# Resistance of Barley to *Puccinia graminis* f. sp. *tritici* and *Puccinia graminis* f. sp. *secalis*

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## ABSTRACT

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Seedlings of barley cultivars possessing the *T*-gene developed low weighted infection types that indicated the plants were resistant when infected with races 113-RTQ, 151-QSH, and 29-HJC of *Puccinia graminis* f. sp. *tritici*. However, four cultivars that lack the *T*-gene had low weighted infection types that were not significantly different from those displayed by the *T*-gene cultivars to either or both race 113-RTQ and 151-QSH. This suggests that these cultivars possess resistance gene(s) that are different from the *T*-gene. Race 29-HJC most clearly distinguished the cultivars with the *T*-gene from those without it. When barleys were infected with race HQ of *P. graminis* f. sp. *secalis*, seedlings of most cultivars developed relatively low weighted infection types; Heitpas-5 and Steptoe had the highest weighted infection types. Barleys possessing the *T*-gene could not be distinguished from those cultivars without the gene to this race of the rye stem rust pathogen. In the field, cultivars with and without the *T*-gene were tested with a composite of races 113-RTQ, 151-QSH, 29-HJC, 151-QFB, and 15-TNM of *P. graminis* f. sp. *tritici*. Terminal rust severities and the type of uredia present on plants indicated that barleys with the *T*-gene were moderately resistant to moderately susceptible to this composite of races. In the group of cultivars lacking the *T*-gene, Heitpas-5, and Black Hull-less were moderately susceptible, whereas the other cultivars were susceptible. In field tests with race HQ of *P. graminis* f. sp. *secalis*, Black Hull-less was resistant and Valkie, Hispont, and Heitpas-5 were moderately resistant. The cultivars with the *T*-gene were susceptible to moderately susceptible and could not be distinguished from some barleys that lack the *T*-gene.

*Additional key words*: disease resistance, rye stem rust, wheat stem rust.

During the past 45 yr, the barley (*Hordeum vulgare* L.) cultivars grown in the upper Mississippi Valley have been considered to be resistant to *Puccinia graminis* Pers. f. sp. *tritici* (9) because they have developed little or no rust, presumably because they have carried the *T*-gene derived from Peatland (CI 5267) and Chevron (CI 1111) (8,11). However, starting in the 1970s, traces of stem rust were found on some of the newer barley cultivars grown in Minnesota and North Dakota, whereas the older cultivars Larker and Chevron remained free of stem rust. This rust was caused by races of *P.g.* f. sp. *tritici* and *P.g.* f. sp. *secalis*.

The occurrence of stem rust on the newer barley cultivars suggested that they might not possess as high a degree of resistance to *P.g.* f. sp. *tritici* as the older cultivars. This seemed possible because, even though the procedures used for developing these cultivars always involved the use of parents that possessed the *T*-gene, the progenies have not been thoroughly screened in stem rust nurseries. We did not consider it likely that the pathogen had become more virulent because isolates obtained from barley have

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elonged to the races found on wheat and the races on wheat and barley have been stable for many years.

The newer barley cultivars might be susceptible to *P.g.* f. sp. *secalis*. This pathogen has largely been ignored in barley improvement programs.

This study was undertaken to provide information about the development of stem rust on *T*-gene and non *T*-gene barley cultivars infected with races of *P.g.* f. sp. *tritici* and *P.g.* f. sp. *secalis*.

## MATERIALS AND METHODS

**Seedling tests.** Studies were made in the greenhouse with Chevron (CI 1111), Larker (CI 10648), 80-TT-29 (CI 16129), and Morex (CI 15773), all of which possess the *T*-gene, and Hispont (CI 8828), Black Hull-less (CI 666), Heitpas-5 (CI 7124), 80-tt-30 (CI 16130), and Steptoe (CI 15229) which lack the *T*-gene. Larker, which has been grown for many years in Minnesota and North Dakota, is representative of older resistant cultivars whereas Morex is representative of the newer cultivars. Chevron is a source of the *T*-gene. Lines 80-TT-29 and 80-tt-30 are near-isogenic except for the presence of the *T*-gene. They were produced from selections from the F29 generation of the cross (Wisconsin Barbless × Chevron) × Composite 11 (J. G. Moseman, *personal communication*). Plants of the test entries were grown in vermiculite in square plastic pots (7 × 7 × 5 cm; 3–8 plants per pot) in a greenhouse at approximately 20 C. When day length was less than 12 hr/day, additional fluorescent light (11,000 lux) was provided. Plants were fertilized after emergence with a formulation of 23-19-17 of N-P-K applied at 0.3 g per pot.

