A Method for Field Evaluation of Wheats for Low Receptivity to Infection by *Puccinia graminis* f. sp. *tritici*

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ABSTRACT

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Uredospores of *Puccinia graminis* f. sp. *tritici* in light mineral oil were applied uniformly with a portable mist blower to a linear arrangement of rows of susceptible wheat accessions. Large differences in amounts of primary infection caused by uniform inoculations with race 15B-2 were consistently detected between the highly receptive wheat line Purdue 5481C1 and the less receptive cultivars Thatcher, Sentry, and Idaed 59. Receptivity changed from high to low with increasing age in Thatcher and Sentry, and from low before anthesis to high afterwards on leaf blades of Idaed 59. Primary uredia were larger on juvenile plants than on older plants of Marquis, Lee, Thatcher, Sentry, and Idaed 59, but were consistently large on Purdue 5481C1. Low receptivity in Idaed 59 appears to be governed by a single dominant gene linked or identical to *Sr Tt-1*, and in Thatcher by two recessive complementary genes. Lee appears to possess a third recessive gene for low receptivity that reacts cumulatively with the two complementary genes in Thatcher to yield lines of very low receptivity.

Additional key words: wheat stem rust, general resistance, slow rusting, adult plant resistance.

The existence of wheat (*Triticum aestivum* L.) cultivars that rust slowly under attack by virulent races of *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. has been known for years (2,4). This slow increase of stem rust is suspected to be due to general resistance. Although similar resistances are used successfully for control of rusts in corn and late blight in potatoes, use of the slow rusting resistances to stem rust in wheat breeding programs has been hampered by the lack of a simple way to evaluate this characteristic. Discontinuities in inoculum densities, differences in racial composition of inocula, and variation in environmental factors often obscure slow-rusting characters in conventional rust nurseries.

A reduced number of sporulating infections is one of the conspicuous characters associated with general resistance against the corn rusts (5) and potato late blight (16). Fast- and slow-rusting wheats differ in numbers of primary uredia produced following uniform inoculations with the stem rust pathogen in the field (1,3,14). Mont and Rowell (11) found that some wheats differed in the receptivity to infection by a virulent race; ie, they differed in the numbers of uredia produced but not in the number of penetrations per unit of plant surface. The receptivity characteristic may be useful for rapid screening of wheat accessions for slow-rusting characters. This paper describes a field method for assessing differences in receptivity to infection among wheats and presents evidence about the inheritance of characters affecting this trait. A preliminary report of these studies has been published (12).

MATERIALS AND METHODS

Six wheat cultivars were tested. Purdue 5481C1 (P5481C1) was used as a reference cultivar because it had been an extremely fast-rusting wheat in epidemiological studies of stem rust at Minnesota since 1963. Marquis (CI 3641), Thatcher (CI 10003), Lee (CI 12488), and Sentry (CI 13102) previously had been shown to differ in number of initial infections from field inoculations with race 15B (1,3). Idaed 59 (CI 13631) was an extremely slow-rusting cultivar in our inoculated spring-wheat-rust nurseries.

Inoculum of isolate number 65-39-2 of race 15B-2 (avirulence/virulence formula *Sr6,8,9a,9b,13,15,17/Sr5,7b,9d,9e,10,11,12,14,16,Tt-1*) of *P. graminis* f. sp. *tritici* was produced in the greenhouse each spring, and 0.5-g lots of uredospores were stored in sealed polyethylene bags at −46 C for use the following summer. On retrieval, the spores were conditioned by immersing the bags in water at 45 C for 5 min. Germination was tested in a drop of a 50:50 (v/v) mixture of light mineral oil (Soltrol 170, Phillips Petroleum Co., Borger, Texas 79007) and pharmaceutical mineral oil on the surface of 1% purified agar in distilled water. Germination in all trials was 85% or more. The seedling reaction of all test wheats except Thatcher to this isolate in the greenhouse has been considered to be susceptible. Thatcher reacts as moderately susceptible with a mixture of types 3 and 2 at 18–24 C.

