Virulence Diversity in the Population of *Bipolaris sorokiniana*

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ABSTRACT

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Spot blotch, caused by *Bipolaris sorokiniana*, is a damaging disease of barley in Canada, especially in the prairie region (Manitoba, Saskatchewan, and Alberta) where most of Canadian crops are produced. Considerable interaction between isolates of the pathogen and barley genotypes necessitates the evaluation of the virulence diversity in the *B. sorokiniana* population in order to deploy effective resistance against the pathogen. The virulence diversity of 127 *B. sorokiniana* isolates from Canada and other countries was evaluated on 12 barley genotypes. Different virulence patterns were detected across *B. sorokiniana* isolates and eight virulence groups were identified using qualitative analysis of the virulence data. Results indicate broader virulence diversity in the pathogen population in the eastern prairie region of Canada, especially in Manitoba, compared with that previously reported. One group of isolates collected from Manitoba displayed a virulence pattern which had not been reported previously. This group was moderately virulent on most differential lines, including American six-rowed barley genotypes considered to possess durable resistance against *B. sorokiniana*. Although the classical method of pathotype identification can be exploited to analyze interactions in the barley-*B. sorokiniana* pathosystem, the continuous range of infection phenotypes found suggests that a quantitative analysis of the complex interactions occurring may be warranted.

Additional keywords: disease assessment, infection response, virulence group designation

Spot blotch, caused by *Bipolaris sorokiniana* (Sacc.) Shoemaker (teleomorph *Cochliobolus sativus* (S. Ito & Kurib.) Drechsler ex Dastur, syn. *Helminthosporium sativum* Pammel C. M. King & Bakke) is a major and damaging foliar disease of barley (*Hordeum vulgare* L.) in Canada. Recently, the prevalence of spot blotch has increased dramatically in the eastern prairie region of Canada. In 2002, this was the predominant disease of barley and affected every field sampled from Manitoba (29). Spot blotch symptoms on barley leaves typically are manifested as oval necrotic lesions surrounded by chlorotic halos. This infection can result in a reduction of photosynthetic area and, eventually, premature senescence of the entire plant. Yield losses up to 30% have been reported for susceptible barley cultivars in Canada (5,15). High humidity with temperatures between 22 and 30°C, conditions commonly found on the Canadian

prairies during the growing season, enhance damage caused by spot blotch (4,7). The pathogen also can attack other parts of barley plants to cause common root rot, seedling blight, and black point (18). Although fungicides can be used to reduce damage from the disease, a more economical and environmentally desirable means of control is through the deployment of resistant cultivars.

Information on the pathogenic variability and virulence present in the *B. sorokiniana* population in a particular region is necessary to develop cultivars with effective resistance against the local population of the pathogen. "Parasitic" specialization in *B. sorokiniana* first was described by Christensen (6), who showed that isolates of the fungus varied considerably in their virulence on a variety of cereals and grasses. Although other virulence studies found diversity among isolates of the pathogen (7,8,14,35), it is only recently that comprehensive studies were begun to examine the differential virulence of *B. sorokiniana* on barley. Levitin et al. (19) reported on host-specific virulence in isolates of *B. sorokiniana* in Russia, but they emphasized that such virulence diversity can be found only among geographically remote populations of the pathogen. In contrast, Fetch and Steffenson (11) identified *B. sorokiniana* isolates with differential virulence on several two-rowed barley genotypes within North Dakota. Valjavec-Gratian and Steffenson (33) further evaluated 36 isolates, mostly collected from

North Dakota, and identified three pathotypes (0, 1, and 2) of *B. sorokiniana*. Subsequently, Zhong and Steffenson (37) found the same three pathotypes among 22 isolates of *B. sorokiniana* collected from three U.S. states, Canada, Poland, Brazil, New Zealand, and Uruguay. In Uruguay, Gamba and Estramill (13) identified three virulence groups of *B. sorokiniana* isolates, based on infection responses (IRs) of 20 Uruguayan barley genotypes. In Australia, Meldrum et al. (21) identified six pathotypes of *B. sorokiniana* among the 34 isolates they tested using 20 differential lines. In Syria, Arabi and Jawhar (3) reported the presence of three virulence groups among 11 *B. sorokiniana* isolates using 10 differential barley genotypes.

In contrast to several published studies on pathogenic diversity in other countries, there are no recent, comprehensive reports documenting the virulence variation present in the Canadian population of *B. sorokiniana*. Several studies regarding the population structure of the *B. sorokiniana* in Canada have been conducted, but attention has been centered on either the pathogen's morphological and cytological characteristics (17,25,31) or the mating-type system (16,30,32). Variability in the population of *B. sorokiniana* in Canada, based on morphological and physiological characters and the virulence patterns of 250 isolates, was reported in an abstract by Dostaler et al. (8). Although they could not find distinct host specialization in the pathogen isolates studied, they reported that pathogen isolates differed in their virulence and could be classified into three discrete groups. Tekauz (28) found that differential virulence was present in the four Manitoba isolates of *B. sorokiniana* tested on 19 barley genotypes, at both seedling and adult-plant stages. The apparent considerable interactions among barley genotypes and isolates of *B. sorokiniana* from the Canadian prairie regions (8,28), coupled with the emergence of a new pathotype (pathotype 2) in North Dakota, a nearby U.S. state (33), underlined the importance of evaluating the current virulence pattern in the pathogen population.

The objective of this study was to assess the virulence diversity of *B. sorokiniana* isolates from Canada and other parts of the world. Because Alberta, Saskatchewan, and Manitoba account for 93% of Canada's annual production of barley (2), most of the Canadian isolates tested in this study were collected there. Particular emphasis was made to identify the virulence diver-

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sity of *B. sorokiniana* in Manitoba, where spot blotch levels recently have increased markedly (29). The classical method of pathotype identification using differential genotypes as described by Stakman et al. (26) was employed to evaluate the virulence diversity of the *B. sorokiniana* isolates. This method, which assumes a "gene-for-gene" interaction between pathogen isolates and host genotypes, has been used in several studies to assess virulence variability of the *B. sorokiniana* population (21,33,37).

MATERIALS AND METHODS

Collection of isolates. In all, 92 Canadian isolates of *B. sorokiniana*, including 75, 8, 5, 3, and 1 isolates collected from Manitoba, Saskatchewan, Alberta, Ontario, and Quebec, respectively, were evaluated for their virulence in this study. Most isolates originated from infected barley leaf tissue, others from either seed of barley or from infected leaf tissue of wheat or oat.

In total, 35 exotic isolates, including 9, 8, 7, 6, 3, and 2 isolates from Australia, Uruguay, Poland, Brazil, the United States, and Mexico, respectively, also were included in the study to compare the virulence of isolates from Canada with that from other parts of the world. Isolates from the United States (ND85F, ND90Pr, and ND93-1) were representative of North Dakota pathotypes 1, 2, and 0, respectively (33). The nine isolates from Australia were from different regions and representative of the six pathotypes of *B. sorokiniana* (21) found there. Most of the exotic isolates originally were isolated from leaf tissue or seed of barley, while a few were from leaf tissue of wheat and rye, or crown tissue of barley.

Differential lines. A differential set of 12 barley lines or cultivars, including 6 Canadian genotypes and 6 genotypes from the United States, was used to test the pathogen isolates. The set included lines ND B112 and ND 5883 and cv. Bowman, which were used previously to characterize the *B. sorokiniana* population in North Dakota (33) and also have been used for identification of *B. sorokiniana* pathotypes in several other studies (13,21,37). The cvs. Conlon, Robust, and Stander, developed in the United States and widely grown in Manitoba, also were included in the study to provide additional information on the virulence of Canadian *B. sorokiniana* isolates. The six Canadian barley genotypes (TR 251, TR 261, Newdale, CDC Stratus, CDC Bold, and AC Metcalfe) were selected based on their differential reactions to *B. sorokiniana* isolates in a previous study (28) or, in the case of AC Metcalfe, its current popularity in western Canada.

Preparation of host plants. Differential lines were seeded 2 weeks prior to inoculation as four clumps of eight seeds per 30-cm-diameter clay pot into a mixture of the

sifted soil, sand, and Turface at the ratio of 4:1:1. Nitrogen-based fertilizer (34-0-0, N-P-K; ammonium nitrate; Crop King, Inc.) at the rate of 5.0 g was added to each pot with the first watering to optimize seedling growth. Plants were grown in a controlled environment cabinet (Convion Model PGW36; Controlled Environments Inc., Winnipeg, Manitoba, Canada) at 17°C with an 18-h photoperiod.

