Age-Dependent Resistance to *Rhizoctonia solani* in Sugar Beet

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Abstract

Rhizoctonia crown and root rot of sugar beet (*Beta vulgaris* L.), caused by *Rhizoctonia solani*, continues to be one of the important concerns for the beet industry in Minnesota and North Dakota. Use of resistant cultivars is an important strategy in the management of *R. solani* in combination with seed treatment and timely fungicide application during the growing season. The objective of this greenhouse study was to determine how sugar beet plants responded to increasing age in resistance to *R. solani*. Each of three seed companies provided three commercial cultivars with varying *R. solani* resistance levels: susceptible, moderately resistant, and resistant. Seed were planted at a weekly interval to create different plant age groups from seed to 10-week-old plants, with growing degree days (GDD) ranging from 0 to 1,519 thermal time (°Cd). Seed and plants were all simultaneously inoculated with *R. solani* AG2-2-infested barley grains. Twenty-eight days after inoculation, plants were pulled and washed, and roots were evaluated for disease severity. All cultivars were highly susceptible to *R. solani* when

inoculated at seed to 3 weeks old (0 to 464°Cd). At 4 and 5 weeks of plant age (617 to 766°Cd), resistant cultivars started to show significant resistance to *R. solani*. Proportion of the affected roots with disease score ≥ 5 followed a sigmoid response, declining with increased GDD in moderately resistant and resistant cultivars, whereas it continued to decline linearly with increased GDD in susceptible cultivars. This study demonstrated that sugar beet cultivars, regardless of their assigned level of *R. solani* resistance, were highly susceptible to the pathogen before they reached the six- to eight-leaf stage at 4 to 5 weeks (617 to 766°Cd) after planting. Therefore, additional protection in the form of seed treatment or fungicide application may be required to protect sensitive sugar beet seed and seedlings in fields with a history of *R. solani* under favorable environmental conditions.

Keywords: cultivar/resistance, disease management, fungi, sugar beet

Rhizoctonia solani is a soilborne plant pathogen widely distributed around the world that causes root diseases on many important economic crops (Anderson 1982). This fungus consists of genetically different isolated populations called anastomosis groups (AGs), which are subdivided into subgroups with different host ranges (Ogoshi 1987). *R. solani* AG 2-2 IIIB, AG 2-2 IV, and AG 4 cause *Rhizoctonia* damping-off and crown and root rot on sugar beet (*Beta vulgaris* L.). *R. solani* AG 2-2 IIIB and IV are the most virulent subgroups and AG 2-2 IIIB seems to be more aggressive than AG 2-2 IV (Bolton et al. 2010). AG 2-2 IIIB, which causes crown and root rot, is typically considered to be the most important on sugar beet in the United States and Europe (Garcia et al. 2001; Strausbaugh et al. 2011). Crown rot infection typically starts on the sugar beet crown but can also occur at or below the soil line. Root rot develops as brown to black, sunken, and circular lesions, which then often coalesce to cover large areas of the root surface. Aboveground symptoms include severe wilting and yellowing of leaves, with black lesions on the base of the petioles (Harveson et al. 2009; Whitney and Duffus 1986; Windels and Nabben 1989). *R. solani* AG 4 is typically associated with damping-off characterized by seedlings with brown to black lesions on the hypocotyl followed by eventual collapse (Windels and Nabben 1989).

R. solani is reported to affect 24% of the sugar beet growing area in the United States and is also a problem for growers in some parts of Europe (Buhre et al. 2009; Garcia et al. 2001; Windels et al. 2009). The yield loss caused by this disease varies greatly from field to field but a significant loss can occur when weather conditions are favorable. Research has shown that entire sugar beet plots can be lost to the disease (Khan et al. 2010; Windels and Brantner 2005) and sometimes entire fields have to be destroyed because of the high severity

of the disease across the entire field (M. F. R. Khan, personal observations) (Strausbaugh 2016). Over 50% of the U.S. sugar beet tonnage (USDA-ERS 2017) comes from Minnesota and North Dakota, where *Rhizoctonia* root rot has been considered to be one of the most serious problems for sugar beet production since 2009 (Stachler et al. 2009). This disease is widespread in other sugar beet production areas such as Colorado, Idaho, Michigan, Montana, Nebraska, Oregon, and Wyoming (Hecker and Ruppel 1977; Kiewnick et al. 2001; Kirk et al. 2008; Ruppel and Hecker 1982; Strausbaugh et al. 2011; Stump et al. 2004).

Disease management of *R. solani* on sugar beet includes cultural practices, fungicide application with recommended rates and seed treatments, and development and use of resistant cultivars. Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) were recommended to be grown in rotation with sugar beet, and this practice reduced the pathogen inoculum compared with other *R. solani*-susceptible hosts such as soybean, *Glycine max* (L.) Merr., and corn (*Zea mays* L.) (Engelkes and Windels 1994; Ithurrart et al. 2004). Azoxystrobin, a quinone outside inhibitor fungicide, provided effective protection to sugar beet from *R. solani* infection when applied before the infection took place (Khan et al. 2010; Kiewnick et al. 2001; Windels and Brantner 2005). Azoxystrobin has been widely used at planting and as a foliar application by sugar beet growers in states such as Montana, Wyoming, Michigan, Minnesota, and North Dakota, where *Rhizoctonia* root rot is common (Kiewnick et al. 2001; Kirk et al. 2008; Stump et al. 2004; Windels and Brantner 2005). Growers typically combine fungicidal seed treatments that include either penthiopyrad, sedaxane, or fluxapyroxad with a foliar application of azoxystrobin to manage *R. solani* (Khan 2018).