For evaluation of receptivity to infection, a suspension of uredospores in light mineral oil was applied uniformly as a mist spray to rows of test plants with a backpack mist-blower. Several modifications were necessary to adapt the mist-blower for this application. The mist-blower used the venturi principal, whereby the air blast atomizes the liquid and the rate of atomization depends upon the diameter of the orifice in the fluid-delivery nozzle. In our equipment an orifice 0.8 mm in diameter delivered 500 ml/1,500 m of row (about 6 L/ha) at an operator speed of 4.9 km hr. Frequent agitation of the spore suspension was necessary to maintain a uniform dispersion at this low rate of delivery. A polyethylene bottle attached to the spray wand was used as the inoculum reservoir to shorten the length of the fluid-delivery tube. During spray application the operator periodically raised the spray wand vertically to shut off the spray, drain the delivery tube, and agitate the spore suspension. Test rows were sprayed uniformly by walking alongside the row at a steady pace with the spray wand aimed toward the plants at a fixed angle.

Entry rows in the test plots were planted in a linear rather than parallel arrangement as in conventional nurseries. All test plots were sprayed 3 wk after planting with 4-*n*-butyl-1,2,4-triazole (Indar, Rohm and Haas Co., Philadelphia, PA 19105) at 0.56 kg/ha. This fungicide is specifically effective against wheat leaf rust (17), and was used for complete control of this disease. Test plants were inoculated before natural stem rust was present or, if it was present, before it exceeded one uredium per 100 tillers. An inoculum concentration of 3 mg/ml was used in trials in which the number of infections was counted, and 6 mg/ml was used in trials in which the number was estimated. Plants in each experiment were inoculated on 3 days in succession so at least one inoculation would be likely to coincide with a favorable infection period. Satisfactory amounts of infection were obtained from 1970 to 1973; the numbers of uredia per leaf on P5481C1 with the low inoculum dose ranged from 10–20 to 50–100 in the different trials. Data on the level of primary infection were recorded 12–14 days later, before secondary spread was apparent.

The amount of primary infection from uniform inoculation of the six wheats was determined experimentally at four plant ages in 1970 and at three ages in 1971 and 1972. In 1970 and 1971, three to four blocks consisting of two replicates of randomized 6-m-long rows of six cultivars were planted on the same day in separate locations remote from each other. In 1970, a block was inoculated individually in the 5th, 6th, 7th, and 8th wk after planting. In 1971, one block was inoculated in the 5th wk, when plants were in the tillering stage; a second block in the 7th wk, at jointing; and a third block in the 9th wk, at heading. In the 1972 test, four replicates of randomized rows of the six cultivars were planted three times at biweekly intervals to yield plants in these three stages of development, and all were then inoculated at one time. Maturation among the oldest plants at the time of inoculation ranged from late anthesis for the early-maturing Idaed 59 to early boot for the late-maturing Sentry. On 20 random tillers in each plot, the number of primary infections were counted on the youngest leaf that had been fully extended at the time of inoculation. Uredia also were counted on the sheath of the sampled leaf in the inoculation trials that had been made at the heading stage. The data for each inoculation trial were subjected to analysis of variance to test the null hypothesis of no difference in counts between the test cultivar and P5481C1. Uredial size was recorded in the numerical scale for the typical uredia associated with the infection types of Stakman et al (15).

For studies of the inheritance of receptivity to infection, reciprocal crosses were made in the greenhouse as follows: P5481C1 with Idaed 59 and Thatcher, and Thatcher with Lee. The single cross Idaed 59/Thatcher also was made. The receptivity to infection of five F_1 plants spaced 15 cm apart was compared with that of five plants of each parent in a field test during 1971. About 500 single seeds from F_1 plants of each cross were space planted 30 cm apart in rows, and the seed was harvested from each F_2 plant in 1972. About 100 seeds from each F_2 plant from the crosses of Idaed 59 with P5481C1, Thatcher with P5481C1, Thatcher with Lee, and Idaed 59 with Thatcher were planted in rows 1.5 m long for evaluation of receptivity in 1973. This test was repeated with each F_2 family planted in hills spaced 0.6 m apart in 1974. No major differences in segregation patterns were observed between the progenies of the reciprocal crosses, so the data were combined for each set of parents. Plot design for each cross consisted of a series of rows 150 m long in which sets of 10 entries of the F_2 families were flanked by an entry of each parental line and an entry of oats to mark each set. The receptivity to infection of each progeny was rated, by comparison with the nearest entries of the parents, as being either similar to the low-receptive parent, similar to the high-receptive parent, distinctly different from either parent, or segregating into a mixture of receptivity types. Chi-square tests were used to determine the probabilities of the segregants observed in the F_2 families fitting hypothetical ratios.