Races 113-RTQ, 151-QSH, 15-TNM, 29-HJC, and 151-QFB of *P.g.* f. sp. *tritici* were studied. They have been some of the most common or virulent races on barley during the last 5 yr. Race HQ of *P.g.* f. sp. *secalis* was also studied because it was a virulent isolate collected from barley. The races of *P.g.* f. sp. *tritici* were increased on seedlings of Line E wheat, and the race of *P.g.* f. sp. *secalis* was increased on Prolific (CI 26) rye. Urediospores were collected, placed in a desiccator (20% relative humidity) at 6 C for 3 days and then at −46 C in polyethylene bags until needed for inoculation. When inoculations were made, all spore lots had a germination percentage over 85%. The racial purity of the races of *P. graminis* was verified in all experiments as described by Roelfs and McVey (10) and Steffenson et al (15).

The fully expanded primary leaves of plants (about 7 days after planting) were inoculated with urediospores suspended in a light-weight mineral oil (2.46 ± 0.05 mg urediospores in 8 ml of oil). After inoculation, the plants were placed in a dark dew chamber at 18 ± 1 C for about 15 hr. Then the chamber was illuminated with fluorescent tubes (10,000 lux), and the temperature was allowed to rise to 27 C and the chamber door was opened to facilitate slow drying of the plant surfaces. When the plants were dry, they were again fertilized (0.3 g per pot of 23-19-17, N-P-K) and placed in a greenhouse at about 18 C or in a growth chamber at 25 C with a relative humidity of over 95%. Illumination was supplied by fluorescent and incandescent lamps (22,600 lux) for 13 hr/day. The experiment was arranged in a completely randomized design with four replicates for each race × cultivar treatment combination.

At 18 and 25 C, mesothetic reactions (a mixture of infection types on a leaf) were noted on all barley cultivars with all races of the pathogens. Two weeks after inoculation, the relative frequency of the individual infection types on the plants was recorded. The scoring of infection types was primarily on the basis of uredium size (Table 1) similar to the system of Miller and Lambert (3). The mesothetic reactions made it difficult to assess differences between entries known to be resistant and susceptible in the field because the cultivars had infection types in common. However, this difficulty was overcome by expressing the disease reactions of the barley entries as a weighted infection type. This was calculated by coding the infection types present (Table 1), ranking them according to relative frequency, and calculating a weighted mean (Table 2).

Data were evaluated by analysis of variance. Differences among treatment means were tested for significance by using Tukey's (13) procedure and the expanded Studentized Q tables of Miller (4).

**Field tests.** The same barley cultivars used in the seedling tests were studied plus Manker (CI 15549) and Beacon (CI 15480) which possess the *T*-gene and Valkie (CI 5748) and Hiproly (CI 3947) which do not. The thirteen entries were planted at St. Paul and Rosemount, MN, during the summers of 1981 and 1982. At both locations, the test entries were planted in a random sequence in hills (10–15 seeds per hill) spaced 32 cm apart. The plot was bordered by susceptible Baart (CI 1697) wheat at St. Paul and Prolific rye at Rosemount. A randomized complete block design was used with each row of test hills constituting a block. There were four blocks in the experiment in 1981 and six in 1982.

A composite of races 113-RTQ, 151-QSH, 29-HJC, 151-QFB, and 15-TNM of *P.g.* f. sp. *tritici* was used to inoculate plants at St. Paul and race HQ of *P.g.* f. sp. *secalis* was used at Rosemount. Inoculum was prepared by mixing 0.2 g of urediospores of each of the five races of *P.g.* f. sp. *tritici*. Plants in the border rows were then inoculated by injecting the stock suspension of 1.0 g of the urediospore mixture in 5.0 liters $H_2O$ into the stems with the aid of a hypodermic syringe before the first node of the stem was visible on most of the test entries. Two weeks later, the plants in the border rows were again inoculated with the urediospore mixture (0.2 mg spores per milliliter of lightweight mineral oil at a rate of about 1.6 ml of oil per meter of row) with a backpack sprayer.

