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Effects of Seeding Rate on Durum Crop Production and Physiological Responses

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ABSTRACT

Seeding rate can be manipulated to optimize the ability of the crop to capture available resources and therefore increase yield. Seeding rate may vary between regions according to the climate conditions, soil type, sowing time, and other agronomic practices. Insufficient information is available for optimum seeding rate on durum wheat (*Triticum turgidum* L. var *durum*) for some production zones, and response to seeding rate is unknown for recently registered durum cultivars in Canada. The objective of this study was to determine the effect of seeding rate (SR) on performance of Canada Western Amber Durum wheat cultivars and study the underlying physiological response to a wide range of SRs. Eight durum wheat cultivars were sown at densities of 163, 217, 272, 326, and 380 seeds m^{-2} to study the effect of SR on several agronomic and physiological traits. Each experiment was planted as a factorial randomized complete block design with three replications near Swift Current and Regina in 2010 and 2011. High genetic and environmental response to SR was observed between cultivars. The results showed an increase in grain yield as the SR increased. The optimum SR for cultivars grown at Swift Current and Regina was 272 to 326 seeds m^{-2} and 217 to 272 seeds m^{-2}. Grain yield showed a positive relationship with carbon isotope discrimination (CID) and leaf area index (LAI). In turn, LAI showed a linear increase with SR. Information generated from this study could enable producers to maximize crop grain profitability by optimizing plant density.

Core Ideas

- Optimum seeding rate on elite durum wheat depends on environment.
- Seeding rate had a significant positive relationship with grain yield, leaf area index, and carbon isotope discrimination.
- Seeding rate should be adjusted for environment and genotype for maximum yield.

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Wheat producers continually seek alternative and improved strategies to increase profitability, manage pest resistance, and protect the environment. There is an interest among agronomists and farmers to exploit the relationship between crop yield and SR (i.e., plant density) to maximize grain yield in cereals (Arduini et al., 2006a; Beres et al., 2016, 2012, 2011; Dorval et al., 2015; Fang et al., 2010; Gooding et al., 2002; Nilsen et al., 2016). The optimization of the SR is considered one of the major factors determining the ability of the crop to capture resources (Lloveras et al., 2004). Because this factor is under the farmer's control in most cropping systems, SR continues to be an important cropping factor for crop producers and best decisions need to be made (Slafer and Satorre, 1999).

Holliday (1960) was the first to graphically depict the relationship between grain yield responses over a wide range of SRs. In wheat, the SR for maximum grain yield was derived from the parabolic response curve which quickly reaches a maximum yield followed by a slow decline at high densities (Beres et al., 2011, 2010; Puckridge and Donald, 1967; Kirby, 1969; Willey and Heath, 1969). Optimum plant densities vary greatly between regions according to climatic conditions (Holliday, 1960; Puckridge and Donald, 1967; Faris and DePauw, 1980; Frederick and Marshall, 1985; Blue et al., 1990; Campbell et al., 1991; Anderson and Sawkins, 1997; Anderson et al., 2004), soil types (Pendleton and Dungan, 1960; Sandhu et al., 1981; Anderson and Sawkins, 1997; Anderson et al., 2004; Gan et al., 2009), sowing time, (Sandhu et al., 1981; Balazs et al., 1992; Sheik et al., 1998), and cultivars (Pendleton and Dungan, 1960; Jones and Hayes, 1967; Puckridge and Donald, 1967; Baker, 1977, 1982; Khokhar et al., 1985; Wajid et al., 2004; Kirkegaard and Hunt, 2010). The use of narrow row spacing and high SR has been shown to enhance yield of winter wheat (Joseph et al., 1985).

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Abbreviations: CID, carbon isotope discrimination; LAI, leaf area index; SR, seeding rate.

This is mainly due to the fact that rapid leaf area development in the season by early capturing light resources has potential to reduce weed pressure due to rapid canopy development, water use efficiency and therefore grain yield (Marshall and Ohm, 1987; Condon et al., 2004). Historically, high SR was used to supress weeds and competition (Fischer and Miles, 1973), although, the use of modern herbicides chemistries and mixes has reduced this need (Davies and Welsh, 2002).

In general, optimum SR increases with the availability of environmental resources (Ciha, 1983; Gooding et al., 2002; Arduini et al., 2006a). However, dense planting does not always increase yield production, because SR also influences inter-plant competition (Holliday, 1960; Park et al., 2003) pathogens, soil moisture, and N availability (Fischer et al., 1976; Read and Warder, 1982). The sowing date, considered the most important factor influencing the optimum SR by growers (Satorre, 1999) is largely governed by the climate and the requirements of a crop rotation. Delay in sowing after the optimal date, consistently reduces yield because it reduces individual plant growth and tiller production in wheat (Darwinkel et al., 1977; Gooding and Davies, 1997; Fielder, 1998). Significant interactions between cultivars, SR, and sowing dates for grain yield in wheat have also been reported (Briggs and Ayten-fisu, 1979; Baker, 1982).

