated with seed yield ($r = 0.41$, 0.41, and 0.39, respectively, $p < 0.100$). At Saint Paul, the fourth rating date (August 27) in the establishment year and the fifth date (August 2) in the production year were moderately correlated with seed yield ($r = 0.42$ and 0.40, respectively, $p < 0.100$).

3.4 | Relationship between turfgrass quality components and seed yield

Multiple regression using scaled data gave insight into turfgrass components correlated with seed yield at each rating date. At Roseau, turfgrass quality on the third rating date was most influenced by crown rust ($\sigma = -0.49$, $p < 0.001$), density ($\sigma = 0.45$, $p < 0.001$), color ($\sigma = 0.18$, $p = 0.030$), and vertical growth ($\sigma = 0.14$, $p = 0.120$). In the seed production year at Roseau, turfgrass quality was best predicted by winter injury ($\sigma = -0.84$, $p < 0.001$) and stem texture ($\sigma = -0.12$, $p = 0.090$) on the first rating and density ($\sigma = 0.55$, $p < 0.001$), winter injury ($\sigma = -0.36$, $p = 0.010$), and stem texture ($\sigma = -0.13$, $p = 0.030$) on the second rating date. At Saint Paul, on the fourth rating date in the establishment year, turfgrass quality was best predicted by density ($\sigma = 0.52$, $p < 0.001$), color ($\sigma = 0.26$, $p = 0.030$), and crown rust ($\sigma = -0.17$, $p = 0.11$). On the fifth rating date in the production year, turfgrass quality at Saint Paul was best predicted by density ($\sigma = 0.58$, $p < 0.001$), color ($\sigma = 0.25$, $p = 0.020$), stem texture ($\sigma = 0.21$, $p = 0.080$), and winter injury ($\sigma = -0.20$, $p = 0.100$).

Considering both locations in the establishment year, turfgrass quality was best predicted by crown rust, density, and color. None of these traits were strongly correlated with seed yield; however, crown rust severity between turfgrass and seed production environments was highly correlated at both Roseau ($r = 0.95$, $p < 0.001$) and Saint Paul ($r = 0.99$, $p < 0.001$) (Figure S3). Considering both locations in the production year, turfgrass quality was best predicted by winter injury, density, and stem texture. Winter injury on an entry mean basis between turfgrass and seed production plots was positively correlated at Roseau ($r = 0.44$, $p = 0.050$) and at Saint Paul ($r = 0.47$, $p = 0.010$). Winter injury was highly correlated with seed yield at Roseau (Figure 2). Density was not correlated with seed yield at Saint Paul but showed a moderate correlation at Roseau ($r = 0.26$, $p = 0.050$). Stem texture was not correlated with seed yield at Saint Paul but showed a weak correlation at Roseau ($r = 0.22$, $p = 0.090$).

3.5 | Relationship between seed maturation and vertical turfgrass growth

Vertical turfgrass growth was not a strong predictor of turfgrass quality in regression models. The vertical growth rate of turfgrass was correlated with earlier stem elongation and flowering in the seed production environment at Saint Paul ($r = 0.56$, $p = 0.010$). In seed production plots, earlier flowering (more advanced growth stage) was correlated with increased seed yield. Despite this faster vertical turfgrass growth being associated with earlier flowering at Saint Paul, the growth rate in turfgrass plots was not associated with higher seed yields ($r = 0.23$, $p = 0.820$).

3.6 | Relationship between fertile tiller number and stem texture

Fertile tiller number and stem texture were important predictors in regression models for both turfgrass quality and seed yield at both locations. On a per-plot basis, fertile tiller number in seed production swards was positively correlated with seed yield per-plot at both locations (Figure 3A). A negative correlation between the proportion of stems in turfgrass plots and quality scores on a per-plot basis was present at both locations (Figure 3B). Although fertile tillers positively correlated with yield and negatively correlated with turfgrass quality, the proportion of stems in turfgrass plots was not correlated with fertile tiller number in seed plots at either location (Figure 3C) on an entry mean basis.