Preparation of inoculum. For isolates obtained from leaf tissue or seed (most western Canadian isolates), tissue sections with putative spot blotch or black point lesions were surface sterilized and incubated for 3 to 4 days to induce fungal sporulation. These then were used to establish single-spore cultures. For isolates obtained from other collections (most exotic isolates), single conidia taken from the original stock (e.g., pure spores, cultures on growth medium, or silica gel) were cultured in the nutritional medium. Surface sterilization, spore culturing, nutritional medium, incubation, and preparation of inoculum followed protocols described by Tekauz (27,28). The concentration of conidial suspensions was adjusted to 3,000 conidia/ml by adding double-distilled water to each sample. A drop of polyoxyethylene-20-sorbitan monolaurate (Tween 20) was added per 50 ml of suspension as a spreader and sticker to facilitate adherence and the even distribution of inoculum on seedling leaves.

Inoculation and disease assessment. Inoculum was applied to 2-week-old plants (GS 13 of Zadoks et al.; 36) using an atomizer nozzle (Model 15; DeVilbiss Co., Somerset, PA) fitted to an electrically driven pressure air pump. Sufficient inoculum was used to cause run-off on seedlings, approximately 10 ml per seedling clump, as described by Tekauz (27,28). Inoculated plants were incubated in darkness for 18 h at 20 to 22°C and 100% relative humidity. They then were grown in growth cabinets under an 18-h photoperiod at 17°C. The second leaf of seedlings was scored for infection response (IR) 10 to 12 days after inoculation using the 1-to-9 IR scale for spot blotch developed by Fetch and Steffenson (12). All of the isolates were tested at least twice, and some were tested three, four, or five times (Table 1). Average IR for each isolate was calculated across replications. To evaluate a gene-for-gene model between isolates and differential lines, average IRs of <4.4 and ≥4.5 were considered as resistant and susceptible reactions, respectively.

Virulence group designation. Isolates were classified into different virulence groups employing the coded triplet nomenclature system of Limpert and Müller (20). In this system, host differentials are ordered in subsets of three (hence coded triplet). The reaction of a differential line to each pathogen isolate is a binary value, where 1 and 0 represent susceptible and

resistant reactions, respectively. The resulting binary value of 1 (susceptible reaction) then is converted to decenary values by a conversion factors 2^0 (equal to 1), 2^1 (equal to 2), and 2^2 (equal to 4) for the first, second, and third differential line in a subset, respectively, whereas a binary value of 0 (resistant reaction) is not converted. The sum of all decenary values in each subset is calculated and the digits are separated by dots. In this study, the 12 differential lines are listed alphabetically and then divided into four subsets of three differentials each, resulting in a four-digit code (e.g., R,R,R; S,R,R; R,S,R; S,S,R can be designated as 0.1.2.3 and R,R,S; S,R,S; R,S,S; S,S,S can be designated as 4.5.6.7). A group of isolates with similar four-digit codes were considered as a "virulence group" to avoid confusion with the three North Dakota "pathotype" groups identified by Valjavec-Gratian and Steffenson (33).

RESULTS

All isolates tested induced spot blotch symptoms on the 12 differential lines, resulting in lesions that varied in their size and foliar coverage (severity). Symptoms varied from minute to small necrotic lesions surrounded by no or very slight marginal chlorosis to large necrotic lesions, usually accompanied by a distinct marginal halo. The lesions exhibited by differential lines to different isolates of *B. sorokiniana* varied continuously, and intermediate IRs (IRs of 4 and 5) of the barley differentials were frequent. In some instances, the extent of the chlorotic halos surrounding necrotic lesions was not as large or typical as illustrated by Fetch and Steffenson (12), and, therefore, the overall size of the necrotic portion of a lesion was used as the main criterion to rate genotype IRs.

Based on IRs induced by the 127 isolates of *B. sorokiniana* on the 12 differential lines, the isolates could be classified into eight virulence groups by the coded triplet nomenclature system (Table 1). Isolates of group 0.0.0.0 displayed low IRs (mostly 2 to 3) on all differential lines and, therefore, were similar to North Dakota pathotype 0 described by Valjavec-Gratian and Steffenson (33). Virulence group 6.0.0.0 was composed of isolates inducing high IRs on cvs. Bowman and CDC Bold and low IRs on the other differentials (Table 1). Isolate ND90Pr (North Dakota pathotype 2) was included in this group. Group 5.7.0.0 isolates induced high IRs on AC Metcalfe, CDC Bold, CDC Stratus, Conlon, and ND 5883 and low ones on Bowman, ND B112, Newdale, Robust, Stander, TR 251, and TR 261 (Table 1). Isolates of group 5.7.4.0 were similar to isolates of group 5.7.0.0, with the addition of virulence on cv. Robust (Table 1). Based on IRs on the three reference differential lines Bowman, ND 5883, and ND B112,

Table 1. Mean infection responses and standard deviations for 12 barley differential lines inoculated with 127 isolates of *Bipolaris sorokiniana*, and corresponding virulence groups (VGs) designated by the coded triplet nomenclature system (four-digit codes)^a