In Europe, the optimum wheat SR range from 200 to 370 seeds m^{-2} (Easson et al., 1993; Gooding et al., 2002; Arduini et al., 2006b) in countries as Ireland, United Kingdom, Belgium, and France to 70 to 150 seeds m^{-2} in Mediterranean countries as Spain and Italy (Lloveras et al., 2004). In the United States, most published research estimated the maximum grain yield for winter wheat at SR ranging from 80 seeds m^{-2} (Black and Bauer, 1990) in North Dakota to 140 seeds m^{-2} in Montana (Holen et al., 2001; Carr et al., 2003). The optimum SR for winter wheat in the Canadian prairies ranged from 175 seeds m^{-2} under dry conditions to 450 seeds m^{-2} under favorable growing conditions (estimated from Pelton, 1969; Tompkins et al. (1991) using an average seed weight of 0.033 mg). In southwestern Saskatchewan, the crop planning guide for 2015 recommend 270 to 365 seeds m^{-2} using an average seed weight of 0.033 mg for winter wheat and 190 to 240 seeds m^{-2} using an average seed weight of 0.042 mg for durum wheat (Saskatchewan Crop Planning Management Guide Farm, 2015). The need to adjust SR according to the genotype has been discussed by many researchers (Briggs and Ayten-fisu, 1979; Faris and DePauw, 1980; Ciha, 1983). These studies suggested that new cultivars should be tested at a wide range of SRs to determine their optimum yields.

Crop response to SR can be measured by the analysis of plant morphological differences (Puckridge and Donald, 1967; Kirby, 1970; Kirby and Faris, 1972; Fischer et al., 1976), by examination of water and light differences in and around the crop (Kirby, 1970; Tompkins et al., 1991; Singh and Uttam, 1997), and by the different abilities of cultivars to compensate for low or high plant density (Osman and Mahmoud, 1981; Hassanein et al., 2001; Stephen et al., 2005).

A significant amount of research has been conducted on the effects of SR on winter wheat in Europe, United States, and Canada; however, little has been published about the relationships between grain yields and optimum SR of durum wheat cultivars, and the analysis of the physiological traits responding to different SR. Little or no information is available on optimum SR and physiological responses in newly registered wheat cultivars. The objectives of this research were (i) to provide a recommended optimum SR for durum wheat to producers, (ii) to determine the SR effects on the performance of the Canadian Western Amber Durum wheat cultivars, and (iii) to study the underlying physiological response to a wide range of SRs.

MATERIALS AND METHODS

Plant Material and Experimental Design

Eight durum wheat cultivars from the Canadian Western Amber Durum Class, Kyle (Townley-Smith et al., 1987), Commander (Clarke et al., 2005a), Strongfield (Clarke et al., 2005b), Brigade (Clarke et al., 2009a), CDC Verona (Pozniak et al., 2009), Eurostar (Clarke et al., 2009b), Enterprise (Singh et al., 2010) and Transcend (Singh et al., 2012) were used to investigate the response to a wide range of SRs. These cultivars represented the predominant Canadian durum wheat cultivars as well as the most recently registered cultivars for the prairie ecosystem when this research was initiated, with the exception of Kyle (released in 1984). Four field experiments were conducted during 2010 and 2011 at two locations, which represented two environmental conditions within the western Canadian prairie (Table 1). Regina typified a dark brown Vertisolic with pH 5.5 clay soil type. Swift Current had a typical Canadian prairie climate with a Swinton loam (Orthic Brown Chernozem) soil type with silt loam texture and a saturated-paste pH of 5.8 in the 0- to 15-cm depth. The background soil test level for 2010 in Regina was 121 and 52 kg ha^{-1} for N and P. Thirty-three kilogram per hectare of 17–19–0–14 and 61 kg ha^{-1} of 34–17–0 and top dress with 48 kg ha^{-1} of 46–0–0 were added to the field. In 2011, the background soil test level was 98 and 38 kg ha^{-1} for N and P. We added 67 kg ha^{-1} of 17–19–0–14 and 179 kg ha^{-1} of 28–26–0. In Swift current, the background soil test level for 2010 was 115 and 38 kg ha^{-1} for N and P. Fifty-six kilogram per hectare of 12–50–0 and top dress 28 kg ha^{-1} of 46–0–0 were added to the field. In 2011, the background soil test level was 66 and 71 kg ha^{-1} for N and P. We added 117 kg ha^{-1} of 34–17–0 and 28 kg ha^{-1} of 21–0-0–24 and top dress of 33 kg ha^{-1} of 46–0–0.

In each experiment, cultivars were planted in a factorial randomized complete block design with three replications in plots of 3.66 m^2 (four rows per plot; 23 cm row width). Plots were trimmed to 3 m in length resulting in an area of 2.74 m^2. Plots were sown between 13 May and 20 May at SRs of 163, 217, 272, 326, 380 seeds m^{-2}. Numbers of seeds per plot were adjusted for percentage germination of seed lot. Plant counts were performed first in the fall by staking and counting two paired 1-m sections of crop row in each plot. The same sections were counted again in spring to determine winter survival and to ensure treatments rates.

Agronomic and Physiological Trait Measurements

Traits measured for all plots were grain yield (kg ha^{-1}), days to physiological maturity (DM, days), plant height (cm), thousand kernel weight (TKW, g), test weight (TW, kg hL^{-1}), grain protein concentration (GPC, %), LAI, chlorophyll content (SPAD), and CID (‰). Days to maturity was recorded when 50% of the spikes had kernels at approximately 30% moisture

Table 1. Site description and agronomic details for the growing conditions.