4 | DISCUSSION

Turfgrass breeding programs predominantly focus on improving turfgrass quality and often assume a tradeoff occurs between increasing quality and seed yield (Bonos & Huff, 2013; Johnson et al., 2003; Meyer & Funk, 1989). Although seed yield is widely recognized as an important trait (Casler et al., 1996), research has shown that increasing fertile tiller number, vertical growth, and duration of flowering may result in reduced aesthetic quality (Hazard et al., 2006;

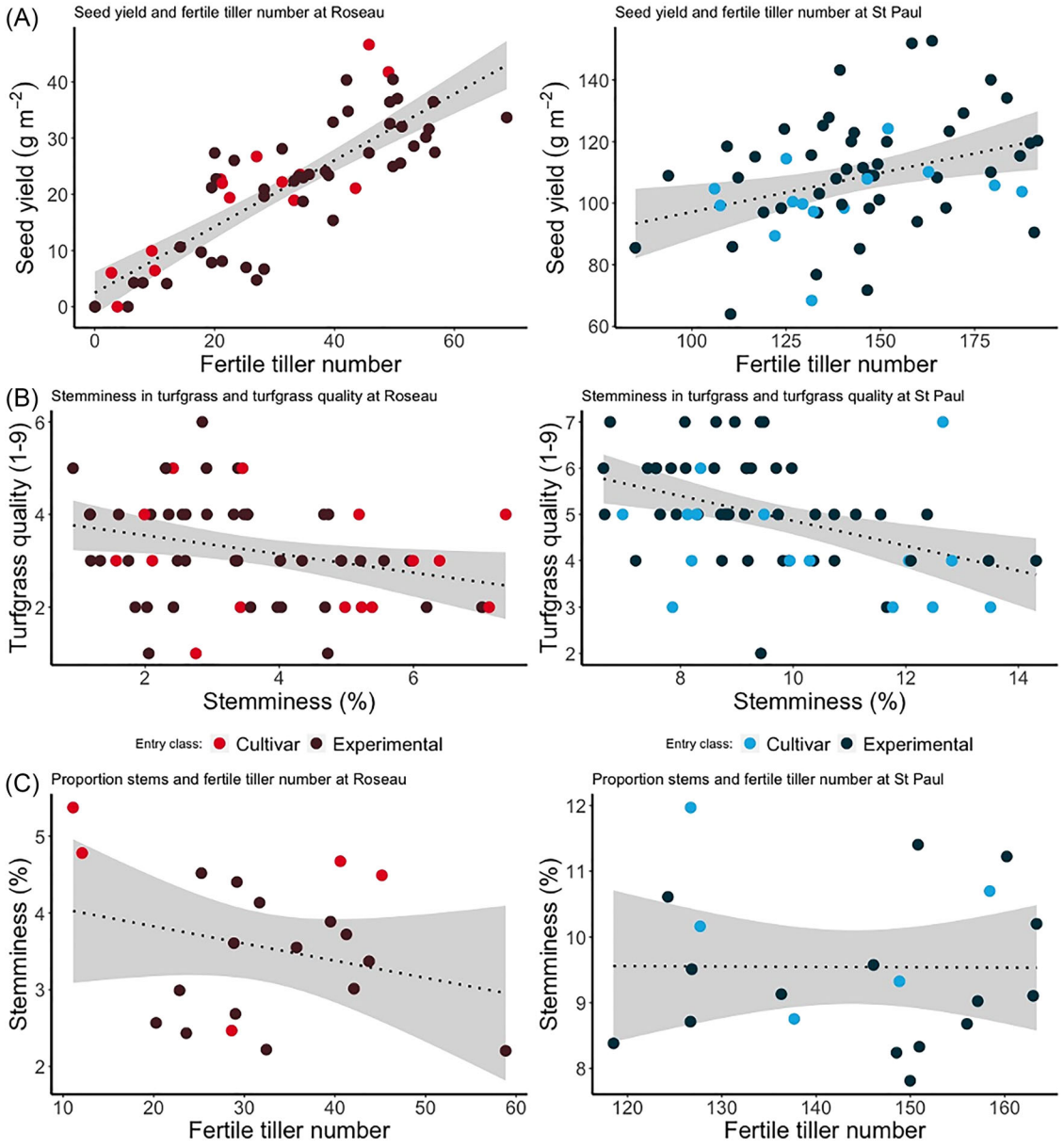

FIGURE 3 (A) Positive linear relationship between fertile tiller number and seed yield in the production year (fitted model: Roseau $\beta_1 = 0.59$***, $R^2 = 0.68$; Saint Paul $\beta_1 = 0.25$**, $R^2 = 0.12$). (B) Negative relationship between turfgrass quality and proportion of fertile tillers (fitted model: Roseau $\beta_1 = -0.20$*, $R^2 = 0.09$; Saint Paul $\beta_1 = -0.27$***, $R^2 = 0.18$). (C) Insignificant relationship between fertile tiller number in seed plots and proportion of fertile tillers (stemminess) in turfgrass plots (fitted model: Roseau $\beta_1 =$ NS; Saint Paul $\beta_1 =$ NS). Symbols for model fit are as follows: *, **, ***; significant at the 0.05, 0.01, and 0.001 probability levels, respectively. NS, not significant

Sampoux et al., 2013; Żurek et al., 2007). This is problematic as seed producers demand higher yields, and screening for seed yield capacity typically does not occur until late in the breeding pipeline; this requires breeders to balance turfgrass quality and seed yield. The two experimental locations in this study included the Minnesota seed production region (Roseau) and the location of the breeding program (Saint Paul). Winter kill (tiller survival) highly impacted research results at Roseau. Often, there is greater winter kill observed at Roseau which is due to the historically colder temperatures and protracted winters (Table 1).

Although there were significant differences between entries for seed yield and turfgrass quality, results showed that turfgrass quality averaged over a year for entry was not correlated with seed yield per plot at either location. This is in contrast with Johnston et al. (2011), who found a negative relationship between average turfgrass quality and an average seed yield over 2 years in Kentucky bluegrass. Turfgrass quality is a complex trait composed of both genetic- and stress-related components that can change dramatically over the growing season (Morris & Shearman, 2006). In the establishment year, variation among entries was found at both locations for almost