Development of sugar beet cultivars resistant to *R. solani* started in the late 1950s, and it has made considerable progress in the level of resistance in sugar beet germplasm (Hecker and Gaskill 1972; Hecker and Smith 1979; Hecker and Ruppel 1983, 1986; Panella et al. 1995). Resistance to *R. solani* is considered to be a quantitative trait conditioned by two major loci and several minor modifying genes (Hecker and Ruppel 1975; Panella 2005). However, immunity to *R. solani* has not been found in sugar beet germplasm (Gaskill 1968). It was reported that the resistance level to *R. solani* was significantly higher in mature plants than young seedlings and that sugar

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beet plants had lower disease severity when they became older (Bolton et al. 2010; Büttner et al. 2004; Engelkes and Windels 1994; Gaskill 1968; Ruppel et al. 1979; Scholten et al. 2001). Breeders have done a good job of developing germplasm with better postemergence resistance to *R. solani*; however, it takes many years to incorporate high levels of resistance in commercial cultivars. Knowing the age at which sugar beet plants become resistant could help growers target the susceptible stage with adequate fungicide protection. As such, the objective of this research was to determine how resistance of sugar beet plants to *R. solani* changes with increasing plant age in a spectrum of susceptible, moderately resistant, and resistant commercial cultivars under greenhouse conditions.

Materials and Methods

Greenhouse and plant material. Experiments were conducted in a greenhouse at North Dakota State University, Fargo, ND, U.S.A. Plastic trays measuring 27 by 13 by 13 cm (T. O. Plastics Inc., Clearwater, MN, U.S.A.) were filled with Sunshine mix 1 peat (Sun Gro Horticulture Ltd.; Alberta, Canada) and 20 g of Osmocote 15-9-12 fertilizer (Scotts Company, Marysville, OH, U.S.A.). Isolates of *R. solani* AG 2-2 IIIB recovered from sugar beet were obtained from Dr. Carol Windels, University of Minnesota. Pure culture of *R. solani* AG 2-2 IIIB was used to produce inoculum by inoculating sterilized barley grains, as described by Noor and Khan (2014). Three seed companies provided commercial cultivars with varying levels of susceptibility to *R. solani*. Company A provided susceptible cultivar AS, moderately resistant cultivar AMR, and resistant cultivar AR; Company B provided susceptible cultivar BS, moderately resistant cultivar BMR, and resistant cultivar BR; and Company C provided susceptible cultivar CS, moderately resistant cultivar CMR, and resistant cultivar CR.

Growing degree days. The plant age at which plants were inoculated was first measured by the nominal weeks after planting immediately before inoculation. Because plants still experienced some daily fluctuations in the greenhouse environments, we also opted to use growing degree days (GDD) (i.e., thermal time [°Cd]) to measure plant age. GDD was calculated by accumulating daily mean temperature above a threshold of 3°C (Qi et al. 2005). The measurement of plant age by GDD is also more realistically applicable to field conditions because temperatures often vary from day to day in the open.

Inoculation and disease severity rating. Sugar beet seed were placed in 2.5-cm-deep furrows in the middle of each tray so as to get 10 plants per tray. Each cultivar was planted at 1-week intervals to have seed and plants from 1 to 10 weeks old. All plants and seed were inoculated on the same day with *R. solani* AG2-2 IIIB-infested barley grains. Inoculation was conducted by placing one inoculated barley grain at 1 cm deep and 1 cm to the side of each plant aged from 1 to 10 weeks. Inoculum was placed 1 cm to the side of each of 10 sugar beet seed in the furrow. The inoculum next to plants, and inoculum and seed were covered with Sunshine mix 1 peat (Sun Gro Horticulture Ltd., Alberta, Canada) (Liu and Khan 2016; Noor and Khan 2014). The negative control was also included for each cultivar at each plant age group using sterilized barley grains but without *R. solani*. Greenhouse conditions were set to allow light for a 12-h photoperiod (600-W high-pressure sodium lamps; P.L. Light Systems, Inc., Beamsville, Ontario, Canada) and daily mean temperature was recorded (Argus Control System Ltd., British Columbia, Canada). Watering was done as required to maintain adequate soil moisture for plant growth and disease development. Twenty-eight days after inoculation, sugar beet roots treated at different age stages were hand harvested and washed under tap water. Disease severity was scored using a 0-to-7 scale, where 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root of older plants completely deteriorated or dead plant or dead seedlings where seed were used, slightly modified from Windels and Nabben-Schindler (1996).