The same procedure was used to inoculate plants with the race of *P.g.* f. sp. *secalis*.

Wheat cultivar McNair 701 (CI 15288), which is immune to races of *P.g.* f. sp. *secalis* and susceptible to the prevalent races of *P.g.* f. sp. *tritici*, was used to detect *P.g.* f. sp. *tritici* in the rye stem-rust nursery. Similarly, cultivar Prolific rye, which is susceptible to races of *P.g.* f. sp. *secalis* but resistant to *P.g.* f. sp. *tritici*, was used to detect *P.g.* f. sp. *secalis* in the wheat stem-rust nursery. At both nurseries and in both years, contamination was nil. This was also borne out when the racial identity of 40 isolates from both nurseries in each year was determined. All rust collections yielded only the races of the pathogens that were originally placed in the nurseries.

The severity of stem rust was evaluated by using the modified Cobb scale (7) when most entries were in the dough stage of growth.

TABLE 1. Description of the infection type code for rating seedlings of barley for resistance to *Puccinia graminis*

| Infection type code | Infection type | Description |
|---|---|---|
| 0 | 0 | Immune: no visible indication of infection. |
| 0.5 | ; | Hypersensitive flecks: no visible sporulation. |
| 1 | 1 | Minute uredia: (not over 1 mm in diameter) surrounded by necrotic areas or chlorosis. |
| 2 | 2 | Small uredia: (from 1 to 2 mm in diameter) associated with chlorosis and sometimes necrosis. |
| 3 | 3 | Medium uredia: (from 2 to 3 mm in diameter) associated with chlorosis. |
| 4 | 4 | Large uredia: (over 3 mm in diameter) often associated with chlorosis. |

TABLE 2. An example showing the calculation of weighted infection type[a] for barley seedlings displaying the mesothetic response (3,4,;,1) to infection by *Puccinia graminis*

| Rank[b] | | Infection type code (ITC)[c] | Rank × ITC |
|---|---|---|---|
| 4 | × | 3 = | 12 |
| 3 | × | 4 = | 12 |
| 2 | × | 0.5 = | 1 |
| 1 | × | 1 = | 1 |
| 10 | | 26/10 = 2.6 weighted infection type | |

[a] General equation: $[\Sigma(\text{Rank} \cdot \text{ITC})]/\Sigma\ \text{Rank}$ = weighted infection type.
[b] The most prevalent infection type is assigned the highest rank value and the least prevalent infection type, the lowest rank value.
[c] Infection type code is listed in Table 1.

In addition, the host response of each entry was estimated according to the size of the uredia and the presence of chlorosis around uredia on the plants. Statistical evaluation of the data was based on an analysis of variance and Tukey's procedure (13) for testing the significance of differences among treatment means. For statistical analysis, the data were transformed by using the Freeman-Tukey (16) transformation to correct for nonconstant variance.

## RESULTS

**Seedling tests.** The tests at 18 C failed to distinguish between cultivars known to be resistant or susceptible in the field because either rust lesions did not develop or the plants gave a low mesothetic reaction (a mixture of infection types with those indicative of a resistant reaction predominating). Thus, it was not possible to distinguish among the cultivars.

At 25 C, all plants gave higher mesothetic reactions than at 18 C; however, because of the gradations in the infection types, it was difficult to judge whether the cultivars were resistant or susceptible on that basis. Therefore, as mentioned earlier, weighted infection types were used to indicate the reactions of the cultivars (Table 3).

TABLE 3. Weighted infection types of barley seedlings with and without the *T*-gene and infected with three races of *Puccinia graminis* f. sp. *tritici* and a race of *P. graminis* f. sp. *secalis* in the greenhouse at 25 C