all turfgrass components, including density, color, vertical growth rate, and crown rust severity (Table 3). Although no differences among entries were found for winter injury, it was predictive of turfgrass quality on a per-plot basis (Figure 2A,B). Spring green-up, defined as the rate (slope) of recovery from winter injury, showed variation among entries at Roseau. This result suggests that entries recovered from damage at variable rates. Winter stress undoubtedly influenced turfgrass ratings and components in the production year. This is apparent by observing the lower *F*-statistics and higher CVs in the production year for most traits compared to the establishment year (Table 3).

Consistent turfgrass quality is dependent on component traits remaining stable throughout the year (Żurek et al., 2007). However, ANOVA showed that turfgrass quality was highly variable over rating dates in both years (Table 2). To provide a deeper understanding of potential tradeoffs, correlations between individual turfgrass rating dates and seed yield were conducted. Several rating dates showed a moderate but positive relationship between turfgrass quality and seed yield ($r = 0.4$–0.42, $p < 0.100$); however, the importance of rating date was not consistent between years and locations. Multiple regression determined that crown rust severity and density were the best predictors of seed yield at both locations in the establishment year and winter injury and density were the most prominent in the production year. Density and stem texture were more likely to be correlated with seed yield simply due to their association with higher levels of survival.

Seed yield, like turfgrass quality, is composed of component traits that are important to maximize yield (Hebblethwaite et al., 1980). Variation among entries existed for almost all seed yield components. Most yield component values were much larger at Saint Paul, likely due to the much lower winter injury (Table 4). Increasing seed component traits such as fertile tiller number and early stem elongation may increase seed yield but increase vertical elongation and reduce the stem texture aesthetic in turfgrass (Elgersma, 1985; Hazard et al., 2006).