Isolate	Rep ^b	Differential line											VG ^c	VG (ND)	
		AC Metcalfe	Bowman	CDC Bold	CDC Stratus	Conlon	ND5883	NDB112	Newdale	Robust	Stander	TR 251			TR 261
WRS1928	2	3 ± 0.7	4 ± 0.7	3 ± 0.0	3 ± 0.7	3 ± 0.7	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1929	2	3 ± 0.7	4 ± 0.7	3 ± 0.7	3 ± 0.7	3 ± 0.7	4 ± 0.7	3 ± 0.0	3 ± 0.7	4 ± 0.7	3 ± 0.0	3 ± 0.7	3 ± 0.7	0.0.0.0	0
WRS1930	3	3 ± 0.9	3 ± 0.0	4 ± 0.5	3 ± 0.0	3 ± 0.3	2 ± 0.3	4 ± 0.4	3 ± 0.9	3 ± 0.0	3 ± 0.5	2 ± 0.3	3 ± 0.5	0.0.0.0	0
WRS1932	2	3 ± 0.7	4 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.0	4 ± 0.7	4 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1937	2	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.0	3 ± 0.7	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1938	4	4 ± 0.7	3 ± 0.5	4 ± 1.0	4 ± 0.9	3 ± 0.5	4 ± 0.6	4 ± 0.5	3 ± 0.5	4 ± 0.8	3 ± 0.5	3 ± 0.6	3 ± 0.0	0.0.0.0	0
WRS1940	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1948	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1949	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1950	2	3 ± 0.0	4 ± 0.0	3 ± 0.4	3 ± 0.4	3 ± 0.0	3 ± 0.0	4 ± 0.0	3 ± 0.4	3 ± 0.0	3 ± 0.0	2 ± 0.4	3 ± 0.0	0.0.0.0	0
WRS1951	2	3 ± 0.7	3 ± 0.4	2 ± 0.2	3 ± 0.7	3 ± 0.2	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.7	2 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1952	2	3 ± 0.2	3 ± 0.5	3 ± 0.0	3 ± 0.2	3 ± 0.4	3 ± 0.2	3 ± 0.2	3 ± 0.4	3 ± 0.4	3 ± 0.2	2 ± 0.0	3 ± 0.0	0.0.0.0	0
WRS1953	2	2 ± 0.0	2 ± 0.4	2 ± 0.2	2 ± 0.2	2 ± 0.0	2 ± 0.4	2 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.2	2 ± 0.0	0.0.0.0	0
WRS1954	2	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1971	2	3 ± 0.2	3 ± 0.2	2 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.5	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1982	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.7	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
WRS1988	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.4	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.4	2 ± 0.0	0.0.0.0	0
WRS1991	2	3 ± 0.7	3 ± 0.7	3 ± 0.0	4 ± 0.7	3 ± 0.7	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.7	3 ± 0.7	2 ± 0.0	3 ± 0.7	0.0.0.0	0
Guelph98.1	3	2 ± 0.6	3 ± 0.6	3 ± 0.3	3 ± 1.0	2 ± 0.6	3 ± 0.5	2 ± 0.0	2 ± 0.0	3 ± 0.6	2 ± 0.0	2 ± 0.6	2 ± 0.0	0.0.0.0	0
Quebec95	2	3 ± 0.0	3 ± 0.0	3 ± 0.0	4 ± 0.7	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	0.0.0.0	0
Ottawa8	2	2 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
Mexico4	2	2 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.7	3 ± 0.7	2 ± 0.0	3 ± 0.7	2 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
Mexico5	3	2 ± 0.0	2 ± 1.2	3 ± 0.6	3 ± 0.6	2 ± 0.0	3 ± 0.6	3 ± 0.6	2 ± 0.6	3 ± 0.6	3 ± 0.6	2 ± 0.6	2 ± 0.6	0.0.0.0	0
UR1T98	2	3 ± 0.2	3 ± 0.4	3 ± 0.7	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.4	3 ± 0.0	3 ± 0.7	3 ± 0.7	2 ± 0.4	3 ± 0.7	0.0.0.0	0
SK1SB98	2	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
AB42000	2	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.2	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.0	2 ± 0.5	2 ± 0.5	0.0.0.0	0
AB52000	2	4 ± 0.5	3 ± 0.1	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	4 ± 0.0	3 ± 0.5	3 ± 0.0	4 ± 0.2	3 ± 0.2	3 ± 1.0	0.0.0.0	0
BRZ176	2	2 ± 0.0	2 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.7	3 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
BRZ178	2	3 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.0	2 ± 0.0	3 ± 0.7	2 ± 0.0	0.0.0.0	0
BRZ193	2	3 ± 0.0	2 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.7	3 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	3 ± 0.0	2 ± 0.0	2 ± 0.0	0.0.0.0	0
AUSSB25	2	2 ± 0.4	3 ± 1.1	2 ± 0.0	2 ± 0.4	3 ± 0.7	3 ± 0.0	3 ± 1.4	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.0	3 ± 0.7	0.0.0.0	0
AUS99074	2	2 ± 0.0	3 ± 0.7	2 ± 0.0	3 ± 0.7	2 ± 0.0	3 ± 0.0	3 ± 0.7	2 ± 0.4	3 ± 0.0	2 ± 0.0	2 ± 0.4	2 ± 0.4	0.0.0.0	0
WRS1909	2	3 ± 0.3	7 ± 0.0	7 ± 0.0	4 ± 0.1	4 ± 0.1	3 ± 0.4	4 ± 0.5	3 ± 0.1	3 ± 0.0	3 ± 0.0	2 ± 0.1	3 ± 0.1	6.0.0.0	2
WRS1978	2	4 ± 0.4	8 ± 0.7	7 ± 0.1	4 ± 0.7	4 ± 0.7	3 ± 0.0	3 ± 0.4	3 ± 0.7	4 ± 0.4	4 ± 0.7	2 ± 0.5	3 ± 0.7	6.0.0.0	2
ND90Pr	2	3 ± 0.3	8 ± 0.0	7 ± 0.4	3 ± 0.0	4 ± 0.4	3 ± 0.0	3 ± 0.0	3 ± 0.7	4 ± 0.2	3 ± 0.2	3 ± 0.6	3 ± 0.4	6.0.0.0	2
WRS1964	2	4 ± 0.2	5 ± 0.7	5 ± 0.1	5 ± 1.2	5 ± 0.8	4 ± 0.1	5 ± 0.9	4 ± 0.4	6 ± 0.5	4 ± 0.4	4 ± 0.7	4 ± 1.1	6.3.5.0	6
WRS1975	3	4 ± 0.0	5 ± 0.3	5 ± 0.6	5 ± 0.3	5 ± 0.6	4 ± 0.5	5 ± 0.1	4 ± 0.5	5 ± 0.3	4 ± 0.7	3 ± 0.3	4 ± 0.2	6.3.5.0	6
WRS1993	2	4 ± 0.0	5 ± 0.2	5 ± 0.1	5 ± 0.2	6 ± 1.1	4 ± 0.2	5 ± 0.5	4 ± 0.0	6 ± 0.4	4 ± 0.4	3 ± 1.2	4 ± 0.0	6.3.5.0	6
WRS1956	3	5 ± 0.8	5 ± 0.8	5 ± 1.0	5 ± 0.6	5 ± 1.2	5 ± 0.6	6 ± 0.9	4 ± 0.8	6 ± 0.5	5 ± 0.6	3 ± 0.0	3 ± 0.6	7.7.5.1	7
WRS1959	3	5 ± 0.9	6 ± 0.8	5 ± 0.7	5 ± 0.4	5 ± 0.4	5 ± 0.7	6 ± 0.6	4 ± 0.4	6 ± 1.0	5 ± 1.0	3 ± 0.0	4 ± 0.4	7.7.5.1	7
WRS1965	3	5 ± 0.3	5 ± 0.1	5 ± 0.6	5 ± 0.1	6 ± 0.4	6 ± 0.4	5 ± 0.3	4 ± 0.2	5 ± 0.9	5 ± 0.6	3 ± 0.5	4 ± 0.5	7.7.5.1	7
WRS1997	4	5 ± 1.0	5 ± 0.3	5 ± 0.6	5 ± 0.5	5 ± 1.0	6 ± 0.4	5 ± 0.9	3 ± 0.8	5 ± 0.5	5 ± 0.5	3 ± 0.6	4 ± 0.7	7.7.5.1	7
WRS1960	3	5 ± 0.9	5 ± 0.0	5 ± 0.6	5 ± 1.0	6 ± 0.5	5 ± 1.0	5 ± 0.6	5 ± 0.1	6 ± 1.0	5 ± 1.0	4 ± 0.0	5 ± 0.7	7.7.7.5	7
WRS1961	3	5 ± 0.9	6 ± 0.1	5 ± 1.2	5 ± 0.9	6 ± 0.6	6 ± 0.7	6 ± 0.1	5 ± 0.5	7 ± 0.6	5 ± 0.3	4 ± 0.5	5 ± 0.7	7.7.7.5	7
WRS1962	3	5 ± 0.1	6 ± 0.6	5 ± 0.3	5 ± 0.6	6 ± 0.3	5 ± 1.0	6 ± 0.6	5 ± 0.4	6 ± 1.0	5 ± 1.0	4 ± 0.6	5 ± 0.5	7.7.7.5	7
WRS1974	3	5 ± 0.7	5 ± 0.1	5 ± 0.6	5 ± 0.3	6 ± 0.4	5 ± 0.3	5 ± 0.6	5 ± 0.5	7 ± 0.4	5 ± 0.3	3 ± 0.5	5 ± 0.1	7.7.7.5	7
WRS1977	3	5 ± 0.8	6 ± 0.4	6 ± 1.4	6 ± 0.9	6 ± 0.7	5 ± 0.0	6 ± 0.6	5 ± 0.4	8 ± 0.5	6 ± 0.7	4 ± 0.4	5 ± 0.2	7.7.7.5	7
WRS1983	5	5 ± 0.8	6 ± 0.4	6 ± 1.1	7 ± 1.2	6 ± 0.5	5 ± 0.6	7 ± 0.4	5 ± 0.3	7 ± 0.3	5 ± 0.8	4 ± 0.6	5 ± 0.9	7.7.7.5	7
WRS1986	3	6 ± 0.4	5 ± 0.5	7 ± 0.9	7 ± 1.3	6 ± 0.4	5 ± 0.3	6 ± 0.6	5 ± 0.3	7 ± 0.3	5 ± 0.9	4 ± 0.1	5 ± 0.7	7.7.7.5	7
WRS1936	4*	5 ± 0.5	3 ± 1.0	5 ± 0.6	5 ± 0.8	5 ± 0.7	8 ± 0.3	3 ± 0.5	4 ± 1.0	4 ± 0.5	3 ± 0.6	3 ± 0.5	3 ± 0.5	5.7.0.0	1
WRS1984	3	5 ± 0.4	4 ± 0.2	5 ± 0.8	5 ± 0.2	5 ± 0.6	6 ± 0.2	4 ± 0.3	2 ± 0.3	4 ± 0.7	4 ± 0.6	2 ± 0.3	3 ± 1.2	5.7.0.0	1
WRS1985	2*	5 ± 0.5	3 ± 0.6	5 ± 0.9	5 ± 0.9	5 ± 0.0	7 ± 0.5	4 ± 0.3	4 ± 0.0	4 ± 0.2	3 ± 0.6	3 ± 0.0	4 ± 0.3	5.7.0.0	1
WRS1994	3	5 ± 1.2	4 ± 0.4	5 ± 0.3	5 ± 0.3	5 ± 0.6	5 ± 0.7	4 ± 0.1	3 ± 0.4	4 ± 0.8	3 ± 0.6	3 ± 0.0	4 ± 0.6	5.7.0.0	1
WRS1996	4	5 ± 0.8	4 ± 0.4	5 ± 0.6	5 ± 0.7	5 ± 0.4	8 ± 0.6	3 ± 0.3	3 ± 0.5	4 ± 0.4	3 ± 0.3	3 ± 0.7	4 ± 0.6	5.7.0.0	1
ND93-1	2	5 ± 0.2	4 ± 0.7	7 ± 1.8	5 ± 0.1	6 ± 0.1	7 ± 1.4	4 ± 0.7	4 ± 0.7	4 ± 0.2	4 ± 0.0	3 ± 0.7	4 ± 0.7	5.7.0.0	1
UR2P98	3	5 ± 1.0	4 ± 0.1	6 ± 1.2	6 ± 1.4	6 ± 1.0	7 ± 1.1	4 ± 0.6	3 ± 0.7	4 ± 0.3	4 ± 0.2	2 ± 1.0	3 ± 0.2	5.7.0.0	1
UR1V99	2	5 ± 0.6	4 ± 0.1	7 ± 0.7	6 ± 0.8	5 ± 0.1	8 ± 0.0	4 ± 0.7	3 ± 0.7	4 ± 0.5	4 ± 0.7	3 ± 0.7	4 ± 0.4	5.7.0.0	1
POL97KD38	2	6 ± 0.0	4 ± 0.0	5 ± 0.4	5 ± 0.0	5 ± 0.1	8 ± 0.1	3 ± 0.2	4 ± 0.7	4 ± 0.0	4 ± 0.0	2 ± 0.0	4 ± 0.2	5.7.0.0	1
BRZ5	2	6 ± 0.0	3 ± 0.0	5 ± 0.2	5 ± 0.2	6 ± 0.2	8 ± 0.0	3 ± 0.0	4 ± 0.7	4 ± 0.1	4 ± 0.0	3 ± 0.0	3 ± 1.4	5.7.0.0	1
BRZ6	2	6 ± 0.4	4 ± 0.7	5 ± 0.5	5 ± 0.4	5 ± 0.0	6 ± 0.5	4 ± 0.0	4 ± 0.7	4 ± 0.5	4 ± 0.7	3 ± 0.0	4 ± 0.0	5.7.0.0	1
AUSSB22	2	5 ± 1.4	3 ± 0.4	5 ± 1.1	5 ± 1.2	5 ± 0.4	8 ± 0.4	4 ± 0.0	3 ± 0.4	4 ± 0.0	3 ± 0.4	2 ± 0.0	3 ± 0.7	5.7.0.0	1
AUS98024	2	5 ± 0.0	4 ± 0.0	5 ± 0.4	5 ± 0.4	5 ± 1.1	8 ± 0.0	4 ± 0.0	3 ± 0.0	4 ± 1.1	4 ± 1.1	3 ± 0.0	4 ± 0.7	5.7.0.0	1