| Cultivar | Possess *T*-gene | *P. g.* f. sp. *tritici* races | | | *P. g.* f. sp. *secalis* race |
|---|---|---|---|---|---|
| | | 113-RTQ | 151-QSH[y] | 29-HJC | HQ |
| Chevron | + | 0.83[z] | 0.15 a | 0.00 a | 1.18 a |
| Larker | + | 1.10 a | 0.28 a | 0.00 a | 1.43 abc |
| 80-TT-29 | + | 1.23 a | 0.45 ab | 0.05 a | 1.38 ab |
| Hispont | − | 1.30 a | 0.40 a | 2.70 c | 1.40 ab |
| Black Hull-less | − | 1.38 a | 1.35 bc | 1.63 b | 1.05 a |
| Morex | + | 1.75 ab | 0.30 a | 0.28 a | 1.08 a |
| Heitpas-5 | − | 2.53 bc | 0.50 ab | 2.53 bc | 2.30 c |
| 80-tt-30 | − | 2.55 bc | 1.00 ab | 2.50 bc | 1.30 ab |
| Steptoe | − | 2.90 c | 2.25 c | 3.15 c | 2.18 bc |

[y] The responses with races 5-TNM and 151-QFB were similar to those shown for race 151-QSH.

[z] Values are means of four replicates. Within the columns means with different letters are significantly different, $P = 0.05$, according to Tukey's procedure.

In tests with *P.g.* f. sp. *tritici*, race 113-RTQ was the most virulent race on cultivars that possessed the *T*-gene (Table 3). On Morex infected with race 113-RTQ and on 80-TT-29 infected with race 151-QSH, the weighted infection types were larger than on the other *T*-gene cultivars but the difference was not significant. However, the two cultivars infected with these two races could not be distinguished statistically from the susceptible isoline 80-tt-30. Race 29-HJC was the most useful of the three races tested for detecting the presence of the *T*-gene since cultivars with and without the gene were well separated (Table 3). On cultivars that lacked the *T*-gene, the weighted infection types varied significantly with the individual races, indicating that these cultivars possess resistance genes other than the *T*-gene. For example, when the cultivars without the *T*-gene were infected with race 113-RTQ, the weighted infection types on Hispont and Black Hull-less did not differ significantly from those on Chevron, the resistant check, though they were numerically larger. Also, when these cultivars were infected with race 151-QSH, the weighted infection types on Hispont, Heitpas-5, and 80-tt-30 did not vary significantly from those on Chevron. The responses with races 15-TNM and 151-QFB were similar to those with race 151-QSH. When the cultivars lacking the *T*-gene were infected with race 29-HJC, other possible resistance genes were not detected except perhaps in Black Hull-less where the weighted infection type was an intermediate one (Table 3).

In tests with *P.g.* f. sp. *secalis*, Black Hull-less was most resistant and Heitpas-5 was most susceptible (Table 3). Among the cultivars which lack the *T*-gene, Black Hull-less, 80-tt-30, and Hispont had significantly lower weighted infection types than Heitpas-5. Cultivars with the *T*-gene had relatively low weighted infection types, and no significant differences were detected among this group. This race of the rye stem rust pathogen did not differentiate among cultivars on the basis of the *T*-gene.

**Field tests.** More stem rust, due to *P.g.* f. sp. *tritici*, developed in 1981 than in 1982 at St. Paul, probably because the weather in 1982 was relatively cool and dry when the disease was developing. In 1981, cultivars with the *T*-gene were moderately resistant to moderately susceptible and the terminal rust severity was low (Table 4). Among cultivars with the *T*-gene, terminal rust severity was significantly greater on Beacon than on Chevron and 80-TT-29. Four of the seven cultivars without the *T*-gene were susceptible, but Black Hull-less, Heitpas-5, and 80-tt-30 had some moderately susceptible reactions. Terminal disease severity in five of these cultivars was more than 30%, the exceptions being in Black Hull-

TABLE 4. Terminal rust severity and host response of selected barley cultivars to a composite of races 113-RTQ, 151-QSH, 29-HJC, 151-QFB, and 15-TNM of *Puccinia graminis* f. sp. *tritici* in the field, 1981 and 1982