Vertical growth in turfgrass swards is an unfavorable attribute, and the texture of second-year perennial ryegrass is particularly reduced by increased stem numbers. In this study, reduced vertical growth was associated with more favorable turfgrass quality scores. Early stem elongation and flowering were correlated with increased seed yields at both locations and this trait has been generally associated with increased seed yields in the past (Elgersma et al., 1994). Growth stage and vertical growth rate in turfgrass plots were positively correlated at Saint Paul (Figure S4). These results lead to the supposition that reducing vertical turfgrass growth rate may increase the time to stem elongation and flowering, thereby possibly negatively affecting seed yield. This hypothesis requires further exploration.

Fertile tiller number in perennial ryegrass is an important seed yield component and has been associated with increased seed yield under certain growing conditions when space is available for crown expansion (Bugge, 1987; Chastain & Young, 1998). This yield component compensation mechanism allows perennial ryegrass to recover from moderate winter damage with little to no yield reduction (Figure 2D) (Young et al., 1996). In the seed production year, stem density was negatively correlated to turfgrass quality (Figure 3). On a per-plot basis, fertile tiller number was highly correlated with seed yield at both locations. Because of the positive correlation between culms and seed yield and the negative correlation between the proportion of stems and turfgrass quality, it seems likely that turfgrass plots with lots of stems would result in seed plots of the same entry having greater numbers of fertile tillers. Surprisingly, fertile tiller number in seed plots and the proportion of stems in turfgrass plots were not correlated (Figure 3C). In Kentucky bluegrass turfgras, Johnson et al. (2003) also found that fertile tiller number was not associated with turfgrass quality ($r = -0.26$, $p > 0.050$). In this study, entries did not consistently differ for fertile tiller number (Table 4) and this trait has been generally associated with low heritability in swards (Bugge, 1987). It is important to reiterate that there was not a single instance in which a turfgrass quality rating date was negatively correlated with seed yield. Certain traits such as growth stage, vertical growth, and fertile tiller number may have been associated with tradeoffs, but the negative impact of these individual components was never prominent enough to cause a negative association between turfgrass quality and seed yield in this study. There may be a tradeoff when breeding for reduced vertical growth in second-year turfgrass swards and fertile tillering growth and development; however, these results were inconsistent across locations. A major limitation of this study was the scant number of entries and the lack of genetic relationship between them. In addition, the entries experienced severe winter damage at both locations. Increasing research sites, such as the Pacific Northwest, and experimental years would improve the data set, but would be logistically challenging.

The following is a recommendation for further study on this topic. A robust design would include a divergent selection scheme where recurrent selection would be made for individuals for both high and low turfgrass quality and high and low seed yield. This could allow the direct observation of changes in the components of seed yield and turfgrass quality and allow for the assessment of genetic correlations between traits in the resulting half-sib offspring. A less time-consuming design would simply assess a diverse panel of germplasm similar to Hulke et al. (2007) for turfgrass quality and seed yield. The scientist would make selections for favorable and unfavorable genotypes to be propagated for half-sib seed production. Clones from selected parents should then be polycrossed with maternal identification maintained and

half-sib families seeded in plots. This would allow for both narrow-sense heritability and genetic correlations to be calculated between turfgrass and seed production swards (Sedcole & Clements, 1973; Waldron et al., 2008).

5 | CONCLUSION

This study explored potential tradeoffs between turfgrass quality and seed yield in perennial ryegrass. No overall correlation between these variables existed, however, turfgrass quality on several individual rating dates was moderately correlated with seed yield. Entry performance for crown rust and winter survival was positively correlated between turfgrass quality and seed production growing environments. Fertile tillering in seed plots was not associated with greater proportions or counts of stems in turfgrass plots. Vertical elongation in turfgrass plots was highly correlated with rapid growth stage advancement in seed plots, although this did not directly impact seed yield. Perennial ryegrass grown for turfgrass or seed in the Upper US Midwest will likely face few major tradeoffs when simultaneously breeding for aesthetic quality and seed yield, although a more rigorous study is warranted.

AUTHOR CONTRIBUTIONS

Garett C. Heineck: Conceptualization; data curation; formal analysis; methodology; writing—original draft; writing—review and editing. **Nancy J. Ehlke**: Conceptualization; funding acquisition; writing—review and editing. **Eric Watkins**: Conceptualization; funding acquisition; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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

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