RESULTS

Comparison of receptivity to infection. The test wheats appeared to be less receptive than P5481C1 to infection at one or more stages of development (Fig. 1). Marquis and Lee appeared to be less receptive than P5481C1, but the results with these two cultivars were more variable among trials than were those with the other cultivars. Blades of Marquis had significantly fewer uredia than those of P5481C1, in eight of 10 inoculations. Sheath infection in Marquis was significantly lower than P5481C1 in only one of three trials. Results with Lee were the most inconsistent. Although the number of uredia on blades of Lee was significantly lower than that on blades of P5481C1 in five of 10 inoculations, the differences were not significant in the last inoculation of 1970, all inoculations of 1971, and the first inoculation of 1972. In sheath infection Lee was similar to P5481C1 in 1970 and 1971, but had significantly fewer uredia than P5481C1 in 1972. The variable results with Marquis and Lee may indicate either that the resolution of the method is inadequate for reliable detection of moderately low levels of receptivity, or that the receptivity of these cultivars is sensitive to an environmental factor.

Low receptivity in Thatcher and Sentry resembled adult plant resistance in that it was observed only in older plants. Numbers of uredia were high, near that of P5481C1, on blades of juvenile plants of these cultivars, but was significantly lower on blades and sheaths of older plants in all inoculations.

The response of Idaed 59 was unique. In the early stages of plant growth, blades of this cultivar had very few uredia that were significantly lower than those on blades of P5481C1. However, in the last inoculations, when Idaed 59 was in the anthesis stage, the number of uredia from the inoculations increased and was very

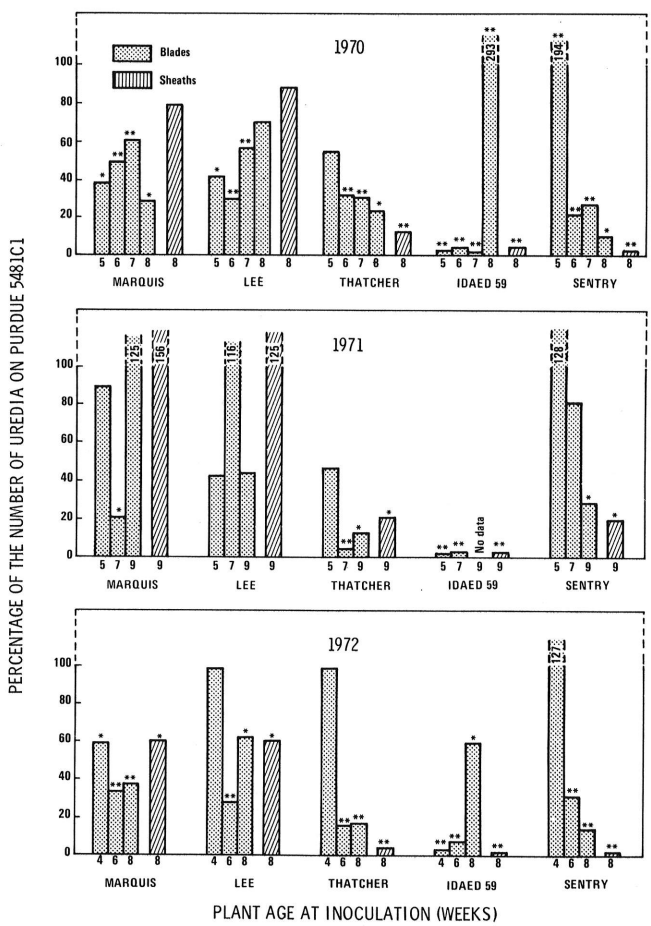

Fig. 1. Receptivity of susceptible wheat cultivars to infection by isolate 65-39-2 of race 15B *Puccinia graminis* f. sp. *tritici*, at different ages of growth under field conditions, expressed as a percentage of the number of uredia on the reference cultivar Purdue 5481C1. Significant differences from P5481C1 are indicated by * ($P = 0.01$).

significantly higher than that on P5481C1 in 1970 but was significantly lower than that on P5481C1 in 1972. No data were obtained in 1971, when the leaves died before uredia appeared. In all years, the number of uredia on sheaths of the plants inoculated at anthesis was extremely low, significantly lower than that on sheaths of P5481C1. In other tests we often observed a shift for leaf blades on Idaed 59, from low to extremely high receptivity to infection after anthesis. Blades of Idaed 59 generally senesce and die shortly after anthesis, a character also observed in a parental line, Illinois #1 Chinese*2 *T. timopheevii* (Zhuk.) Zhuk. Thus, the reversals of the receptivity of the blades at the late inoculations may result from the changes of senescence.