Site description	Swift Current			Regina		
Coordinates	50°15′ N, 107°44′ W			50°40′ N, 104°56′ W		
Soil classification	Orthic Brown Chernozem			Dark Brown Vertisolic		
Soil texture	Swinton Loam			mostly >60% clay		
Soil pH (0–15-cm depth)	5.8			5.5		
Year	2010	2011	Long -term mean	2010	2011	Long -term mean
Annual precipitation, mm	655	411	366	503	408	363
Seasonal rainfall, mm	409	299	256	485	265	220
April to July rainfall, mm	366	250	198	262	230	213
Average maximum temperature , °C	19.0	21.7	18.5	20.4	22.7	19.6
Average minimum temperature, °C	8.3	8.7	6.0	8.0	8.5	5.7
Average temperature, °C	13.7	15.2	12.4	14.2	15.8	12.7
Sowing date	17 May	13 May		15 May	20 May	
Harvest date	1 Oct.	16 Sept.		2 Oct.	6 Sept	
Total days	137	126		140	109	

on a wet weight basis. When all plots reached physiological maturity (Zadoks et al., 1974), plant height was determined by measuring the distance between the base of the stem and the top of the spike excluding awns. The entire plot area was harvested with a Wintersteiger Elite combine (Wintersteiger AG, Salt Lake City, UT) when the plants in the experimental plots attained a maximum of 18% moisture on a wet weight basis. Grain samples were dried to about 12% moisture prior to weighing. Thousand kernel weight was estimated by adjusting the weight of 200 kernels by a factor of 5X. Test weight was measured using a 0.57 L chondrometer. For grain protein concentration (GPC), 25-g subsamples of grain from each plot were equilibrated for 7 d at 45% relative humidity and 22°C, ground with an UDY cyclone sample mill with a 1-mm screen, and equilibrated for a further 7 d under the same moisture and temperature conditions. Grain protein concentration was measured using a FOSS-6500 Near-Infrared Reflectance Spectrophotometer (NIRS) calibrated with reference samples using a Leco-N Analyzer (LECO FP-528). Prediction of GPC by NIRS was confirmed by analysis of 50 samples selected at random from each of the field trials.

Leaf area index was measured using the LAI-2200 plant canopy analyzer (LI-COR Inc., Lincoln, NE). The LAI-2200 measures the attenuation of diffuse sky radiation at five zenith angles simultaneously with a "fish-eye" optical sensor that calculates LAI and mean foliage tilt angle (MTA). Twelve measurements, three above and nine below the canopy, were made per plot to determinate canopy light interception; LAI and MTA of the foliage were computed from these measurements (Lang et al., 1985; Perry et al., 1988). To prevent direct sunlight on the sensor of LAI-2000, samples below and above-canopy radiation were made in the direction facing away from the sun (i.e., with the sun behind the operator) using a view restrictor of 45°. The measurements were taken either under clear skies with low solar elevation (i.e., within the 2 h following sunrise or preceding sunset) or under overcast conditions at anthesis (Zadoks stage 65).

Chlorophyll content was measured at anthesis (Zadoks stage 65) on 10 healthy flag leaves per plot, with a portable soil plant analysis development device (SPAD-502, Minolta Camera Co), which generates a measure predictive of chlorophyll concentration (Yadawa, 1986).

Carbon isotope discrimination is a measure of the ^{13}C to ^{12}C ($^{13}C/^{12}C$) in plant material compared to the same ratio in the atmosphere (Farquhar et al., 1989). When measured in plant dry matter, CID integrates transpiration efficiency, the ratio of net photosynthesis to water transpired (biomass production), over the period during which the dry matter is assimilated (Araus et al., 2004). For each plot, a sample of approximately 2 g of mature kernels was oven-dried and finely ground with an UDY mill with a 1-mm screen. The $^{13}C/^{12}C$ ratio of samples was determined by the Lethbridge Research Center of Agriculture and Agri-Food Canada, Lethbridge, AB. Canada. Samples weighing 0.6 to 0.8 mg were combusted in an elemental analyzer (Carlo Erba NA 2100 manufactured by CE Instruments in Milan, Italy), and the $^{13}C/^{12}C$ ratio was measured with an isotope ratio mass spectrometer (Optima manufactured by VG Isotech in Middlewich, UK) operated in continuous flow mode. Stable CID was expressed as $\delta^{13}C$ values (Farquhar et al., 1989), where $\delta^{13}C$ (‰) = [(R sample/R standard)-1] ′ 1000, and R is the $^{13}C/^{12}C$ ratio. Secondary standards of graphite, sucrose, and polyethylene foil (IAEA, Vienna, Austria) calibrated against Peedee belemnite (PDB) carbonate were used for comparison. The accuracy of the $\delta^{13}C$ measurements was ±0.1 ‰. Carbon isotope discrimination was further calculated using the equation CID = $(\delta_a - \delta_p)/(1 + \delta_p)$, where *a* and *p* refer to air and plant, respectively (Farquhar et al., 1989). On the PDB scale, free atmospheric CO_2 has a current deviation, δ_a, of approximately −8.0‰ (Farquhar et al., 1989). Weeds were chemically controlled following best management practices at each site.