Nonparametric analysis. The experimental layout was a split-plot design, with cultivar as the whole-plot factor and plant age

before inoculation as the subplot factor. Each treatment had three replicates and the trial was repeated once. Replicate mean disease severity score was obtained by averaging disease scores (DS) from 10 individual plants in each tray. Data were analyzed by nonparametric methods using the SAS procedures of Proc Rank and Proc Mixed (version 9.3; SAS Institute Inc., Cary, NC, U.S.A.). The relative effects of disease severity for each treatment and their confidence intervals at 95% confidence were calculated using 'F1_LD_F1' and 'LD_CI' macros (Shah and Madden 2004).

Proportion of affected plants with DS ≥ 5. Among the eight classes of DS, we considered that affected plants with DS ≥ 5 were critical in causing economical yield losses in sugar beet. Thus, we calculated proportion of affected plants with DS ≥ 5 in the combined two repeated experiments out of all treated plants, expressed as percentage in each treatment for plant age group.

Regression analysis. A logistic equation was fitted first to the percentage of affected plants with DS ≥ 5 (DS₅%) for each individual variety. Because the observed maximum DS₅% was at 100% when plants were inoculated at apparent 0°Cd GDD, the fitted logistic equation was of the following formula:

$$DS_5\% = Y_0 + \left[(100 - Y_0) / \left(1 + e^{c[GDD - T_0]} \right) \right] \quad (1)$$

In equation 1, DS₅% is the percentage of affected plants with DS ≥ 5, Y_0 is the minimum DS₅% at a given GDD when the ability of increasing plant age to resist or tolerate *R. solani* reached its maximum, c is the rate of reduction in DS₅% due to the increased plant age prior to inoculation (i.e., as GDD increases), $100 - Y_0$ measures the maximum reduction in DS₅% that the enhanced resistance of increased plant age can bring, GDD is the accumulated thermal time from sowing to the time when inoculation occurred, and T_0 is the GDD at which the reduction in DS₅% reaches half the value of $100 - Y_0$.

Table 1. Test statistics for effects of the plant ages from seed stage to 10 weeks old and the cultivars susceptible, moderately resistant, and resistant to *Rhizoctonia solani* from each of three seed companies on the disease severity of sugar beet simultaneously inoculated by *R. solani* AG 2-2 IIIB^a

Effect	Analysis of variance-type statistic ^b			
	df _N	df _D	ATS	P value
Cultivar	7.74	43.33	0.94	0.478
Plant age	4.65	∞	227.04	<0.001**
Cultivar × plant age	20.51	∞	3.27	<0.001**

^a Sugar beet plants were evaluated 28 days after inoculation and the data were analyzed using nonparametric analysis in SAS.

^b df_N = numerator degrees of freedom, df_D = denominator degrees of freedom, ATS = ANOVA-type statistic, and asterisks (**) indicate significant at the 0.001 probability level.

Fig. 1. Daily mean temperature and accumulated growing degree days (GDD; °Cd) above 3°C at various nominal plant age week (WK) groups from 0 to 10 when inoculation took place.

Table 2. Median disease severity, relative effect, and its confidence interval for the disease severity on sugar beet caused by *Rhizoctonia solani* AG 2-2 IIIB^a