(continued on next page)

^a Single-digit codes for the isolates, based on infection responses of North Dakota differential lines ND 5883, Bowman, and ND B112 (ND), also are listed for comparison.

^b Rep = replication. Mean infection responses were calculated by averaging infection responses of the corresponding replications using the 1-to-9 rating scale of Fetch and Steffenson (12). Replications means were rounded up to whole numbers. Asterisks (*) indicate that isolates were tested in an additional replication with only four of the differential lines, including Bowman, ND B112, Stander, and TR 251.

^c VGs designated according to the coded triplet nomenclature system of Limpert and Müller (20).

Table 1. (continued from preceding page)

Isolate	Rep ^b	Differential line												VG ^c	VG (ND)
		AC Metcalfe	Bowman	CDC Bold	CDC Stratus	Conlon	ND5883	NDB112	Newdale	Robust	Stander	TR 251	TR 261		
AUS98137	2	6 ± 0.7	4 ± 0.0	6 ± 0.4	6 ± 0.7	6 ± 0.0	8 ± 0.0	4 ± 0.4	4 ± 0.7	4 ± 0.0	4 ± 0.0	3 ± 0.4	4 ± 0.7	5.7.0.0	1
WRS1908	3*	6 ± 1.0	4 ± 0.5	6 ± 0.1	6 ± 0.7	6 ± 0.8	7 ± 0.5	4 ± 0.6	4 ± 0.6	5 ± 0.5	4 ± 0.8	3 ± 0.6	4 ± 0.5	5.7.4.0	1
WRS1934	2	7 ± 0.8	4 ± 0.1	8 ± 0.3	7 ± 0.3	6 ± 0.1	7 ± 0.1	3 ± 0.0	3 ± 0.4	5 ± 0.0	4 ± 0.1	3 ± 0.4	4 ± 0.0	5.7.4.0	1
WRS1941	3*	6 ± 0.2	4 ± 1.0	5 ± 0.5	6 ± 1.1	6 ± 0.9	8 ± 0.1	4 ± 0.3	4 ± 0.1	5 ± 0.9	4 ± 0.6	3 ± 0.1	4 ± 0.5	5.7.4.0	1
WRS1943	2*	6 ± 0.7	4 ± 0.0	7 ± 0.4	7 ± 1.2	6 ± 0.2	8 ± 0.2	4 ± 0.0	3 ± 0.5	5 ± 0.0	4 ± 0.3	3 ± 0.2	4 ± 0.1	5.7.4.0	1
WRS1944	2*	6 ± 0.2	4 ± 0.5	8 ± 0.0	7 ± 1.8	7 ± 0.7	7 ± 0.5	4 ± 0.3	4 ± 0.0	5 ± 0.4	4 ± 0.7	3 ± 0.2	4 ± 0.1	5.7.4.0	1
WRS1945	2*	6 ± 0.1	4 ± 0.3	7 ± 0.9	7 ± 0.2	6 ± 0.1	8 ± 0.2	4 ± 0.3	4 ± 0.4	5 ± 0.1	4 ± 0.1	4 ± 0.4	4 ± 0.5	5.7.4.0	1
WRS1955	2*	6 ± 0.5	4 ± 0.0	6 ± 0.2	6 ± 0.0	7 ± 0.1	8 ± 0.7	4 ± 0.0	3 ± 0.0	5 ± 0.5	4 ± 0.2	3 ± 0.7	4 ± 0.5	5.7.4.0	1
WRS1957	2*	6 ± 0.1	4 ± 0.6	6 ± 0.4	6 ± 0.5	7 ± 0.9	8 ± 0.7	4 ± 0.6	4 ± 0.0	5 ± 0.4	4 ± 0.6	3 ± 0.0	3 ± 0.5	5.7.4.0	1
WRS1958	2*	6 ± 0.5	4 ± 0.8	6 ± 0.9	5 ± 0.1	6 ± 0.4	8 ± 0.0	4 ± 0.7	3 ± 0.0	5 ± 0.5	4 ± 0.7	3 ± 0.0	4 ± 0.5	5.7.4.0	1
WRS1966	2*	6 ± 0.2	4 ± 0.4	6 ± 0.4	6 ± 1.4	6 ± 0.5	8 ± 0.0	4 ± 0.5	4 ± 0.7	5 ± 0.4	4 ± 0.3	3 ± 0.2	4 ± 0.0	5.7.4.0	1
WRS1967	3*	7 ± 0.3	4 ± 0.4	6 ± 0.7	6 ± 0.6	6 ± 0.3	8 ± 0.5	4 ± 0.4	3 ± 0.0	5 ± 0.0	4 ± 0.7	3 ± 0.6	4 ± 0.9	5.7.4.0	1
WRS1968	2*	7 ± 0.4	4 ± 0.8	6 ± 0.7	6 ± 1.3	6 ± 0.0	7 ± 0.1	4 ± 0.3	4 ± 0.0	5 ± 0.1	4 ± 0.3	3 ± 0.0	4 ± 0.4	5.7.4.0	1
WRS1969	3	6 ± 0.5	4 ± 0.3	8 ± 0.4	7 ± 0.8	6 ± 0.7	8 ± 0.4	4 ± 0.3	4 ± 0.2	5 ± 0.3	4 ± 0.5	3 ± 0.3	4 ± 0.8	5.7.4.0	1
WRS1970	2	5 ± 0.0	4 ± 0.5	7 ± 0.3	7 ± 0.0	6 ± 0.3	8 ± 0.0	4 ± 0.5	4 ± 0.6	5 ± 0.2	4 ± 0.1	3 ± 0.7	4 ± 0.9	5.7.4.0	1
WRS1976	3	6 ± 1.0	4 ± 0.0	7 ± 1.1	6 ± 0.4	6 ± 0.7	8 ± 0.2	4 ± 0.0	4 ± 0.6	5 ± 0.4	4 ± 0.1	3 ± 0.6	4 ± 0.6	5.7.4.0	1
WRS1981	3	5 ± 0.6	4 ± 0.0	6 ± 0.6	6 ± 0.7	5 ± 0.6	8 ± 0.3	4 ± 0.3	4 ± 0.0	5 ± 0.6	4 ± 0.3	4 ± 0.5	4 ± 0.6	5.7.4.0	1
Guelph98.2	3	6 ± 0.3	4 ± 1.3	6 ± 0.1	6 ± 0.1	6 ± 0.4	7 ± 0.6	4 ± 1.0	4 ± 0.6	5 ± 0.0	4 ± 0.5	3 ± 0.0	4 ± 0.1	5.7.4.0	1
ND85F	3*	6 ± 0.5	4 ± 0.3	6 ± 1.2	6 ± 0.8	6 ± 0.3	7 ± 0.9	4 ± 0.6	4 ± 0.3	5 ± 0.0	4 ± 0.6	3 ± 0.0	4 ± 0.2	5.7.4.0	1
UR5T99	2*	5 ± 0.1	3 ± 0.5	6 ± 0.4	6 ± 0.8	7 ± 0.7	8 ± 0.6	4 ± 0.5	3 ± 0.5	5 ± 0.2	4 ± 0.2	4 ± 0.1	4 ± 0.5	5.7.4.0	1
UR2T98	2	6 ± 1.1	4 ± 1.4	7 ± 0.2	8 ± 0.7	6 ± 0.5	9 ± 0.0	4 ± 0.4	3 ± 0.3	5 ± 0.0	4 ± 0.4	3 ± 0.5	4 ± 1.0	5.7.4.0	1
UR3T98	2	7 ± 0.1	4 ± 0.0	6 ± 0.3	6 ± 0.3	5 ± 0.0	8 ± 0.0	4 ± 0.3	3 ± 0.9	5 ± 0.9	4 ± 0.7	3 ± 0.4	4 ± 0.4	5.7.4.0	1
UR2V98	2	7 ± 0.9	4 ± 0.0	6 ± 0.2	8 ± 0.2	8 ± 0.1	8 ± 0.0	4 ± 1.4	4 ± 0.2	5 ± 0.0	4 ± 0.4	3 ± 0.4	4 ± 1.4	5.7.4.0	1
UR1P98	2	6 ± 0.2	4 ± 0.0	6 ± 0.2	7 ± 0.2	7 ± 0.5	8 ± 0.0	4 ± 1.4	4 ± 0.7	5 ± 0.2	4 ± 0.0	3 ± 1.4	4 ± 1.4	5.7.4.0	1
POL97KD21	2	6 ± 0.0	4 ± 0.0	6 ± 0.5	7 ± 0.0	7 ± 0.2	8 ± 0.1	4 ± 0.3	4 ± 0.2	5 ± 0.3	4 ± 0.0	3 ± 0.6	4 ± 0.4	5.7.4.0	1
POL97KD33	3	6 ± 1.0	4 ± 0.5	7 ± 0.4	7 ± 1.1	7 ± 0.5	8 ± 0.9	4 ± 0.5	4 ± 0.0	5 ± 0.6	4 ± 0.5	4 ± 0.9	4 ± 0.7	5.7.4.0	1
POL97KD26	2	6 ± 1.4	4 ± 1.4	6 ± 0.4	6 ± 0.5	7 ± 0.4	7 ± 0.9	4 ± 1.4	4 ± 0.7	5 ± 0.6	4 ± 0.7	3 ± 1.3	4 ± 0.4	5.7.4.0	1
POL97KD29	2*	7 ± 0.1	4 ± 0.4	6 ± 0.2	6 ± 0.4	7 ± 0.4	8 ± 0.4	4 ± 0.5	4 ± 0.0	5 ± 0.4	4 ± 0.6	4 ± 0.7	4 ± 0.3	5.7.4.0	1
POL97KD37	2*	7 ± 0.5	4 ± 0.5	7 ± 0.3	8 ± 0.0	6 ± 0.1	8 ± 0.6	4 ± 0.5	4 ± 0.0	5 ± 0.2	4 ± 0.1	4 ± 0.1	4 ± 0.4	5.7.4.0	1