Statistical Analysis

The data were analyzed using PROC Mixed (SAS Institute, 1984) with a mixed model (McCulloch et al., 2008) for each trait separately. In each of these mixed models, replications were considered as random effects whereas environmental variables, SR and cultivars were considered as fixed effects. Variance components were estimated by residual maximum likelihood. The respective error terms in Table 2 were also obtained PROC MIXED to detect the significance of the main and interaction effects. The pairwise differences in Table 3 were obtained using the LSMEANS statement with Tukey test for multiple testing corrections.

Table 2. *F* values of the combined analysis of variance for eight durum wheat cultivars grown in Regina and Swift Current during 2010 and 2011 environments.

Effect	df	Yield	DM†	Height	GPC	TW	TKW	SPAD	CID	LAI	MTA
Year	1	193***	23,886***	23.7***	93.6***	3760***	1.44 ns‡	0.15ns	11,285***	1621***	38.2***
Location (loc)	1	842***	2,673***	735***	0.40ns	1644***	397***	0ns	2,185***	793***	0.30ns
Year×loc	1	3.09ns	–	12.8***	1439***	89.4***	40.88***	19.6***	316***	469***	18.2***
Rep(year×loc)	8	11.6***	5.75***	7.9***	23.0***	5.37***	1.89ns	1.27ns	12.6***	27.1***	3.85***
Cultivar	7	21.5***	38.4***	205***	32.9***	84.7***	104***	4.25***	171***	25.0***	5.11***
Cultivar×year	7	4.85***	1.39ns	9.96***	4.67***	15.0***	20.0***	0.57ns	13.7***	6.02***	0.80ns
Cultivar×loc	7	10.7***	4.37***	4.05***	3.63***	5.83***	6.14***	0.40ns	5.17***	5.63***	0.76ns
Cultivar×year×loc	7	2.05*	–	2.00ns	0.91ns	11.79***	11.7***	0.06ns	4.17***	2.32*	1.90ns
Rate	4	38.8***	15.8***	0.73ns	1.88ns	2.43*	7.54***	1.1ns	9.34***	36.7***	1.19ns
Rate×year	4	0.24ns	0.98ns	1.88ns	1.78ns	0.44ns	0.34ns	0.05ns	0.41ns	3.04**	1.12ns
Rate×loc	4	1.46ns	2.10ns	0.65ns	0.78ns	4.7**	3.51**	0.04ns	2.78*	1.05ns	0.29ns
Rate×year×loc	4	3.93ns	–	1.40ns	2.35ns	0.86ns	1.25ns	0.23ns	3.49**	2.12ns	0.39ns
Cultivar×rate	28	0.96ns	0.91ns	0.74ns	1.05ns	0.89ns	1.12ns	0.18 ns	0.86ns	0.97ns	0.81ns
Cultivar×rate×year	28	0.87ns	1.25ns	0.75ns	0.97ns	0.59ns	0.82ns	0.2ns	1.06ns	0.74ns	0.69ns
Cultivar×rate×loc	28	0.45ns	0.77ns	0.93ns	1.05ns	0.82ns	1.03ns	0.14ns	0.63ns	0.62ns	1.29ns
Cultivar×rate×year×loc	28	1.21ns	–	1.47ns	0.79ns	1.16ns	1.09ns	0.17ns	1.22ns	1.22ns	0.94ns

* P < 0.05.

** *P* < 0.01.

*** *P* < 0.001.

† DM: days to maturity, GPC: grain protein content (%), TW: test weight, TKW: thousand kernel weight, CID: carbon isotope discrimination, LAI: leaf area index, MTA: Mean tilt angle.

‡ ns, *P* ≥ 0.05.

RESULTS

Environment Characterization

The maximum, minimum, and mean temperatures, and total rainfall during the crop growth cycle are shown in Table 1. An overview of the weather conditions for both environments during the growing season indicates that precipitation varied between years. Swift Current was slightly cooler both years and received more total rainfall than Regina in 2011. Precipitation and temperature at both Swift Current and Regina in each year exceeded the long-term average on both the seasonal and the April–July range rainfall (Table 1). Between locations and years, the difference in the average temperatures was less than 1°C. June had the highest precipitation, and July was the hottest month for both environments.

Statistical Analysis

The combined ANOVA for yield and related traits revealed that the effects of year, location, genotype, and SR were highly significant (Table 2). Based on our four locations, the SR ′ genotype interaction was nonsignificant for all traits. Seeding rate × location was nonsignificant except for TW, TKW, and CID. The location × SR × genotype interaction was nonsignificant for all agronomic and physiological traits. The ANOVA results indicate that most of the variation was due to the main effects, year, location, SR, and cultivars, and that the two-way interactions are mainly due to changes in magnitude rather than reversals in order (Table 2 and Supplemental Table S1). Highly significant differences were observed for agronomic and physiological traits (Table 3) with the exception of height and MTA among locations, SR, and cultivars. The location and SR, which affects the growing plant environment, significantly influenced all traits.

Effect of Seeding Rate on Agronomic Traits

Yield increased as SR increased across environments and years (Table 3, Fig. 1). The relationship between grain yield and SR for all four environments is presented in Fig. 1. The highest yield for all cultivars occurred at the Regina environment in both years. The maximum yield in Swift Current and Regina was first reached at a SR of 326 and 272 seeds m^{-2}, respectively (Table 3, Fig. 1). Increasing the sowing density beyond those rates resulted in little or no change in yield, but a significant decrease in DM at Regina (Table 3). In 2010, the differences in grain yield between the lowest and the highest SR in Swift Current and Regina were 17.8 and 9.15%, respectively. In 2011, Regina showed a greater difference (14.2%) than Swift Current (10%) between the lowest and the highest yield for all cultivars. Height did not show significances differences among years and locations except at Swift Current in 2011 (Table 3). On average, the height differences were stronger in Swift Current (13.9%) than Regina (11.8%).