Company (cultivar)	Resistance level ^b	Plant age ^c	MDS ^d	REDS ^e	95% CI ^f
Company A (AS)	S	Seed	7.0	0.803	0.721–0.865
Company A (AS)	S	1 week old	7.0	0.754	0.606–0.859
Company A (AS)	S	2 weeks old	7.0	0.704	0.491–0.853
Company A (AS)	S	3 weeks old	7.0	0.778	0.663–0.861
Company A (AS)	S	4 weeks old	5.5	0.578	0.369–0.762
Company A (AS)	S	5 weeks old	4.4	0.439	0.278–0.615
Company A (AS)	S	6 weeks old	5.8	0.562	0.441–0.676
Company A (AS)	S	7 weeks old	5.5	0.532	0.407–0.653
Company A (AS)	S	8 weeks old	4.4	0.442	0.277–0.621
Company A (AS)	S	9 weeks old	4.8	0.478	0.334–0.626
Company A (AS)	S	10 weeks old	3.8	0.431	0.309–0.561
Company A (AS)	S	Control	0.0	0.072	0.058–0.089
Company A (AMR)	MR	Seed	7.0	0.709	0.494–0.857
Company A (AMR)	MR	1 week old	7.0	0.780	0.662–0.865
Company A (AMR)	MR	2 weeks old	7.0	0.722	0.509–0.865
Company A (AMR)	MR	3 weeks old	7.0	0.758	0.608–0.862
Company A (AMR)	MR	4 weeks old	0.1	0.184	0.081–0.369
Company A (AMR)	MR	5 weeks old	0.7	0.220	0.130–0.349
Company A (AMR)	MR	6 weeks old	1.9	0.266	0.180–0.376
Company A (AMR)	MR	7 weeks old	2.2	0.291	0.182–0.431
Company A (AMR)	MR	8 weeks old	2.5	0.314	0.200–0.456
Company A (AMR)	MR	9 weeks old	2.7	0.324	0.214–0.459
Company A (AMR)	MR	10 weeks old	3.1	0.364	0.267–0.474
Company A (AMR)	MR	Control	0.0	0.072	0.058–0.089
Company A (AR)	R	Seed	7.0	0.750	0.586–0.863
Company A (AR)	R	1 week old	7.0	0.763	0.613–0.867
Company A (AR)	R	2 weeks old	7.0	0.784	0.593–0.899
Company A (AR)	R	3 weeks old	7.0	0.776	0.652–0.865
Company A (AR)	R	4 weeks old	0.0	0.165	0.082–0.309
Company A (AR)	R	5 weeks old	0.8	0.180	0.105–0.294
Company A (AR)	R	6 weeks old	1.0	0.234	0.154–0.341
Company A (AR)	R	7 weeks old	2.7	0.298	0.212–0.402
Company A (AR)	R	8 weeks old	1.7	0.275	0.156–0.437
Company A (AR)	R	9 weeks old	2.5	0.333	0.223–0.466
Company A (AR)	R	10 weeks old	2.3	0.310	0.221–0.416
Company A (AR)	R	Control	0.0	0.072	0.058–0.089
Company B (BS)	S	Seed	7.0	0.827	0.745–0.886
Company B (BS)	S	1 week old	7.0	0.805	0.668–0.893
Company B (BS)	S	2 weeks old	7.0	0.863	0.838–0.885
Company B (BS)	S	3 weeks old	7.0	0.756	0.608–0.860
Company B (BS)	S	4 weeks old	3.3	0.446	0.215–0.703
Company B (BS)	S	5 weeks old	5.9	0.589	0.443–0.720
Company B (BS)	S	6 weeks old	4.1	0.414	0.259–0.590
Company B (BS)	S	7 weeks old	5.3	0.508	0.313–0.700
Company B (BS)	S	8 weeks old	4.5	0.470	0.329–0.616
Company B (BS)	S	9 weeks old	4.2	0.455	0.304–0.616
Company B (BS)	S	10 weeks old	3.7	0.400	0.271–0.544
Company B (BS)	S	Control	0.0	0.072	0.058–0.089
Company B (BMR)	MR	Seed	7.0	0.772	0.649–0.860
Company B (BMR)	MR	1 week old	7.0	0.827	0.747–0.886
Company B (BMR)	MR	2 weeks old	7.0	0.746	0.587–0.858
Company B (BMR)	MR	3 weeks old	7.0	0.740	0.531–0.876
Company B (BMR)	MR	4 weeks old	7.0	0.663	0.449–0.826
Company B (BMR)	MR	5 weeks old	5.3	0.531	0.352–0.701
Company B (BMR)	MR	6 weeks old	3.4	0.395	0.261–0.547
Company B (BMR)	MR	7 weeks old	4.0	0.410	0.284–0.549

(Continued on next page)

^a Inoculation was simultaneously done on nine sugar beet cultivars with three resistance levels (susceptible, moderately resistant, and resistant to *R. solani*) from seed stage up to 10-week-old plants. Disease severity was evaluated 28 days after inoculation and the data were analyzed using nonparametric analysis in SAS.

^b S, MR, and R indicate that sugar beet cultivars were susceptible, moderately resistant, or resistant, respectively, to *R. solani*.

^c Inoculation was done using seed and plants at different plant ages from 1 to 10 weeks old. The corresponding physiological age measured in growing degree days was 0, 157, 313, 464, 617, 766, 919, 1,067, 1,220, 1,368, and 1,519°Cd (thermal time) for 0 (seed) to 10 weeks (for 10-week-old plants) at 1-week intervals, respectively. “Control” represents the negative control where sterilized barley was used.

^d Median disease severity.

^e Relative effect of disease severity (Shah and Madden 2004).

^f Upper–lower values of 95% confidence interval (CI) for treatment relative effect.

For susceptible cultivars, the DS₅% showed a continuous decline with increasing GDD. Therefore, a simple linear relation was fitted to the DS₅% as:

$$DS_5\% = 100 - b \times GDD \quad (2)$$

to describe the data. Here, *b* is the slope measuring the reduction rate in the DS₅% as per 1 degree day's increase in GDD. The parameters in both equation 1 and equation 2 were estimated using the SAS procedures of PROC NLIN (version 9.3; SAS Institute Inc.)

Results

No significant difference was observed between repeats according to Levene's test ($P = 0.93$); therefore, the data were combined. There

were statistically significant effects ($P \leq 0.001$) of plant age and its interaction with cultivar on root rot severity caused by *R. solani* (Table 1).

GDD. The recorded mean daily temperature fluctuated between 23.4 and 27.6°C during the preparation of various plant age groups immediately before inoculation (Fig. 1). As a result, the weekly accumulated GDD varied from 148 to 157°Cd. This supported the idea that plant age should be more accurately measured by thermal time than by days or weeks. The accumulated GDD for each plant age week group is shown in Figure 1, with GDD varying from 1,519°Cd at the end of the 10th week for 10-week-old plants to 157°Cd for 1-week-old plants and 0°Cd for seed (week 0), when inoculation occurred.