POL97KD32	2	6 ± 0.7	4 ± 0.0	7 ± 0.7	8 ± 0.0	6 ± 0.3	8 ± 1.1	3 ± 0.1	4 ± 0.4	5 ± 0.0	4 ± 0.2	3 ± 0.2	3 ± 0.5	5.7.4.0	1
SK2A98	2	6 ± 0.9	4 ± 0.7	5 ± 0.5	5 ± 0.4	6 ± 0.2	8 ± 0.0	4 ± 0.7	3 ± 0.5	5 ± 0.5	4 ± 0.2	3 ± 1.4	4 ± 0.9	5.7.4.0	1
SK2T98	2	6 ± 0.5	4 ± 0.4	7 ± 0.0	7 ± 0.2	6 ± 0.0	8 ± 0.4	4 ± 0.2	3 ± 0.0	5 ± 0.2	4 ± 0.7	4 ± 0.7	4 ± 0.6	5.7.4.0	1
AB12000	3	6 ± 0.6	4 ± 0.4	7 ± 0.5	7 ± 0.6	8 ± 0.6	8 ± 0.6	4 ± 0.4	3 ± 0.6	5 ± 0.1	4 ± 0.6	3 ± 0.6	4 ± 0.9	5.7.4.0	1
AB22000	3	6 ± 0.6	4 ± 0.3	5 ± 0.5	5 ± 0.3	6 ± 0.1	7 ± 0.6	3 ± 0.3	3 ± 0.5	5 ± 0.0	4 ± 0.6	2 ± 0.5	3 ± 0.6	5.7.4.0	1
AB32000	3	5 ± 0.4	4 ± 0.3	6 ± 0.0	6 ± 0.1	6 ± 0.4	7 ± 0.5	4 ± 0.0	3 ± 0.3	5 ± 0.0	4 ± 0.7	3 ± 0.6	3 ± 0.6	5.7.4.0	1
BRZ4	2*	6 ± 0.7	4 ± 0.3	6 ± 0.4	6 ± 0.0	5 ± 0.0	8 ± 0.4	4 ± 0.5	3 ± 0.0	6 ± 0.7	4 ± 1.2	3 ± 0.7	4 ± 0.6	5.7.4.0	1
AUS98042	2	6 ± 0.0	4 ± 0.4	6 ± 0.0	7 ± 0.4	6 ± 0.4	8 ± 0.0	4 ± 0.7	3 ± 0.4	6 ± 0.7	4 ± 0.4	3 ± 0.7	4 ± 0.4	5.7.4.0	1
AUS99108	2	6 ± 0.7	4 ± 0.7	6 ± 0.0	6 ± 0.4	7 ± 1.4	8 ± 0.0	3 ± 0.4	4 ± 0.7	6 ± 0.7	4 ± 0.4	3 ± 0.7	4 ± 0.4	5.7.4.0	1
AUS99109	2	6 ± 0.7	4 ± 0.0	7 ± 0.7	7 ± 0.0	8 ± 0.7	8 ± 0.0	4 ± 0.0	4 ± 0.0	5 ± 0.4	4 ± 0.4	4 ± 0.7	4 ± 0.0	5.7.4.0	1
WRS1903	2*	6 ± 0.1	5 ± 0.8	7 ± 0.5	8 ± 0.2	6 ± 0.4	8 ± 0.5	5 ± 1.0	4 ± 0.1	5 ± 1.1	4 ± 0.7	3 ± 0.1	5 ± 1.0	7.7.5.4	7
WRS1910	3*	6 ± 1.7	5 ± 1.6	7 ± 1.4	6 ± 2.1	6 ± 1.4	7 ± 0.5	5 ± 1.1	4 ± 0.3	6 ± 0.5	4 ± 0.7	3 ± 0.9	5 ± 0.3	7.7.5.4	7
WRS1911	3*	6 ± 1.9	5 ± 1.1	7 ± 1.1	7 ± 1.5	6 ± 0.3	7 ± 1.4	5 ± 0.5	4 ± 0.0	5 ± 0.3	4 ± 0.5	3 ± 0.4	5 ± 0.6	7.7.5.4	7
WRS1927	2*	7 ± 0.3	5 ± 0.7	8 ± 0.1	8 ± 0.4	7 ± 0.3	7 ± 0.4	5 ± 0.6	4 ± 0.3	5 ± 0.1	4 ± 0.3	3 ± 0.3	5 ± 0.4	7.7.5.4	7
WRS1933	2*	7 ± 0.9	5 ± 0.6	7 ± 1.1	7 ± 1.1	7 ± 1.0	8 ± 0.3	5 ± 0.6	4 ± 0.0	5 ± 0.0	4 ± 0.4	3 ± 0.0	5 ± 0.5	7.7.5.4	7
WRS1935	3	6 ± 1.2	5 ± 0.5	7 ± 1.2	7 ± 1.3	7 ± 0.6	8 ± 0.1	6 ± 0.2	4 ± 0.4	5 ± 0.3	4 ± 0.0	3 ± 0.8	5 ± 1.1	7.7.5.4	7
WRS1939	2	7 ± 0.0	5 ± 0.4	8 ± 0.7	7 ± 2.1	8 ± 0.7	8 ± 0.0	5 ± 0.0	4 ± 0.4	5 ± 0.2	4 ± 0.0	3 ± 0.0	6 ± 0.7	7.7.5.4	7
WRS1942	2*	6 ± 0.4	5 ± 0.8	8 ± 0.7	8 ± 0.0	7 ± 0.7	8 ± 0.2	5 ± 0.8	4 ± 0.4	5 ± 0.9	4 ± 0.1	3 ± 0.0	5 ± 1.0	7.7.5.4	7
WRS1946	3	6 ± 0.4	5 ± 0.0	7 ± 1.0	7 ± 0.8	6 ± 0.3	8 ± 0.3	5 ± 0.3	4 ± 0.5	5 ± 0.5	4 ± 0.6	4 ± 0.3	5 ± 0.5	7.7.5.4	7
WRS1947	3*	6 ± 0.6	5 ± 0.6	6 ± 0.4	6 ± 0.4	6 ± 0.3	8 ± 0.3	5 ± 0.7	4 ± 0.2	5 ± 0.3	4 ± 0.2	3 ± 0.2	5 ± 0.3	7.7.5.4	7
WRS1963	2*	6 ± 0.8	5 ± 0.3	7 ± 0.1	6 ± 0.0	6 ± 0.1	8 ± 0.0	5 ± 0.9	4 ± 0.0	6 ± 0.1	4 ± 0.1	4 ± 0.7	5 ± 0.6	7.7.5.4	7
WRS1972	2	6 ± 0.0	6 ± 0.7	7 ± 0.8	7 ± 0.3	7 ± 0.4	8 ± 0.4	6 ± 0.7	4 ± 0.9	5 ± 1.1	4 ± 1.3	3 ± 0.2	5 ± 0.7	7.7.5.4	7
WRS1973	2*	7 ± 0.7	5 ± 0.5	7 ± 0.5	7 ± 0.7	7 ± 2.0	8 ± 0.7	5 ± 0.5	4 ± 0.7	5 ± 0.2	3 ± 0.5	3 ± 1.1	5 ± 0.5	7.7.5.4	7
WRS1979	3	5 ± 0.4	5 ± 0.6	6 ± 1.5	8 ± 0.6	6 ± 0.6	8 ± 0.1	5 ± 0.4	4 ± 0.8	5 ± 0.1	4 ± 0.5	4 ± 0.5	5 ± 0.9	7.7.5.4	7
WRS1980	2*	6 ± 0.1	5 ± 0.5	6 ± 1.0	6 ± 0.0	6 ± 0.1	8 ± 0.1	5 ± 0.4	4 ± 0.4	6 ± 0.7	4 ± 0.1	3 ± 0.0	5 ± 0.6	7.7.5.4	7
WRS1987	2	6 ± 0.3	5 ± 0.0	7 ± 0.7	7 ± 0.7	7 ± 1.3	7 ± 0.2	5 ± 0.2	4 ± 0.2	5 ± 1.2	4 ± 1.4	3 ± 0.0	5 ± 0.7	7.7.5.4	7
WRS1989	2*	6 ± 0.3	5 ± 1.0	6 ± 0.8	6 ± 0.8	6 ± 0.1	8 ± 0.1	5 ± 1.0	4 ± 0.0	5 ± 0.6	4 ± 0.8	4 ± 0.7	5 ± 0.5	7.7.5.4	7
WRS1990	2*	6 ± 0.1	5 ± 0.3	7 ± 1.4	7 ± 2.1	6 ± 1.1	8 ± 0.2	6 ± 0.3	4 ± 0.1	5 ± 0.4	4 ± 0.4	3 ± 0.4	5 ± 1.0	7.7.5.4	7
WRS1992	3	5 ± 0.5	5 ± 1.0	7 ± 1.2	7 ± 1.2	6 ± 1.0	8 ± 0.0	5 ± 0.9	4 ± 1.0	5 ± 0.3	4 ± 0.3	3 ± 0.8	5 ± 1.0	7.7.5.4	7
WRS1995	2*	6 ± 0.7	5 ± 0.3	7 ± 1.4	7 ± 1.4	6 ± 0.7	7 ± 0.9	5 ± 1.5	4 ± 0.4	5 ± 0.5	4 ± 0.5	3 ± 0.0	5 ± 0.7	7.7.5.4	7
SK1A98	2*	6 ± 0.5	5 ± 0.4	7 ± 1.2	6 ± 0.4	7 ± 0.6	8 ± 0.1	5 ± 0.6	3 ± 0.0	5 ± 0.4	4 ± 0.2	3 ± 0.0	5 ± 0.7	7.7.5.4	7
SK2N98	3	7 ± 1.0	5 ± 0.3	7 ± 0.4	6 ± 1.7	8 ± 0.3	8 ± 0.4	5 ± 0.3	4 ± 0.8	6 ± 0.4	4 ± 0.3	3 ± 0.3	5 ± 1.2	7.7.5.4	7
SK1CR98	2*	6 ± 0.4	5 ± 0.4	6 ± 0.1	6 ± 0.7	7 ± 1.5	8 ± 0.1	5 ± 0.6	3 ± 0.0	5 ± 0.2	4 ± 0.5	3 ± 0.0	5 ± 0.6	7.7.5.4	7
SK2CR98	2*	6 ± 0.0	5 ± 1.2	7 ± 0.2	6 ± 0.2	6 ± 0.2	8 ± 0.5	5 ± 0.9	4 ± 0.4	5 ± 0.4	4 ± 0.7	4 ± 0.0	5 ± 0.1	7.7.5.4	7
SK1N98	2	6 ± 0.0	5 ± 0.2	6 ± 0.6	7 ± 1.9	6 ± 0.7	8 ± 0.7	5 ± 0.0	4 ± 0.2	5 ± 0.4	4 ± 0.5	3 ± 0.0	5 ± 0.2	7.7.5.4	7
AUS98153	2	7 ± 0.7	5 ± 0.4	7 ± 1.1	7 ± 1.1	7 ± 0.4	8 ± 0.0	5 ± 0.2	4 ± 0.2	5 ± 0.4	4 ± 0.0	4 ± 0.0	5 ± 0.7	7.7.5.4	7
Reactions															
Susceptible	...	89	43	95	92	92	89	40	7	78	11	0	33	...	...
Resistant	...	38	84	32	35	35	38	87	120	49	116	127	94	...	...