Grain protein concentration ranged from 11.8 to 14.7% and from 12.2 to 14.1% in Swift Current and Regina. In general, GPC decreased with increasing SR up to 380 seeds m^{-2} although this trend was not significant in Swift Current and Regina 2010 (Table 3). The maximum value for GPC obtained was 14.7% at 163 seeds m^{-2} at the Swift Current location.

There was a variable response to SR and environment for TW. Test weight showed significant differences among SR in all locations and years with the exception of Swift Current in 2010. The first significant maximum TW value obtained was at 217 seeds m^{-2} for both locations and years.

In general, SR entailed a decrease on TKW. Thousand kernel weight was negatively correlated with grain yield, in Swift Current in both years ($R^2 = 0.81^*$, 0.64) (Fig. 2). Between environments, Regina showed on average 6.4% higher values of TKW than Swift Current (Table 3) although no significant differences were observed among years in this environment.

The slopes for grain yield displayed similar values when averaged across environment and years, resulting in greater slopes at Regina than Swift Current (Table 4). Maximum and minimum SR slopes observed in Regina 2011 and Swift Current 2010. Days to maturity decreased significantly in both locations with a steeper slope at Regina than at Swift Current.

Effect of Seeding Rate on Physiological Traits

Soil Plant Analyzer Development values showed the same pattern for both locations and years (Table 3). Statistically significant differences in SPAD were noted in 2011 for both locations (Table 3). The highest SPAD values were observed at the SR of 163 seeds m^{-2} at all locations and years. The highest LAI values were recorded in 2011 for both environments, and Regina showed the maximum value at 326 seeds m^{-2} (Table 3). Leaf area index had a strong positive relationship with grain yield (Fig. 2a and 2b) and explained most of the observed variability in grain yield (between 89 and 98%) for both locations and years. There was a positive relationship between LAI and SR when comparing years and locations (Table 4). In general, CID and LAI increased as SR increased across environments (Table 3). Carbon isotope discrimination increased significantly across all environments except Regina in 2010. In turn, CID showed a high significantly positive correlation with grain yield (Fig. 2c and 2d). This relationship was particularly large in 2011 in Regina (Fig. 2d, $R^2 = 0.98$***). Mean foliage tilt angle did not change when SR increased, except at RG-2010.

Effect of Seeding Rate on Genotype Performance

There was no SR × cultivar interaction for grain yield, nor for any other trait measured. The highest yield occurred at Regina; associated with more rainfall and the lowest mean temperature across years (Tables 1 and 3). There was a variable response of the cultivars depending on SR, environment, and

Table 3. Least square means values for agronomic and physiological traits for each seeding rate averaged over eight cultivars grown at Swift Current and Regina in 2010 and 2011. Levels not connected with the same letter are significantly different.

SR†	Yield	DM	Height	GPC	TW	TKW	SPAD	CID	LAI	MTA
Seeds m^{-2}	kg ha^{-1}	days	cm	%	kg hL^{-1}	g	-	‰	-	°
SC-2010										
163	3047c‡	–	81.2a	12.0a	76.1a	41.4a	51.6a	18.2b	1.13c	64.1a
217	3236bc	–	79.7a	11.8a	75.9a	40.2ab	49.5a	18.3ab	1.19c	65.5a
272	3369b	–	80.0a	11.8a	76.0a	39.6b	48.8a	18.3b	1.25bc	65.5a
326	3690a	–	81.1a	11.9a	75.5a	39.3b	49.2a	18.4ab	1.50a	65.3a
380	3708a	–	81.6a	11.9a	75.8a	39.4b	49.4a	18.5a	1.38ab	68.3a
LSM§	3410	–	80.7	11.9	75.9	39.7	49.7	18.3	1.3	65.74
SE	98	–	1.4	0.20	0.59	0.45	2.5	0.11	0.1	2.5
SC-2011										
163	3668c	102.2a	78.5b	14.7a	79.3ab	41.8a	53.3a	15.5a	2.46c	60.2a
217	3935ab	102.2a	81.1ab	14.5a	79.6a	41.5ab	52.9a	15.8a	2.76b	59.9a
272	3874a	102.2a	80.7ab	14.4a	79.3ab	41.0ab	52.2b	15.6a	2.72b	60.9a
326	4010a	102.0a	81.4ab	14.5a	79.2b	40.7ab	52.2b	15.7a	2.92ab	61.2a
380	4077a	101.7a	79.7a	14.7a	79.2b	40.3b	52.1b	15.7a	2.99a	61.2a
LSM	3913	102	80.3	14.6	79.3	41.1	52.5	15.7	2.8	60.7
SE	74	0.2	1.0	0.2	0.2	0.4	0.3	0.06	0.1	1.0
RG-2010										
163	4110b	117.2a	92.5a	13.9a	77.5b	43.7a	52.7a	18.9a	2.29b	61.9b
217	4340ab	116.4ab	92.8a	13.9a	78.1a	44.3a	52.3a	18.9a	2.47ab	62.6a
272	4518a	115.8bc	91.6a	14.0a	78.1a	43.7a	52.2a	19.0a	2.55a	63.5a
326	4503a	115.6bc	91.5a	14.1a	77.9ab	43.4a	52.2a	19.1a	2.54a	63.2a
380	4524a	115.0c	91.0a	14.0a	78.1a	43.4a	52.0a	19.0a	2.55a	64.9a
LSM	4399	116	92	14	78	44	52	19	2	63
SE	98	0.3	1.3	0.1	0.2	0.5	0.4	0.1	0.1	1.2
RG-2011										
163	4336c	95.9a	87.9a	12.8a	82.3b	43.2a	51.3a	16.9c	2.63c	62.7a
217	4647b	95.3ab	89.1a	12.5ab	82.7a	43.0a	50.4ab	17.0b	2.79bc	62.8a
272	4895ab	95.1ab	88.3a	12.3ab	82.7a	42.9a	49.3c	17.1ab	2.95ab	62.1a
326	5010a	94.5b	89.2a	12.3ab	82.7a	43.1a	49.3c	17.2ab	3.14a	61.4a
380	5057a	94.5b	89.2a	12.2b	82.7a	42.6a	49.4c	17.2a	3.10a	62.4a
LSM	4789	95	88.7	12.4	82.6	43.0	49.9	17.1	2.9	62.3
SE	126	0.4	1.4	0.2	0.1	0.4	0.4	0.05	0.1	0.9