Table 2. (Continued from previous page)

Company (cultivar)	Resistance level ^b	Plant age ^c	MDS ^d	REDS ^e	95% CI ^f
Company B (BMR)	MR	8 weeks old	3.2	0.389	0.263–0.533
Company B (BMR)	MR	9 weeks old	4.6	0.494	0.322–0.667
Company B (BMR)	MR	10 weeks old	2.9	0.367	0.244–0.512
Company B (BMR)	MR	Control	0.0	0.072	0.058–0.089
Company B (BR)	R	Seed	7.0	0.816	0.707–0.890
Company B (BR)	R	1 week old	7.0	0.827	0.744–0.887
Company B (BR)	R	2 weeks old	7.0	0.827	0.744–0.887
Company B (BR)	R	3 weeks old	7.0	0.780	0.654–0.869
Company B (BR)	R	4 weeks old	1.9	0.329	0.165–0.552
Company B (BR)	R	5 weeks old	2.0	0.302	0.164–0.490
Company B (BR)	R	6 weeks old	1.7	0.279	0.178–0.412
Company B (BR)	R	7 weeks old	1.8	0.275	0.183–0.392
Company B (BR)	R	8 weeks old	4.2	0.504	0.313–0.694
Company B (BR)	R	9 weeks old	2.7	0.352	0.204–0.536
Company B (BR)	R	10 weeks old	2.3	0.400	0.276–0.538
Company B (BR)	R	Control	0.0	0.072	0.058–0.089
Company C (CS)	S	Seed	7.0	0.746	0.590–0.857
Company C (CS)	S	1 week old	7.0	0.827	0.746–0.886
Company C (CS)	S	2 weeks old	7.0	0.735	0.562–0.857
Company C (CS)	S	3 weeks old	7.0	0.731	0.546–0.859
Company C (CS)	S	4 weeks old	4.9	0.506	0.264–0.745
Company C (CS)	S	5 weeks old	3.8	0.423	0.282–0.578
Company C (CS)	S	6 weeks old	4.8	0.499	0.378–0.621
Company C (CS)	S	7 weeks old	6.2	0.631	0.515–0.734
Company C (CS)	S	8 weeks old	4.6	0.502	0.382–0.621
Company C (CS)	S	9 weeks old	4.4	0.459	0.362–0.560
Company C (CS)	S	10 weeks old	5.5	0.525	0.404–0.643
Company C (CS)	S	Control	0.0	0.072	0.058–0.089
Company C (CMR)	MR	Seed	7.0	0.747	0.583–0.861
Company C (CMR)	MR	1 week old	7.0	0.827	0.745–0.887
Company C (CMR)	MR	2 weeks old	7.0	0.735	0.559–0.858
Company C (CMR)	MR	3 weeks old	7.0	0.733	0.546–0.861
Company C (CMR)	MR	4 weeks old	1.5	0.345	0.176–0.566
Company C (CMR)	MR	5 weeks old	2.6	0.394	0.222–0.597
Company C (CMR)	MR	6 weeks old	4.3	0.461	0.307–0.623
Company C (CMR)	MR	7 weeks old	6.5	0.633	0.505–0.745
Company C (CMR)	MR	8 weeks old	4.9	0.498	0.367–0.630
Company C (CMR)	MR	9 weeks old	4.7	0.475	0.376–0.575
Company C (CMR)	MR	10 weeks old	4.0	0.435	0.322–0.556
Company C (CMR)	MR	Control	0.0	0.072	0.058–0.089
Company C (CR)	R	Seed	7.0	0.827	0.745–0.886
Company C (CR)	R	1 week old	7.0	0.827	0.745–0.886
Company C (CR)	R	2 weeks old	7.0	0.827	0.745–0.886
Company C (CR)	R	3 weeks old	7.0	0.746	0.581–0.861
Company C (CR)	R	4 weeks old	5.6	0.542	0.312–0.756
Company C (CR)	R	5 weeks old	0.5	0.214	0.127–0.341
Company C (CR)	R	6 weeks old	2.1	0.300	0.187–0.445
Company C (CR)	R	7 weeks old	4.5	0.470	0.350–0.593
Company C (CR)	R	8 weeks old	1.1	0.275	0.145–0.461
Company C (CR)	R	9 weeks old	2.7	0.334	0.212–0.485
Company C (CR)	R	10 weeks old	1.8	0.262	0.153–0.413
Company C (CR)	R	Control	0.0	0.072	0.058–0.089

Effects of sugar beet plant age by weeks. Inoculation with *R. solani*-infested barley grains killed seedlings and resulted in various degrees of root rot symptoms on all nine sugar beet cultivars tested in this study, indicating that the artificially produced inoculum was effective to cause infections. In the negative controls, plants had clean roots without damping-off and root rot symptoms caused by *R. solani*, leading to the expected zero disease severity and lowest relative effect (Table 2). For all cultivars, inoculation of 3-week-old sugar beet plants or earlier (0 to 464°Cd) resulted in almost a complete loss of plant stand, with the highest disease severity

Fig. 2. Relationship between the percentage of affected plants with disease score ≥ 5 ($DS_5\%$) and plant age measured by growing degree days (GDD) at inoculation for resistant cultivars from three different companies. Curves were described by the estimates for parameters in the logistic equation $DS_5\% = Y_0 + [(100 - Y_0)/(1 + e^{-(GDD - T_0)})]$. Sugar beet resistant cultivars (AR, BR, and CR) at plant ages from seed stage to 10 weeks old were simultaneously inoculated by *Rhizoctonia solani* AG 2-2 IIB. Disease severity was evaluated 28 days after inoculation using a scale as follows: 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root completely deteriorated or dead plant or seedling.