both of these groups would be classified as North Dakota pathotype 1 (Table 1). Isolates of group 7.7.5.4 induced high IRs on most of the differential lines except for Newdale, Stander, and TR 251 (Table 1). Isolates of group 7.7.5.4 had similarities to isolates of group 5.7.4.0 except for their virulence, albeit of a moderate level and rated mostly as 5, on Bowman, ND B112, Robust, and TR 261 (Table 1). Isolates of virulence groups 5.7.4.0 and 7.7.5.4 exhibited higher virulence on cvs. AC Metcalfe, CDC Bold, CDC Stratus, and Conlon (mostly 6 to 7), and very high virulence on line ND 5883, inducing large necrotic lesions with distinct chlorotic halos characteristic of IRs of 8 and 9, as described by Fetcher and Steffenson (12).

Virulence group 7.7.7.5 was composed of isolates inducing high IRs on all differential lines except TR 251. The few isolates designated as virulence group 7.7.5.1 exhibited low IRs on Newdale, TR 251, and TR 261, and high IRs on all other differentials. Group 6.3.5.0 also was composed of only a few isolates that induced high IRs on Bowman, CDC Bold, CDC Stratus, Conlon, ND B112, and Robust but low IRs on AC Metcalfe, ND 5883, Newdale, Stander, TR 251, and TR 261 (Table 1).

Two of the three reference isolates from North Dakota, ND85F, and ND90Pr (pathotypes 1 and 2, respectively), exhibited a virulence pattern corresponding to isolates of virulence groups 5.7.4.0 and 6.0.0.0. However, isolate ND93-1 (representative of North Dakota pathotype 0) was virulent on some differential lines in this study, including line ND 5883, which previously were reported to be resistant to this isolate (33). The virulence pattern of isolate ND93-1 (North Dakota pathotype 0) was completely different from that of the low virulence isolates of virulence group 0.0.0.0, identified in this study. The nine reference isolates from Australia (21) had virulence patterns similar to those of

four of the eight virulence groups (0.0.0.0, 5.7.0.0, 5.7.4.0, and 7.7.5.4) identified in this study. None of the reference Australian isolates of *B. sorokiniana* induced IR on the 12 barley differential lines that were similar to those of isolates of groups 6.0.0.0 (North Dakota pathotype 2), 6.3.5.0, 7.7.5.1, or 7.7.7.5.

The number and frequency of isolates collected from different provinces in Canada and other countries assigned to each virulence group are listed in Table 2. From a total of 127 isolates tested, 32 (25%) exhibited low virulence on all differential lines (group 0.0.0.0). Isolates in groups 5.7.4.0, 7.7.5.4, 5.7.0.0, 7.7.7.5, 7.7.5.1, 6.3.5.0, and 6.0.0.0 composed 38 (30%), 26 (21%), 14 (11%), 7 (6%), 4 (3%), 3 (2%), and 3 (2%) of total isolates, respectively. Isolates assigned to virulence groups 6.3.5.0, 7.7.5.1, and 7.7.7.5 were collected only from Manitoba. Of the three isolates designated as virulence group 6.0.0.0, two were collected in Manitoba and the third was the reference isolate ND90Pr (pathotype 2) from North Dakota.