† SR: seeding rate, DM: days to maturity, GPC: grain protein concentration, TW: test weight, TKW: thousand kernel weight, SPAD: Soild Plant Analysis development, CID: carbon isotope discrimination, LAI: leaf area index, MTA: mean tilt angle.

‡ Means within a column not sharing a lowercased letter differ significantly at the $P < 0.05$ levels.

§ LSM: Least square means.

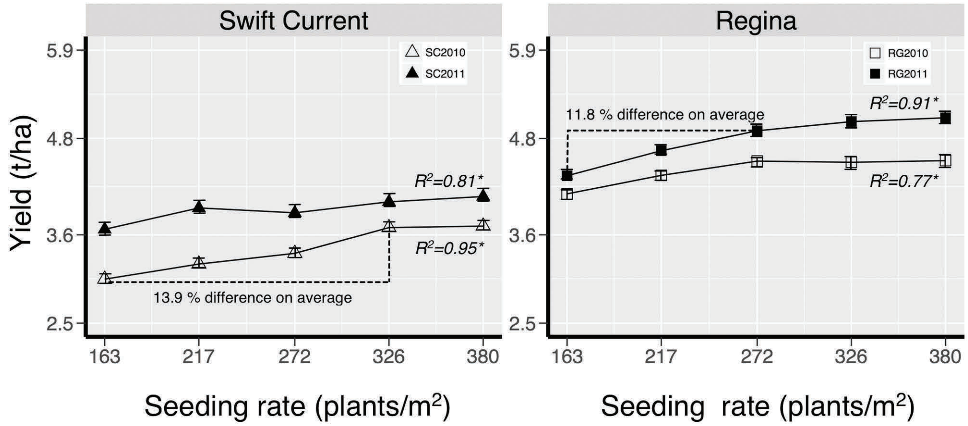

Fig. 1. Response of grain yield to seeding rates for each environment and year. Each point represents the mean value from eight cultivars in each seeding rate conducted in 2010 and 2011.

