Effects of Seeding Rate on Durum Crop Production and Physiological Responses

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Abstract
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Disciplines
Agricultural Economics | Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

Comments

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ABSTRACT
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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 (Sláfer 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).
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 suppress 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 (Holten 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 Uttram, 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 L$^{-1}$), 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.
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 was measured using a FOSS-6500 Near-Infrared Reflectance Analyzer (FOSS, Silver Spring, MD). Grain protein concentration was predicted 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 13C/12C ratio was measured using an isotope ratio mass spectrometer (Optima manufactured by VG Isotech in Middlewich, UK) operated in continuous flow mode. Stable C13 was expressed as δ13C values (Farquhar et al., 1989), where δ13C (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000, and R is the 13C/12C 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 δ13C measurements was ±0.1‰. Carbon isotope discrimination was further calculated using the equation CID = (\delta_a - \delta_p)/(1 + \delta_p), where \delta_a and \delta_p refer to air and plant, respectively (Farquhar et al., 1989). On the PDB scale, free atmospheric CO2 has a current deviation, δC, 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.
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.

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.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Yield</th>
<th>DM†</th>
<th>Height</th>
<th>GPC</th>
<th>TW</th>
<th>TKW</th>
<th>SPAD</th>
<th>CID</th>
<th>LAI</th>
<th>MTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>4</td>
<td>4.04*</td>
<td>15.8***</td>
<td>0.73ns</td>
<td>1.88ns</td>
<td>2.43*</td>
<td>7.54***</td>
<td>1.1ns</td>
<td>9.34***</td>
<td>36.7***</td>
<td>1.19ns</td>
</tr>
<tr>
<td>Location (loc)</td>
<td>3</td>
<td>12.8***</td>
<td>1439***</td>
<td>89.4***</td>
<td>40.88***</td>
<td>19.6***</td>
<td>316***</td>
<td>469***</td>
<td>18.2***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rep(year × loc)</td>
<td>12</td>
<td>4.14***</td>
<td>54.9***</td>
<td>4.7***</td>
<td>2.8***</td>
<td>3.51***</td>
<td>0.45ns</td>
<td>1.23ns</td>
<td>2.32***</td>
<td>0.98ns</td>
<td></td>
</tr>
<tr>
<td>Cultivar</td>
<td>7</td>
<td>21.5***</td>
<td>38.4***</td>
<td>205***</td>
<td>32.9***</td>
<td>84.7***</td>
<td>104***</td>
<td>4.25***</td>
<td>171***</td>
<td>5.11***</td>
<td></td>
</tr>
<tr>
<td>Cultivar × year</td>
<td>7</td>
<td>4.85***</td>
<td>1.39ns</td>
<td>9.96***</td>
<td>4.67***</td>
<td>15.0***</td>
<td>20.0***</td>
<td>0.57ns</td>
<td>13.7***</td>
<td>6.02***</td>
<td></td>
</tr>
<tr>
<td>Cultivar × location</td>
<td>7</td>
<td>10.7***</td>
<td>4.37***</td>
<td>4.05***</td>
<td>3.63***</td>
<td>5.83***</td>
<td>6.14***</td>
<td>0.40ns</td>
<td>5.17***</td>
<td>5.63***</td>
<td></td>
</tr>
<tr>
<td>Cultivar × year × loc</td>
<td>7</td>
<td>2.05*</td>
<td>2.00ns</td>
<td>0.91ns</td>
<td>1.179***</td>
<td>11.7***</td>
<td>0.06ns</td>
<td>4.17***</td>
<td>2.32***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rep(year × loc × rate)</td>
<td>8</td>
<td>11.6***</td>
<td>5.75***</td>
<td>7.9***</td>
<td>23.0***</td>
<td>5.37***</td>
<td>1.89ns</td>
<td>1.27ns</td>
<td>27.1***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cultivar × year × rate</td>
<td>7</td>
<td>4.85***</td>
<td>1.39ns</td>
<td>9.96***</td>
<td>4.67***</td>
<td>15.0***</td>
<td>20.0***</td>
<td>0.57ns</td>
<td>13.7***</td>
<td>6.02***</td>
<td></td>
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<tr>
<td>Cultivar × location × rate</td>
<td>7</td>
<td>10.7***</td>
<td>4.37***</td>
<td>4.05***</td>
<td>3.63***</td>
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<td>0.40ns</td>
<td>5.17***</td>
<td>5.63***</td>
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<tr>
<td>Cultivar × year × loc × rate</td>
<td>7</td>
<td>2.05*</td>
<td>2.00ns</td>
<td>0.91ns</td>
<td>1.179***</td>
<td>11.7***</td>
<td>0.06ns</td>
<td>4.17***</td>
<td>2.32***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.05.
** P < 0.01.
*** P < 0.001.
‡ ns, P > 0.05.
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.

<table>
<thead>
<tr>
<th>SR†</th>
<th>Yield</th>
<th>DM</th>
<th>Height</th>
<th>GPC</th>
<th>TW</th>
<th>TKW</th>
<th>SPAD</th>
<th>CID</th>
<th>LAI</th>
<th>MTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds m(^{-2})</td>
<td>kg ha(^{-1})</td>
<td>days</td>
<td>cm</td>
<td>%</td>
<td>kg hL(^{-1})</td>
<td>g</td>
<td>%</td>
<td></td>
<td></td>
<td>°</td>
</tr>
<tr>
<td>SC-2010</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>163</td>
<td>3047C‡</td>
<td>81.2a</td>
<td>12.0a</td>
<td>76.1a</td>
<td>41.4a</td>
<td>51.6a</td>
<td>18.2b</td>
<td>1.13c</td>
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<td>217</td>
<td>3236bc</td>
<td>79.7a</td>
<td>11.8a</td>
<td>75.9a</td>
<td>40.2ab</td>
<td>49.5a</td>
<td>18.3ab</td>
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<td>75.8a</td>
<td>39.4b</td>
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<td>68.3a</td>
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<td>LSM§</td>
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<td>SE</td>
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<td>0.05</td>
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‡ Means within a column not sharing a lowercased letter differ significantly at the P < 0.05 levels.
§ LSM: Least square means.

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1985
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.
Agronomy Journal

lower SR practices of earlier eras. Achieved if higher sowing densities are used compared to the yield potential of modern durum cultivars can only be reports (Beres et al., 2011; Nilsen et al., 2016) are an indication as SR increased within the SR used (Supplemental Fig. S1 and Durum class cultivars presented a continuing yield response was 18-fold. This indicates that the Canadian Western Amber 2.33-folds, whereas in the study by Faris and DePauw (1980) it in this study. For example, the SR ranged in our study was and the minimum SR in those experiments were larger than this might be due to the fact that the range between the maximum Holliday (1960) and Faris and DePauw (1980) studies. This ex- pects 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).

**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-folds. 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 show 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 genet- ics 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).

### 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.

<table>
<thead>
<tr>
<th>Environment</th>
<th>Year</th>
<th>Trait</th>
<th>Equation</th>
<th>R²</th>
<th>r</th>
<th>P value</th>
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<td>2010</td>
<td>Grain yield</td>
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<td>95.3</td>
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<tr>
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<td></td>
<td>LAI</td>
<td>y = 0.003 × SR + 0.88</td>
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<td>y = 3.7 × SR+3462</td>
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<td>DM</td>
<td>y = –0.005 × SR + 102.7</td>
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<td>LAI</td>
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<td>DM</td>
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† R²: 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).
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 caryophyll 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.

**ACKNOWLEDGMENTS**

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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.

**REFERENCES**