All isolates designated as group 7.7.5.4 were collected from either Manitoba or Saskatchewan, except isolate AUS98153 from Australia. In contrast, isolates designated as group 5.7.4.0, with similar virulence to isolates of North Dakota pathotype 1, had a wide geographic distribution in all provinces of Canada and all other countries, except for Quebec and Mexico, from which only one and two isolates, respectively, were tested. The highest frequencies of isolates in this virulence group were detected in Alberta, Poland, and Uruguay, composing 60, 86 and 63%, respectively, of the total isolates collected in those regions. Isolates of group 5.7.0.0, similar to North Dakota pathotype 1, were found in Manitoba at a low frequency (7%), but were not found in other provinces of Canada. In contrast, isolates of this group composed a larger proportion of

the isolates collected from Australia, Brazil, Poland, and Uruguay (33, 33, 14, and 25%, respectively).

Of the 127 isolates evaluated in this study, 86, 18, and 1 isolate were collected from barley leaf, seed, and crown tissues, respectively (Table 3). Ten, five, and one isolates were collected from leaves of wheat, oat, and rye, respectively, while the host origins of the remaining six isolates was unknown (Table 3). Isolates of all virulence groups were found among *B. sorokiniana* isolates collected from barley leaf tissue. Of the 18 isolates collected from barley seed, 11% were classified in group 0.0.0.0, whereas 89% were more virulent and classified in virulence groups 5.7.0.0, 5.7.4.0, and 7.7.5.4. The majority of the isolates collected from leaves of wheat (70%) and oat (60%) and one isolate each from rye leaf and barley crown had low virulence on the differential lines used here and were classified as virulence group 0.0.0.0.

DISCUSSION

Different virulence patterns were detected across *B. sorokiniana* isolates collected from several provinces in Canada, and from other countries. Based on the low-virulence or high-virulence phenotypes on 12 differential barley lines, eight virulence groups were identified from 127 isolates of *B. sorokiniana*. The greatest amount of pathogenic variability among *B. sorokiniana* isolates was observed in Manitoba, where all eight virulence groups were represented. Isolates designated as groups 7.7.7.5, 7.7.5.1, and 6.3.5.0 were found only in collections from Manitoba. In addition, isolates of group 7.7.5.4 were found only in Manitoba, Saskatchewan, and Australia. These results may indicate a broader variability in the pathogen in the eastern prairie region of Canada, especially in Manitoba. However, this likely can be attributed to the higher number of isolates

Table 2. Number and percentage of *Bipolaris sorokiniana* isolates collected (or obtained) from different provinces of Canada or other countries assigned to eight virulence groups

Provinces, country ^b	No. per virulence group (%) ^a								Total
	0.0.0.0	6.0.0.0	6.3.5.0	7.7.5.1	7.7.7.5	5.7.0.0	5.7.4.0	7.7.5.4	
MB, Canada	18 (24)	2 (3)	3 (4)	4 (5)	7 (9)	5 (7)	16 (21)	20 (27)	75
SK, Canada	1 (13)	0	0	0	0	0	2 (25)	5 (62)	8
AB, Canada	2 (40)	0	0	0	0	0	3 (60)	0	5
ON, Canada	2 (66)	0	0	0	0	0	1 (33)	0	3
QC, Canada	1 (100)	0	0	0	0	0	0	0	1
Australia	2 (22)	0	0	0	0	3 (33)	3 (33)	1 (11)	9
Brazil	3 (50)	0	0	0	0	2 (33)	1 (17)	0	6
Mexico	2 (100)	0	0	0	0	0	0	0	2
Poland	0	0	0	0	0	1 (14)	6 (86)	0	7
Uruguay	1 (13)	0	0	0	0	2 (25)	5 (63)	0	8
ND, United States	0	1 (33)	0	0	0	1 (33)	1 (33)	0	3
Total	32	3	3	4	7	14	38	26	127
Total (%) ^c	25	2	2	3	6	11	30	21	...

^a Virulence groups designated according to the coded triplet nomenclature system of Limpert and Müller (20). Percentage in parentheses represents proportion of the isolates of each designated virulence group in the province or country collected.

^b MB, SK, AB, ON, QC, and ND represent Manitoba, Saskatchewan, Alberta, Ontario, and Quebec provinces in Canada and North Dakota in the United States, respectively.

^c Total percentage represents proportion of the isolates of each designated virulence group in the total of 127 isolates of *B. sorokiniana* evaluated.

tested from Saskatchewan ($n = 9$) and from Manitoba ($n = 75$). Duveiller et al. (9) reported that the probability of detecting an isolate that differs from the others increases with the number of isolates tested, and that this is more likely to occur with isolates from locations distinct from one another.

The small number of isolates collected from cereals other than barley (seven, three, and one from wheat, oat, and rye, respectively) in this study does not allow for a definitive evaluation of host specificity among *B. sorokiniana* isolates. Nonetheless, most of the isolates collected from wheat and oat, and one Australian isolate collected from rye, were weakly virulent on the 12 barley differential lines used in this study and were designated as virulence group 0.0.0.0. Nelson and Kline (23) pointed out that most species of *Helminthosporium* can attack a wide variety of gramineous hosts. In their study, they reported that *Helminthosporium sorokinianum* (syn. *B. sorokiniana*) conidia isolated from barley could infect 13 different gramineous species, including barley, rice, sorghum, and 10 wild relatives. Likewise, Misra (22) stated that *B. sorokiniana* can infect several hosts and, thus, can be transferred from one cereal crop to another. Based on the differential responses of 25 species in 22 genera of the Gramineae, Nelson and Kline (24) found intraspecific variation in the pathogenicity of eight *H. sorokinianum* isolates collected from different regions of Canada and the United States. All eight isolates were pathogenic on barley and sorghum, seven on wheat, and five on rice, but none infected corn. However, Nelson and Kline (23,24) used the term “pathogenic” for any lesions found on host plants and made no attempt to interpret quantitative or qualitative variation (i.e., lesion size and type) representative of the virulence of isolates.

The occurrence of virulence groups such as 0.0.0.0, 5.7.0.0, 5.7.4.0, and 7.7.5.4 in isolates originating from both barley leaves and kernels indicates that tissue specificity is unlikely to occur in aboveground tissues. This is in agreement with Valjavec-Gratian and Steffenson (33), who found no tissue specificity among isolates collected from barley leaves and kernels. Because only one root-derived isolate was evaluated in

this study, no comment can be made regarding specificity of *B. sorokiniana* isolates collected from barley crowns and roots versus aerial tissues. However, the low virulence of this single isolate (group 0.0.0.0), accompanied with evidence of low virulence for the only root-derived isolate of *B. sorokiniana* used in the study of Valjavec-Gratian and Steffenson (33), suggests that further research on tissue specificity between root isolates and isolates from aerial parts of cereal plants is warranted.

The small number of isolates tested from geographical regions outside Canada and the virulence groups identified among these likely do not represent the total variability in the *B. sorokiniana* population in those regions (i.e. in Australia, Poland, Mexico, and so on). Nonetheless, isolates classified in virulence groups 5.7.4.0, 5.7.0.0, and 0.0.0.0 appear to have a wider distribution in the world than isolates of other groups. Based on IRs on Bowman, ND 5883, and ND B112, virulence groups 5.7.4.0 and 5.7.0.0 equate to North Dakota pathotype 1, and virulence group 0.0.0.0 to North Dakota pathotype 0 (33). Our results agree with Valjavec-Gratian and Steffenson (33) and Zhong and Steffenson (37), who also reported the presence of isolates designated as pathotype 1 and 0 in countries other than the United States (i.e., Brazil, Uruguay, Poland, and Canada). Although we did not evaluate any isolates from China, Japan, or New Zealand in this study, the occurrence of pathotypes 1 and 0 in those countries has been reported (33,37).

In our study, the proportion of virulence groups 5.7.4.0 and 5.7.0.0 was 30 and 11%, respectively. If isolates of group 7.7.5.4 (with relatively close virulence patterns to isolates of groups 5.7.4.0 and 5.7.0.0) are added, the proportion with virulence similar to North Dakota pathotype 1 becomes 62%. In contrast, the proportion of isolates of group 0.0.0.0 was 25%. This also was the case in Australia, where Meldrum et al. (21) found that percentage of pathotypes 177, 377, and 737, corresponding to North Dakota pathotype 1, was 59%, and a relatively smaller proportion (35%) of the isolates was similar to North Dakota pathotype 0. However, our findings are in contrast to those of Val-

javec-Gratian and Steffenson (33), who found a very high proportion of pathotype 0 (68%), and a very low proportion of pathotype 1 (9%), among 22 isolates of *B. sorokiniana* collected from different parts of North Dakota. In addition, isolate ND93-1 (North Dakota pathotype 0) exhibited a virulence pattern completely different from that of low-virulence isolates (group 0.0.0.0) in our study, but similar to that of isolates of group 5.7.0.0, the equivalent of North Dakota pathotype 1.