| Cultivar | Possess *T*-gene | Terminal rust severity and host response | | | |
|---|---|---|---|---|---|
| | | 1981 | | 1982 | |
| Chevron | + | 1.0[y]a | MR-MS[z] | 0.3 a | R-MR |
| 80-TT-29 | + | 1.9 a | MR-MS | 0.6 ab | MR-R |
| Morex | + | 4.5 ab | MS-MR | 1.2 ab | MR-MS |
| Larker | + | 5.3 ab | MR-MS | 0.5 ab | MR-R |
| Heitpas-5 | − | 7.5 ab | MS-S | 1.6 ab | MR-MS |
| Manker | + | 8.8 ab | MS-MR | 0.8 ab | MR-MS |
| Black Hull-less | − | 12.5 abc | MS | 0.8 ab | MR-MS |
| Beacon | + | 17.5 bcd | MS-MR | 0.9 ab | MR-R |
| Valkie | − | 35.0 cde | S | 3.0 bc | S-MR |
| Hispont | − | 40.0 de | S | 2.0 abc | S-MR |
| 80-tt-30 | − | 42.5 def | S-MS | 6.5 c | MS-S |
| Steptoe | − | 52.5 ef | S | 21.7 d | MS-S |
| Hiproly | − | 77.5 f | S | 38.3 e | S-MS |

[y] Values are Cobb's percent rust severity and are the means of four replicates in 1981 and six replicates in 1982. Within columns, means with different letters are significantly different, $P = 0.05$, according to Tukey's procedure.

[z] Host responses: S = large uredia (>3 mm long) without chlorosis, MS = medium uredia (2–3 mm long) often associated with chlorosis, MR = small uredia (1–2 mm long) associated with much chlorosis, and R = minute uredia (<1 mm long) often surrounded with necrosis.

TABLE 5. Terminal rust severity and host response of selected barley cultivars to race HQ of *Puccinia graminis* f. sp. *secalis* in the field, 1981 and 1982

| Cultivar | Possess *T*-gene | Terminal rust severity and host response | | | |
|---|---|---|---|---|---|
| | | 1981 | | 1982 | |
| Black Hull-less | − | 2.8[y]a | R-MS[z] | 2.0 a | R-MS |
| Valkie | − | 17.5 b | MR-MS | 11.7 bc | MS-S |
| Heitpas-5 | − | 20.0 b | MS-MR | 4.8 ab | MR-MS |
| Hispont | − | 22.5 bc | MS-MR | 22.2 cd | MR-MS |
| 80-TT-29 | + | 35.0 bcd | S | 31.7 de | MS-S |
| 80-tt-30 | − | 35.0 bcd | S | 40.0 efg | MS-S |
| Larker | + | 42.5 cde | S | 33.3 def | MS-S |
| Chevron | + | 47.5 de | S | 38.3 efg | MS-S |
| Morex | + | 47.5 de | S | 41.7 efg | MS-S |
| Steptoe | − | 55.0 de | S | 53.3 gh | MS-S |
| Manker | + | 57.5 de | S | 48.3 efg | S-MS |
| Beacon | + | 67.5 e | S | 50.0 fgh | MS-S |
| Hiproly | − | 67.5 e | S | 70.0 h | S |

[y] Values are Cobb's percent rust severities and the means of four replicates in 1981 and six replicates in 1982. Within the columns means with different letters are significantly different, $P = 0.05$, according to Tukey's procedure.

[z] Host responses: S = large uredia (> 3 mm long) without chlorosis, MS = medium uredia (2–3 mm long) often associated with chlorosis, MR = small uredia (1–2 mm long) associated with much chlorosis, and R = minute uredia (<1 mm long) often surrounded with necrosis.

less and Heitpas-5 which had terminal rust severities that were not significantly different from cultivars with the *T*-gene. Since the epidemic developed poorly in 1982, it was difficult to draw conclusions about the resistance of the cultivars; but, in general, differences between cultivars with and without the *T*-gene could be seen with the same two exceptions: Black Hull-less and Heitpas-5.

Black Hull-less was the cultivar most resistant to *P.g.* f. sp. *secalis* in both years whether resistance was measured by terminal rust severity or by host response (Table 5). Heitpas-5, Hispont, and Valkie had relatively low terminal rust severities and moderately resistant host responses. All other cultivars had susceptible to moderately susceptible reactions and relatively high terminal rust severities. The *T*-gene was ineffective against this race of *P. g.* f. sp. *secalis* as specifically exemplified by the reaction of the near-isogenic lines.

## DISCUSSION

Mesothetic responses were frequently observed in seedlings of barley inoculated with *P. graminis* making it difficult to distinguish the resistance of the cultivars by use of the classical infection type method used in wheat (12). Miller and Lambert (3) and Patterson et al (6) also encountered this difficulty. The weighted infection type was useful for classifying plants into resistant and susceptible categories. The weighted infection type was calculated from the kind and relative frequency of individual infection types observed in the mesothetic reaction.