Fig. 3. Relationship between the percentage of affected plants with disease score ≥ 5 ($DS_5\%$) and plant age measured by growing degree days (GDD) at inoculation for moderately resistant cultivars from three different companies. Curves were described by the estimates for parameters in the logistic equation $DS_5\% = Y_0 + [(100 - Y_0)/(1 + e^{-(GDD - T_0)})]$. Sugar beet moderately resistant cultivars (AMR, BMR, and CMR) at plant ages from seed stage to 10 weeks old were simultaneously inoculated by *Rhizoctonia solani* AG 2-2 IIB. Disease severity was evaluated 28 days after inoculation using a scale as follows: 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root completely deteriorated or dead plant or seedling.

scores and the highest relative effect. The 4- or 5-week-old plants (617 to 766°Cd) became more resistant to *R. solani* with varying degrees depending on the cultivar: five cultivars (AR, AMR, BR, CMR, and CR) had a significantly lower relative effect compared with earlier plant age treatments; the other four cultivars (AS, BS, BMR, and CS) showed a reduced disease severity but it was not significant. For 6-week-old (919°Cd) to 10-week-old (1,519°Cd) plants, cultivars were observed to have overlapping confidence intervals for relative effect, indicating that the cultivars had developed similar levels of resistance. However, the 6- to 10-week-old (919 to 1,519°Cd) plants had relative effects that were worse than the negative controls (Table 2).

Response of proportion of affected plants to plant age by GDD.

The logistic equation of equation 1 was well fitted to describe the proportion of affected plants with $DS \geq 5$ for both moderately resistant and resistant commercial cultivars provided by all three companies (Figs. 2 and 3). *F* tests of the estimated parameters of each cultivar gave evidence that the fitted logistic equation was statistically significant ($P < 0.001$) (Table 3). Apparently, enhanced resistance of increased plant age at about 600°Cd GDD showed a more marked reduction in resistant cultivar AR from Company A than BR from Company B. As the GDD increased further beyond 600°Cd, the contributing effect of plant age on resistance to *R. solani* gradually reduced, and became negligible when the plant age reached about 800°Cd GDD. Thus, regardless of the plant age beyond 800°Cd, *R. solani* can cause a minimum (i.e., Y_0) of 8.9, 15.0, and 23.4% of affected plants with $DS \geq 5$ in resistant cultivars from Company A, Company B, and Company C, respectively. As a result, the estimated maximum reduction (i.e., $100 - Y_0$) in $DS_5\%$ was 91.1, 85.0, and 76.6 from Company A, Company B, and Company C, respectively.

A similar response pattern was found in the moderate resistant cultivars (Fig. 3; Table 3). All moderately resistant cultivars had a much higher minimum (i.e., Y_0) and a lower maximum reduction (i.e., $100 - Y_0$) of $DS_5\%$ compared with resistant cultivars from a corresponding seed company (Table 3). Among all six moderately resistant and resistant cultivars, it was apparent that cultivars were more resilient and tolerant from Company A, followed by Company B and Company C.

The $DS_5\%$ showed a continuous and linear decrease with the plant age measured by GDD in susceptible cultivars (Fig. 4). A simple linear relation of equation 2 was better fitted to these observations than the logistic response of equation 2. The estimated slopes (i.e., b) are given in Table 4 and were all tested to be statistically significant ($P < 0.001$). Susceptible cultivars from Company A responded to increasing plant age by reducing about 3.7% of affected plants with $DS \geq 5$ per increase of 100°Cd GDD. However, susceptible cultivars from Company B and Company C responded similarly by reducing 4.6 and 4.4% of affected plants, respectively, with $DS \geq 5$ per increase of 100°Cd GDD (Table 4).

Discussion

Nine sugar beet commercial cultivars from three seed companies were evaluated to determine at what age after planting they expressed significant resistance to *R. solani* so that strategies can be developed to provide protection when they are most susceptible. In the current study, inoculation was done on the same day to seed and plants from 1 week up to 10 weeks of age. In a previous study that determined the relationship between sugar beet plant age and disease severity, Engelkes and Windels (1994) reported that disease resistance was more clearly expressed in simultaneous inoculations compared with consecutive inoculations. In our study, inoculation was done by placing the inoculum into the soil near the sugar beet seed or taproots. Other researchers have also placed the inoculum close to the seed or roots when evaluating *R. solani* resistance in sugar beet (Engelkes and Windels 1994; Gaskill 1968; Pierson and Gaskill 1961; Ruppel et al. 1979).