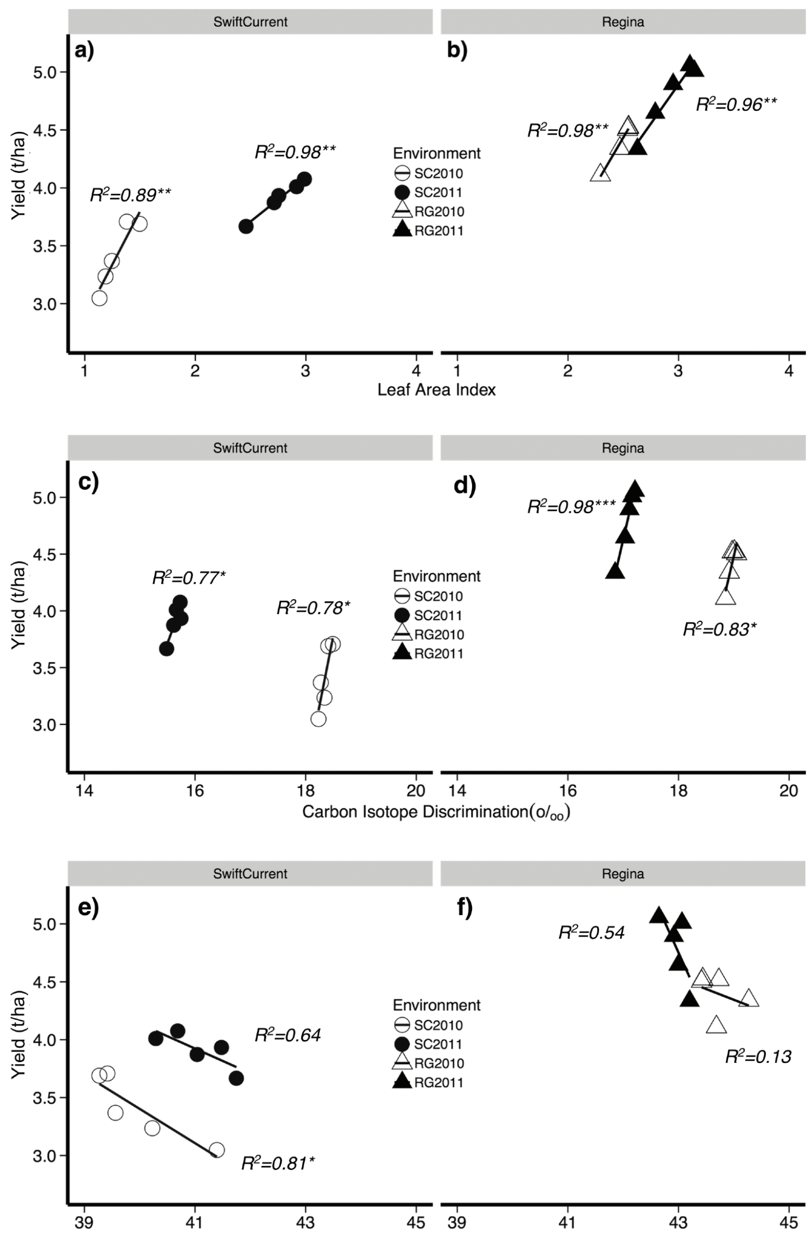

Fig. 2. Relationship between leaf area index (LAI), carbon isotope discrimination (CID), and thousand kernel weight (TKW) with grain yield for each environment and year. Each point represents the mean value from eight cultivars in each seeding rate conducted in Swift Current (SC) and Regina (RG) by year.

Table 4. Best fit regression equations for the average response of yield, days to maturity (DM), and leaf area index (LAI) to seeding rates in each environment and year.

Environment	Year	Trait		R^2†	*r*‡	*P* value§
Swift Current	2010					
		Grain yield	*y* = 7.4 × SR + 2514	95.3	0.97	0.0043
		DM	.	.	.	.
		LAI	*y* = 0.003 × SR + 0.88	73.2	0.85	0.0641
Swift Current	2011					
		Grain yield	*y* = 3.7 × SR+3462	81.1	0.90	0.0369
		DM	*y* = –0.005 × SR + 102.7	74.2	–0.86	0.0604
		LAI	*y* = 0.005 × SR + 2.16	87.1	0.93	0.0204
Regina	2010					
		Grain yield	*y* = 4.1 × SR+ 3899	76.9	0.87	0.0506
		DM	*y* = –0.02 × SR + 118.6	96.5	–0.98	0.0027
		LAI	*y* = 0.002 × SR + 2.18	72.1	0.85	0.0687
Regina	2011					
		Grain yield	*y* = 7.5 × SR + 3881	91.1	0.95	0.0115
		DM	*y* = –0.01 × SR + 96.8	93.1	–0.96	0.0079
		LAI	*y* = 0.005 × SR + 2.27	91.1	0.95	0.0116

† R^2: Proportion of the variation explained by the regression model. Coefficient of determination.
‡ ***r***: correlation coefficient value.
§ *P* value: is the probability of obtaining a result equal to or more extreme that what was observed when the hypothesis null is true.

year, showing that the eight cultivars chosen clearly represent a wide range of grain yield. Mean values of yield components and related traits for eight durum cultivars grown under four different environments are shown in Supplemental Tables S1 and S2. The overall yield ranged from 3112 to 5378 kg ha^{-1}. The highest average grain yield was observed at Regina, and average grain yield at Swift Current in 2010 was the lowest. Brigade, the highest yielding cultivar in three of the four environments, displayed the highest DM, LAI, and CID and the lowest GPC. The grain yield of Eurostar was superior over all cultivars at Swift Current in 2011 and showed similar performance to Brigade at Swift Current in 2011. Kyle was the lowest yielding and one of the early maturing cultivars at Regina both years (Supplemental Table S2).

DISCUSSION

Yield

Within the range of SRs used, grain yield increased with increasing SR, which is consistent with Nilsen et al. (2016) and Beres et al. (2011). Figure 1 shows that yield response to plant density was more linear rather than the quadratic response cited by (Pan et al., 1994). The linear relationship found in our experiments between SR and grain yield does not coincide with Holliday (1960) and Faris and DePauw (1980) studies. This might be due to the fact that the range between the maximum and the minimum SR in those experiments were larger than in this study. For example, the SR ranged in our study was 2.33-folds, whereas in the study by Faris and DePauw (1980) it was 18-fold. This indicates that the Canadian Western Amber Durum class cultivars presented a continuing yield response as SR increased within the SR used (Supplemental Fig. S1 and Table S2). These findings and results reported from recent reports (Beres et al., 2011; Nilsen et al., 2016) are an indication that the yield potential of modern durum cultivars can only be achieved if higher sowing densities are used compared to the lower SR practices of earlier eras.