In studies with seedlings at 18 C, mostly low mesothetic reactions were found whereas at 25 C, higher mesothetic reactions resulted. We conclude that the reaction of some barleys to stem rust is temperature sensitive and that this characteristic may tend to suppress rust development in cool growing areas.

The cultivars tested as seedlings in this study produced mesothetic responses to all cultures of *P. graminis*. Therefore, all of the entries probably possess some degree of seedling resistance to most isolates of the pathogen as was also reported by Patterson et al (6). Indeed, when compared to susceptible wheats like Line E and McNair 701, none of the barleys tested were completely susceptible.

Race 29-HJC best distinguished cultivars that possess the *T*-gene from those that do not, and this race could be useful for detecting the presence of this gene in seedlings. Hispont, Black Hull-less, and Heitpas-5, which lack the *T*-gene, appeared to possess genetic factor(s) for stem rust resistance that are different from the *T*-gene. This also appeared to be true for the susceptible isoline 80-tt-30 infected with race 151-QSH. Moseman (5) also reported that Hispont was resistant to some cultures of *P. graminis*. In addition, Heitpas-5 has been reported to possess a genetic factor governing stem rust resistance that was different from the *T*-gene carried by Chevron (6). Studies on the inheritance of resistance in cultivars that possess genes for stem rust resistance that are different from the *T*-gene could provide useful information for breeding programs.

In the field, barley cultivars with the *T*-gene were distinguished from most without it when tested with a composite of races of *P.g.* f. sp. *tritici*. Among cultivars with the *T*-gene, Chevron was the most resistant but only compared with Beacon was this difference statistically significant. The genetic mechanisms that account for Beacon being more susceptible than Chevron are not known. Black Hull-less and Heitpas-5 both possess some adult plant resistance to *P.g.* f. sp. *tritici* even though they do not possess the *T*-gene.

The *T*-gene is unique among stem rust resistance genes in that it has been effective for a long time in spring barley cultivars grown in the United States. In contrast, in wheat, during the same period, a number of resistant cultivars have become susceptible when new races of the wheat rust pathogen have appeared. A number of factors may have contributed to this longevity of stem-rust resistance in barley: most seedlings of barley that possess the *T*-gene appear to possess some resistance to the wheat and rye stem-rust pathogens; barley is usually planted early in the season when the weather is cool which suppresses stem rust development; the inoculum from the southern United States reaches the barley late in the season when plants are beginning to mature; barley is protected from a local increase of wheat stem rust inoculum because the wheat cultivars of the region are resistant to stem rust and epidemics of rye stem rust in barley do not develop because inoculum is limited and there is little rye planted in the area; and one or more genetic factors in addition to the *T*-gene may control the reaction to stem rust as indicated by Lejeune (2) who used a cross with Chevron.

The agreement between the weighted infection type of seedlings infected with race 29-HJC of *P.g.* f. sp. *tritici* in the greenhouse and the terminal rust severity to a composite of races in the field was generally good. An exception was Heitpas-5, which had a high weighted infection type to race 29-HJC in the greenhouse, but a relatively low terminal rust severity in the field. In contrast, the agreement between the weighted infection type of seedlings infected with *P.g.* f. sp. *secalis* in the greenhouse and the terminal rust severity in the field was not close. Most cultivars were resistant as seedlings but susceptible in the field. This confirms the work of Johnson and Buchannon (1) who advocated evaluating cultivars for resistance to the rye stem-rust pathogen in the field.

Black Hull-less possesses a high degree of resistance to *P.g.* f. sp. *secalis* in the field (Table 5) which agrees with the report of Johnson and Buchannon (1). The resistance of Black Hull-less to the race used in this study is governed by a single recessive gene in adult plants (14). Heitpas-5, Hispont, and Valkie also have some resistance to *P.g.* f. sp. *secalis*, but the inheritance of this resistance was not studied. The other barleys tested, including those with the *T*-gene, were susceptible to *P.g.* f. sp. *secalis*. Johnson and Buchannon (1) also found that cultivars with the *T*-gene were susceptible to *P.g.* f. sp. *secalis* in the field.

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