These results indicated that uniform inoculation in the field revealed major differences in receptivity to infection by *P. graminis* f. sp. *tritici* among cultivars. Receptivity, however, was not constant in the test cultivars. In Thatcher and Sentry, receptivity changed from high in juvenile plants to low in older plants. In Idaed 59, the receptivity of leaf blades changed from low before anthesis to high afterward, but the receptivity of leaf sheaths at the same time was low. Thus, the timing of inoculation can be critical for evaluation of receptivity.

Differences in uredial size were apparent among the cultivars, particularly after inoculation of older plants. These differences were most apparent in 1972 when the cultivars were inoculated simultaneously at three ages and infections developed in all under the same environmental conditions (Table 1). Observations were made 12 days after the last of the three inoculations, which caused the greatest amount of infection in this test. The average daily temperature between inoculation and observation was 19 C. Uredia were consistently largest on P5481C1, and there were no apparent differences among plants of different ages. On the other cultivars, uredia on juvenile plants were distinctly larger than those on the older plants. Uredial size changed less on Marquis than on the other cultivars. On Thatcher and Sentry the reduced uredial size on the older plants was correlated with the decrease in receptivity, but on Idaed 59 the uredia remained small at anthesis even though receptivity increased at that stage. Similar trends in uredial size were observed in the 1970 and 1971 trials.

TABLE 1. Relative sizes of primary uredia on leaves of test cultivars of different ages inoculated uniformly with *Puccinia graminis* f. sp. *tritici* in 1972

	Uredial size[a] on plants of indicated age at inoculation[b]			
	Blades			Sheaths
Cultivar	4 wk	6 wk	8 wk	8 wk
Purdue 5481C1	3	3	3	3
Marquis	23	12	12	12
Lee	2	1=2	1−2−	1−2−
Thatcher	23	1−2+	1=2−	1=2−
Idaed 59	2−	1=	1=2−	1=2
Sentry	3−	1=	1=	1=2

[a]Scale, the approximate size of uredia associated with the infection types of Stakman et al (15): 1=, minute uredia, to 4, very large uredia; two digits express the range in uredial size on a single plant.

[b]Plant development at the different ages was: 4 wk, all with pseudostem erect; 6 wk, ranging from second node of stem formed on Sentry to boot formed on Idaed 59; 8 wk, ranging from ligule of flag leaf visible on Sentry to beginning of flowering on Idaed 59.

TABLE 2. The amount of infection on parents and F_1 plants from crosses between cultivars with different receptivity to infection by *Puccinia graminis* f. sp. *tritici* in field tests

Low-rusting parent		High-rusting parent		F_1 plant
Cultivar	Mean score[a]	Cultivar	Mean score[a]	Mean score[a]
Idaed 59[b]	1	Purdue 5481C1	3	1.2
Thatcher	1	Purdue 5481C1	3	3
Idaed 59[b]	1	Thatcher	3	1.6
Thatcher	1	Lee	3	3

[a]Within each cross, 3 = highest, 2 = intermediate, and 1 = lowest number of infections.

[b]Data for crosses with Idaed 59 as a parent are from plants inoculated 7 wk after planting; all other data are from plants inoculated 9 wk after planting.

Inheritance of receptivity to infection. The amount of primary infection on individual F_1 plants was compared with that on the parents after uniform field inoculation (Table 2). Only the F_1 plants from crosses with Idaed 59 had low receptivity, which suggests that low receptivity was dominant in Idaed 59. The F_1 plants from the other crosses resembled the parent with high receptivity, which suggests that low receptivity was recessive in Thatcher and Lee.

The families from F_2 plants were evaluated by the method in 1973 (Table 3). The distinctiveness of the receptivity phenotype of the plants in the various families influenced the accuracy of scoring. Families in which all plants were uniformly very high or very low in receptivity were most distinctive and easily recognized. Families segregating for receptivity charcters were difficult to recognize and, therefore, were likely to be misscored as similar to the parent in which the receptivity character was dominant. Thus, the families that were scored most accurately were those with high receptivity when low receptivity was dominant and those with low receptivity when high receptivity was dominant.