The optimum SR of the five tested in this experiment varied for each environment (Fig. 1, Table 2). Our results shows that a high yield can be achieved in a particular environment by adjusting SR within that environment as was previously demonstrated in barley (*Hordeum vulgare* L.) and bread wheat (Faris and DePauw, 1980; Van Den Boogaard et al., 1996). The higher SR resulted in the highest yields in each environment, which also agrees with durum and bread wheat SR responses reported by Beres et al. (2011). There were not statistically yield difference between the 217 to 272 seed m^{-2} SR and 272 to 380 seed m^{-2}, although the latter showed the highest grain yield. The optimum SRs for cultivars grown at Swift current was 272 to 326 seeds m^{-2} and 217 to 272 seeds m^{-2} in Regina. Nevertheless, the optimum rates found in this experiment are different from the recommendations of earlier reports in Canada and the United States (Black and Bauer, 1990; Saskatchewan Crop Planning Management Guide Farm, 2015). This might be due to the fact that the precipitation at both Swift Current and Regina in each year exceeded the long-term average.

Agronomic Traits

The genotype Kyle was used as a control to include old genetics to test whether or not semi-dwarf and tall cultivars demand different SR and to observe any changes in the adaptation of newer cultivars to SR. The hypothesis (Sharma and Smith, 1987; Budak et al., 1995) of having tall plants less responsive to SR than semi-dwarf has not been observed in our results, where different heights do not require different SRs (Table 3). The curvilinear response between SR and days to maturity found in previous studies Wilson and Swanson (1962), Johnson et al. (1966), and Faris and DePauw (1980) have also been observed in our experiment, where days to maturity generally decreased as SR increased (Table 3, Fig. 2). The reduction of DM in Regina was due to the higher temperatures during the growing cycle in comparison with Swift Current (Table 3).

Although GPC was generally negatively correlated with yield, the total protein per cultivar was greatest at the SR, which gave the highest yield. This indicates that the negative correlation between yield and protein is not strong in these cultivars, probably due to adaptation of those cultivars to the Canadian prairies (Table 4). Test weight showed a different response to SR according to the location indicating that inter-plant competition could have altered the grain filling. However, the physiological results do not coincide with this assumption, indicating that factors other than inter-plant competition caused the underlying differences in TW. Leaf area index and CID at Regina showed the highest value across years being likely the most feasible explanation for the increase of TW in this environment.

Kernel weight was significantly affected by environment, genotype, and by SR. Overall, TKW decreased as SR increased at Swift Current but not at Regina (Table 3, Fig. 2). In general, TKW reduced significantly with increased SR, which is corroborated by Faris and DePauw (1980), as SR resulted in a larger sink as more seeds were produced per unit area, as SR increased resulting in source becomes the limiting factor.

Physiological Traits

When the relationship between grain yield and the measured traits was examined, a linear increase of yield was observed with increases in SR; this was primarily due to the increase of LAI and CID (Table 3, Fig. 2) in all environments. The LAI is an indicator of biomass and biomass is highly correlated with grain yield (Marti et al., 2007). The most probable explanation is that earlier canopy closure at high SR reduced the amount of water lost by evaporation, and in this way, maximized the proportion of the available water used by the plant.

Carbon isotope discrimination can be considered an indicator of the water status of plants (Farquhar et al., 1989; Acevedo, 1993; Araus et al., 1997) and is strongly influenced by environmental and physiological factors (Condon et al., 1992). In this study, CID was positive and highly correlated with yield across environments and cultivars (Fig. 2), which corroborated previous reports in durum wheat (Villegas et al., 2000). Transpiration efficiency, the main factor driving the negative relationship between CID and yield in drought environments (Condon et al., 1990), was not affected in these environments by increasing SR. The fact that we did not find significant differences in MTA across years and locations except in Regina 2010 indicates that, in general, SR did not change the distribution of light over the leaves in the canopy. Regina in 2010 was characterized with high rainfall that could have affected the downward rotation of the lamina around its ligular zone (Ledent, 1977) and could have been the reason for the differences in MTA in this location. In general, in all environments, higher MTA results in higher LAI and higher yield (Table 2). Therefore, cultivars with more vertical leaves on the tillers of the adult plant would be optimal because more erectophile profile enhances photosynthesis and dry matter production by greater sunlight capture (Duncan, 1971; Bingham and Lupton, 1987).

CONCLUSIONS

Seeding rate affected grain yield and its effects varied according to the environment. With the range of SRs used, there were no significant interactions of SR with any other factor. Seeding rate had a significant positive relationship with grain yield, LAI, and CID. For all cultivars studied under the western Canadian prairie conditions, the response curve to the different SRs was linear in each environment. Generally, the higher SRs resulted in the highest yields in each environment. In the environments tested, SRs of 272 to 380 seeds m^{-2} resulted in the highest grain yields. These densities are higher than those recommended to producers in the United States and Canada for durum wheat, suggesting that SR should be adjusted for environment and genotype for maximum yield. In the Canadian Prairie, higher sowing densities result in earlier canopy closure and improved crop competitiveness. In this sense, LAI and CID (water status of the plant) are the main physiological traits influencing grain yield, when increasing SR.

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SUPPLEMENTAL MATERIAL

Fig. S1. Relationship between grain yield and seeding rate for each genotype tested in Swift Current (SC) and Regina (RG) in 2010 and 2011.

Table S1. *F* values from the ANOVA of eight durum wheat cultivars grown under two different environments (Swift Current and Regina) during two growing seasons (2010 and 2011).

Table S2. Least square means values of yield and related traits for eight durum cultivars grown under two different environments (Swift Current and Regina) during two growing seasons (2010 and 2011) at different seeding rates. Levels not connected with the same letter are significantly different.

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