Plant age measured by calendar days or weeks can be misleading when plants experience fluctuating temperatures under different growing conditions; for example, growing plants in the open or in

fields. Although temperature was set at 22°C under the greenhouse, the recorded daily mean temperature still varied appreciably between 23.4 and 27.6°C. Consequently, the accumulated weekly thermal time (i.e., GDD) was not constant between respective week intervals. Therefore, thermal time was calculated to measure plant age for each week age group from 0 to 10 weeks (Fig. 1).

Inoculation of seed and plants up to 3 weeks of age (i.e., 0 to 464°Cd from planting) resulted in severe damping-off, which killed most of the seedlings after emergence as well as young plants compared with the negative controls. This result was consistent with a previous study by Gaskill (1968), who reported that inoculation of *R. solani* to sugar beet seedlings resulted in disease severity that was too severe to measure the survival difference between populations. Our study showed that all three seed companies designated sugar beet cultivars as “resistant” that were highly susceptible to the inoculation of *R. solani* at the seed and young seedling stages (i.e., before GDD of 464°Cd from planting).

None of the resistant cultivars expressed a good level of resistance until they were 4 weeks from planting (i.e., 617°Cd GDD). Host plants with increased age have elevated resistance to the pathogen *R. solani* in sugar beet (Bolton et al. 2010; Engelkes and Windels 1994; Ruppel and Hecker 1988), bean (Bateman and Lumsden 1965), corn (Ruppel 1985), and other crops (Yang and Verma 1992). Researchers indicated that inoculation at 21 to 35 days post-thinning differentiated the varied degrees of *R. solani* resistance in sugar beet fields (Gaskill 1968; Pierson and Gaskill 1961). Because we wanted to assess at what age commercial sugar beet cultivars expressed sufficient resistance to prevent severe *R. solani* infection, we sought to inoculate commercial cultivars with a range of plant ages from seed (0°Cd) to 10 weeks old (1,519°Cd). Temperatures above a threshold of 3°C are required to start the germination process and sugar beet seedlings typically emerge within 5 days under optimal conditions (Milford et al. 1985b,c). Thereafter, leaves appear and expand in linear relationship with the physiological thermal time (i.e., GDD above 3°C) (Milford et al. 1985a,b,c). In our greenhouse study, emergence took place in about 5 days after planting, with cotyledonary leaves after 1 week (157°Cd). Each week thereafter, about two new leaves were produced. Because the resistance emerged at 4 weeks (617°Cd) after planting when sugar beet plants were at the six- to eight-leaf stage, the plants were able to express their maximum resistance to *R. solani*. These results are consistent with previous research, which shows that plants should not be screened for resistance prior to the six- to eight-leaf growth stage whether in the greenhouse or the field (Büttner et al. 2004; Gaskill 1968; Ruppel et al. 1979; Scholten et al. 2001).

The fact that sugar beet crops expressed elevated *R. solani* resistance with increased age could be associated with the interaction between some enzymes secreted by the pathogen and the cell wall maturation process of the host. *R. solani* is known to produce pectic and cellulolytic enzymes that degrade the cell wall of the host to

facilitate infection (Bugbee 1990, 1993). Recent work also reported that high numbers of secreted proteins and cell-wall-degrading enzymes were found by genomic analysis of *R. solani* AG2-2 IIIB (Wibberg et al. 2016). Research has shown that the *R. solani* enzymes

Fig. 4. Relationship between the percentage of affected plants with disease score ≥ 5 ($DS_5\%$) and plant age measured as growing degree days (GDD) at inoculation for susceptible varieties from three different companies. Curves were described by the fitted simple linear equations (equation 2: $DS_5\% = 100 - b \times GDD$). Sugar beet susceptible cultivars (AS, BS, and CS) at plant ages from seed stage to 10 weeks old were simultaneously inoculated by *Rhizoctonia solani* AG 2-2 IIIB. Disease severity was evaluated 28 days after inoculation using a scale as follows: 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root completely deteriorated or dead plant or seedling.

Table 4. Estimated slopes (i.e., b) for susceptible cultivars when a simple linear relation (equation 2) was fitted to the percentage of affected plants with disease score ≥ 5 ($DS_5\%$) against plant age measured by growing degree days (GDD) at inoculation^a

Company (cultivar)	Slope ^b	R^2	F-test significance
Company B (BS)	-0.0460 (0.00328)	0.8703	$P < 0.001$
Company C (CS)	-0.0436 (0.00352)	0.8313	$P < 0.001$
Company A (AS)	-0.0374 (0.00179)	0.9316	$P < 0.001$

^a Equation 2: $DS_5\% = 100 - b \times GDD$. Disease score: 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root completely deteriorated or dead plant or seedling.

^b Slope is the reduction rate in the $DS_5\%$ as per one degree day's increase in GDD.