The differences found across studies (above) may be due to a number of factors: the inoculation methods, inoculation conditions, genetic differences in seed stocks, or experimental error among raters. Duveiller et al. (10) demonstrated that measuring *B. sorokiniana* pathogenicity at the seedling stage is extremely sensitive to experimental conditions. Duveiller et al. (9) also stated that inoculum calibration and an unequal amount of inoculum sprayed on the leaves can be two major sources of experimental error when evaluating *B. sorokiniana* pathogenicity at the seedling stage. The different reaction spectrum produced by isolate ND93-1 in our study also could have resulted from an error in the labeling of the isolate cultures at the original (T. Fetch, *personal communication*) or destination laboratories.

Isolates designated as virulence groups 7.7.7.5, 7.7.5.1, and 6.3.5.0 were collected only in Manitoba. These can be regarded as new virulence groups of *B. sorokiniana* based on their virulence specificity on the differential lines in this study. Their common attribute was an intermediate level of virulence (usually rated as an IR of 5, and rarely as 4 or 6) on differential line ND 5883, compared with groups 7.7.5.4, 5.7.4.0, and 5.7.0.0 that had a higher virulence (usually an IR of 8) on ND 5883. The other characteristic of isolates of these three groups was their higher virulence on ND B112 and its derivatives, Bowman, Robust, and Stander, compared with that of groups 5.7.4.0 and 5.7.0.0; however, their virulence on these differential lines was similar to that of isolates of virulence group 7.7.5.4. None of the *B. sorokiniana* isolates collected in Manitoba prior to 2002 had the same virulence pattern as isolates in these groups. This suggests that these virulence groups may have evolved

Table 3. Number and percentage of 127 isolates of *Bipolaris sorokiniana* collected from different host plants or plant parts assigned to eight virulence groups

Host source	No. per virulence group (%) ^a								Total
	0.0.0.0	6.0.0.0	6.3.5.0	7.7.5.1	7.7.7.5	5.7.0.0	5.7.4.0	7.7.5.4	
Seed, barley	2 (11)	0	0	0	0	2 (11)	9 (50)	5 (28)	18
Leaf, wheat	7 (70)	0	0	0	0	0	1 (10)	2 (20)	10
Leaf, rye	1 (100)	0	0	0	0	0	0	0	1
Leaf, oat	3 (60)	0	0	0	0	1 (20)	0	1 (20)	5
Leaf, barley	15 (17)	3 (3)	3 (3)	4 (5)	7 (8)	9 (10)	27 (31)	18 (21)	86
Crown, barley	1 (100)	0	0	0	0	0	0	0	1
Unknown	3 (50)	0	0	0	0	2 (33)	1 (17)	0	6

^a Virulence groups designated according to the coded triplet nomenclature system of Limpert and Müller (20). Percentage in parentheses represents proportion of the isolates of each virulence group collected from different host plants or plant parts.

recently or that their frequency previously was too low to be readily detected in the population. Although the frequency of these virulence groups was only 14% of the total of 75 isolates collected in Manitoba, they composed 32% of the 43 isolates of *B. sorokiniana* collected in 2002. The isolates were collected primarily from central regions of Manitoba in 2002, but a few were collected from western regions of the province during the annual barley leaf spot disease survey that year (A. Tekauz, unpublished). Additional collections from western and other parts of Manitoba should be made to determine the extent of the occurrence of these isolates of unique virulence.

Isolates designated as group 6.0.0.0 in this study can be equated to North Dakota pathotype 2 (33). Excluding isolate ND90Pr, only two isolates collected in Manitoba were classified as such. Fetch and Steffenson (11) and Valjavec-Gratian and Steffenson (33) documented a markedly higher virulence in isolates of pathotype 2 on cv. Bowman and two-rowed derivatives of Bowman in North Dakota. The sensitivity of the Canadian two-rowed cultivar CDC Bold to isolates of group 6.0.0.0 likewise was detected in this study. CDC Bold was developed from the cross SB88403 × Tyra, where accession SB88403 is a line from the University of Saskatchewan, Crop Development Centre, Canada with the pedigree of Deuce × Bowman (*B. Rossnagel, personal communication*). Based on a genetic study of the cross Bowman × ND 5883, a clear gene-for-gene interaction between line ND 5883 and isolate ND90Pr (pathotype 2) was identified and a single recessive gene in line ND 5883 conferred the resistance to isolate ND90Pr (34). It may be that a dominant allele from Bowman at the same locus possibly encodes for a product (i.e., receptor) that cannot recognize the specific elicitor released by isolate ND90Pr. If true, caution is warranted when using the cv. Bowman in crosses in the regions where isolates of group 6.0.0.0 (North Dakota pathotype 2) predominate.

Of the 22 isolates of *B. sorokiniana* collected from North Dakota, 23% were classified as pathotype 2 (33) whereas, in our study, this pathotype (virulence group 6.0.0.0) composed only 3% of isolates collected from Manitoba. This suggests that isolates of this pathotype likely are more prevalent and widely distributed in North Dakota than in Manitoba. This type of virulence was not detected among *B. sorokiniana* isolates from other Canadian provinces or from other countries. This finding is in agreement with that of Valjavec-Gratian and Steffenson (33) and Zhong and Steffenson (37), who did not detect this pathotype among isolates collected from other U.S. states or countries. Although Gamba and Estramil (13) reported a virulence profile similar to that of

North Dakota pathotype 2 among Uruguayan isolates of *B. sorokiniana*, none of the eight isolates from Uruguay tested in this study or the five Uruguayan isolates tested by Zhong and Steffenson (37) displayed the same virulence pattern as isolates of group 6.0.0.0 (North Dakota pathotype 2). Therefore, it is probable that virulence group 6.0.0.0 (North Dakota pathotype 2) of *B. sorokiniana* is specific to North Dakota and Manitoba regions where cv. Bowman or its derivatives are widely grown. Testing of advanced barley lines developed from a Bowman pedigree with an isolate of virulence group 6.0.0.0 would be prudent before their release as a new barley cultivar. This is especially pertinent for Manitoba and North Dakota, where the presence of the “susceptible” Bowman gene could result in substantial crop damage from isolates of this virulence group.

In contrast, breeding for resistance against the predominant virulence groups of *B. sorokiniana*, also having higher virulence, likely will be a more difficult task than breeding for virulence group 6.0.0.0 (North Dakota pathotype 2) resistance. These higher virulence groups were much more frequent in western Canada than isolates of either groups 0.0.0.0 or 6.0.0.0 (North Dakota pathotypes 0 and 2, respectively). Our results demonstrated a great diversity in the virulences of isolates other than those in groups 0.0.0.0 and 6.0.0.0. This diversity does not lend itself to categorize all of these isolates in a simple unique virulence group (i.e., pathotype 1). Using an IR of 5 as the cut-off point (as applied by Valjavec-Gratian and Steffenson [33,34] and Zhong and Steffenson [37]) to differentiate among low-virulence and high-virulence responses, the number of virulence groups of *B. sorokiniana* in this study would increase to 32 (*data not shown*). This can be attributed to the many intermediate-level IRs induced on the differential lines by most of these virulent isolates. Beginning in the early 1990s, and in conjunction with the emergence of pathotype 2 in North Dakota, research groups accepted that “virulence” (i.e. the gene-for-gene model) was implicit in this particular pathosystem, and used an arbitrarily chosen cut-off point of 5 (33,34,37) or 4 (21) to distinguish between resistant and susceptible phenotypes. Here, we chose to use a cut-off point of 4.5 to analyze our data using the classical approach. However, because of the continuous range of infection phenotypes, irrespective of the cut-off point used, this likely still would not provide the best analysis of the interactions occurring.

In summary, our findings demonstrate that complex interactions exist between many *B. sorokiniana* isolates and their barley host, and that this requires additional evaluation. The detection of a continuous range of IRs of 2 to 9 on different

barley genotypes induced by virulent isolates, together with frequently observed intermediate IRs of 4 and 5 among genotypes, suggest that such isolates may not demonstrate a distinct gene-for-gene interaction with differential barley lines. Although the classical method of pathotype identification can be exploited to analyze interactions in the barley-*B. sorokiniana* pathosystem, our results demonstrate that, in a pathosystem with primarily quantitative variation, the virulence group or pathotype designation may be largely artificial, limiting the validity of conclusions. In this article, we have demonstrated that qualitative analysis is inadequate for analyzing this host-pathogen system, although a specific gene-for-gene-like interaction does occur between isolates of pathotype 2 and cv. Bowman. Therefore, the virulence of *B. sorokiniana* isolates may be better analyzed using quantitative approaches to differentiate among them and to clarify their relatedness. An analysis of the data using several quantitative approaches and how these compare with the qualitative gene-for-gene results described here will be presented in a follow-up article. The term “aggressiveness,” which depicts the amount of disease produced in a particular susceptible host-pathogen interaction (1), may be preferred to “virulence” to determine the pathogenicity of *B. sorokiniana* isolates quantitatively. As such, the use of the most aggressive isolates in specific regions or provinces is desirable to provide the most effective screening of lines in barley breeding programs.

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