Table 3. Parameter estimates for moderately resistant and resistant cultivars when the logistic equation (equation 1) was fitted to the percentage of affected plants with disease score ≥ 5 ($DS_5\%$) against plant age measured by growing degree days (GDD) at inoculation^a

Resistance level, company (cultivar)	Y_0^b	c^c	T_0^d	$(100 - Y_0)^e$	F-test significance
Resistant					
Company B (BR)	14.9638 (1.6142)	0.0216 (0.0035)	560.9 (11.29)	85.04	$P < 0.001$
Company C (CR)	23.3981 (1.0947)	0.0270 (0.0094)	607.0 (6.03)	76.60	$P < 0.001$
Company A (AR)	8.9476 (1.4096)	0.0380 (0.0081)	532.7 (15.52)	91.05	$P < 0.001$
Moderate					
Company B (BMR)	35.2540 (3.0699)	0.0092 (0.0021)	779.0 (29.31)	64.75	$P < 0.001$
Company C (CMR)	39.9121 (1.4670)	0.0396 (0.0155)	529.3 (27.31)	60.09	$P < 0.001$
Company A (AMR)	19.0958 (1.6226)	0.0387 (0.0160)	519.6 (24.21)	80.90	$P < 0.001$

^a Equation 1: $DS_5\% = Y_0 + [(100 - Y_0)/(1 + e^{c(GDD - T_0)})]$. DS: 0 = no disease, 1 = crown area slightly scurfy, 2 = <5% infection, 3 = 6 to 25% infection, 4 = 26 to 50% infection, 5 = 51 to 75% infection, 6 = >75% infection, and 7 = the root completely deteriorated or dead plant or seedling.

^b Parameter Y_0 is the minimum $DS_5\%$ at a given GDD when the ability of increasing plant age to resist or tolerate *R. solani* reached its maximum.

^c Parameter c is the rate of reduction in $DS_5\%$ due to the increased plant age prior to inoculation.

^d Parameter T_0 is the GDD at which the reduction in $DS_5\%$ reaches half the value of $100 - Y_0$.

^e Parameter $100 - Y_0$ is the measurement of maximum reduction in the $DS_5\%$.

are less likely to degrade the cell wall when host plants grow to maturity (Bateman et al. 1969). Bateman and Lumsden (1965) indicated that the conversion of pectin to calcium pectate during tissue maturation rendered the cell wall resistant to polygalacturonase secreted by *R. solani*. More molecular studies should be conducted to determine how the *R. solani* enzymes interact with the cell wall components.

In Minnesota and North Dakota, root rot caused by *R. solani* is one of the most important yield-limiting diseases (Carlson et al. 2010, 2015). One possible reason for more reports of *Rhizoctonia* spp. could be due to relatively higher average daily soil temperatures favorable for infection by the pathogen at or soon after planting. In recent years (2014 to 2016), the soil temperature at the 10-cm soil depth was above 18°C—considered to be the average daily soil temperature that is favorable for infection by *R. solani* (Khan et al. 2010)—when sugar beet planting was completed in Minnesota and North Dakota (NDAWN; <https://ndawn.ndsu.nodak.edu/>). The current study shows that none of the resistant cultivars provided a marked resistance to *R. solani* before reaching the six- to eight-leaf stage (at 4 and 5 weeks of age and 617 to 766°Cd after sowing), indicating that planting resistant cultivars alone is not adequate to protect sugar beet seedlings from infections of *R. solani* inoculum activated by favorable environmental conditions at planting or soon thereafter. In this case, effective fungicides such as sedaxane, registered in North America and Europe, can be applied on sugar beet seed to prevent severe infection caused by *R. solani* early in the growing season. Producers in North America have the options of using fungicidal seed treatments or fungicide application at planting or foliarly in a timely manner to effectively control *R. solani* and protect sugar beet seedlings (Liu and Khan 2016; Windels and Brantner 2005). As such, in areas with a history of high *R. solani* disease severity, the practice of using fungicides such as azoxystrobin in-furrow or labeled fungicidal seed treatment (Khan 2018) could be used to prevent infection of sugar beet at a vulnerable stage in the early season.

Our results demonstrated that, when screening cultivars for resistance to *R. solani*, different seed companies should adopt a common protocol. This protocol should include a standard plant age such as the six- to eight-leaf growth stage or an age measured by thermal time to establish when plants should be inoculated. This is to avoid the confounding effects of plant age on the resistance level assigned to cultivars in their respective breeding program. The results also demonstrated that, even though cultivars were classified to be resistant to *R. solani*, if virulent inocula were prevalent, the proportion of affected plants would be no different from susceptible cultivars when infection happened before plants experienced a GDD of 617°Cd after planting. Results also implied that, even though resistant cultivars have experienced a sufficiently long thermal time after planting, *R. solani* can still lead to a minimum percentage of affected plants which could be severe enough to cause economic yield losses. The range in resistance responses found in commercial sugar beet cultivars is likely due to the difficulty in trying to maintain the multigenic root rot resistance in all the parental lines. Commercial sugar beet hybrids are frequently generated using a three-way cross (Skaracis and Smith 1984), which makes maintaining multigenic resistance in all the parental lines difficult because other desirable traits such as sucrose yield and resistance to other diseases must also be maintained. We recommend that, when cultivars are screened for resistance to virulent strains of *R. solani*, indicators such as percentage of affected plants above an economically important DS should be more useful than a mean disease severity rating. Thus, chemical control will be needed to prevent *R. solani* root rot in sugar beet where this disease is endemic until resistance can be improved and uniformity is maintained within commercial cultivars.

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