Clear-cut results were observed with the cross between Idaed 59 and P5481C1. The ratio of families with high receptivity to all others (families with low receptivity plus segregating families in which low-receptive plants predominated) fit ($P > 0.50$) the expected ratio for the segregation of a single dominant gene for low receptivity from Idaed 59. No families were observed with receptivity distinctively lower or higher than that of the low- or high-receptive parents, respectively.

The small fraction of [F_2] families with low receptivity from the cross between Thatcher and P5481C1 fit ($P > 0.10$) the expected ratio for the segregation of two complementary recessive genes for low receptivity from Thatcher. No families were observed in which a distinctive level of receptivity could be ascribed to either of the two recessive genes alone. One family, however, had receptivity distinctively lower than that of Thatcher and the other families in the low receptivity category.

The most complex array of phenotypes for receptivity was found among the families from the cross between Idaed and Thatcher. The results above indicate that this cross combined a dominant gene for low receptivity from Idaed 59 with two complementary recessive genes for low receptivity from Thatcher. Idaed 59 and Thatcher both had low receptivity when inoculated at the boot to the heading stage of development, but in the parental reference rows in this nursery the Idaed 59 plants had discernably less infection than the Thatcher plants. Of the families, 105 were scored similar to Idaed 59; 162, similar to Thatcher; 318, segregating; and 138, distinctively higher in receptivity than either parent.

The observed ratio of 105 low : 618 all other for this cross did not fit ($P < 0.005$) the ratios of 1 low : 3 all other that would be expected if all low-receptive families were homozygous for the low receptivity gene from Idaed 59, or 19 low : 45 all other that would be expected if all low-receptive families were homozygous for the low receptivity genes from Idaed 59, Thatcher, or both. Furthermore, the observed ratio of 138 distinctively high : 585 all other did not fit ($P < 0.005$) the ratio of 1 high : 3 all other that would be expected if all high-receptive families were homozygous recessive for the receptivity gene from Idaed 59. Likewise, the observed ratio did not fit ($P < 0.05$) the ratio of 7 high : 57 all other that would be expected if all distinctively high-receptive families lacked the dominant gene for low receptivity from Idaed 59 and were homozygous for one or both of the dominant alleles of the complementary genes for low receptivity in Thatcher. Those families from F_2 plants with a genotype homozygous for the recessive allele of the receptivity gene from Idaed 59 and heterozygous for the complementary genes in Thatcher would have a ratio of 15 plants with distinctively high receptivity to 1 plant with the low receptivity of Thatcher, and such families probably were scored as distinctively high. These potentially segregating families that were possibly misclassified as high would include 4/64 of the population. The 4/64 added to the

7/64 described above would yield an expected fraction of 11/64 with high receptivity. The number of families that were scored as distinctively high fits ($P > 0.10$) the ratio of 11 high : 53 all other. The absence in this cross of any families with receptivity distinctively lower than that of Idaed 59 suggests that the gene for low receptivity from Idaed 59 is epistatic to the complementary genes from Thatcher.

Of the families from the cross between Thatcher and Lee, 577 were scored high in receptivity, like Lee; 359, segregating; 143, low, like Thatcher; and 17, distinctively lower than Thatcher. The relatively large number of families in the low categories suggested that a recessive gene from Lee was complementary with either of the two recessive genes from Thatcher and would give similar levels of low receptivity with either. The observed ratio of 160 low : 936 all others fit ($P > 0.25$) the ratio of 10 low : 54 all other that would be expected if low receptivity occurred in families with genotypes homozygous for any two or for all three recessive genes. Furthermore, the number of families with distinctive receptivity, lower than that of Thatcher, fit ($P > 0.95$) the expected ratio for a cumulative relationship in the type that is homozygous for all three recessive factors.

DISCUSSION

The present study demonstrated that receptivity to infection with *P. graminis* f. sp. *tritici* is one of the components of resistance of the slow-rusting cultivars examined. Differences in receptivity among cultivars in the field were evaluated from the relative amount of primary infection per unit of plant surface produced by uniform application of inoculum. The method used appears to be adequate for recognition of genetic factors that consistently reduced infection to less than 50% of that on a highly receptive fast-rusting cultivar. About 200 field entries per hour can be evaluated for large differences in receptivity with sufficient accuracy for identification of those with receptivity low enough to be potentially useful. In addition, the method revealed differences among cultivars in the size of primary uredia on adult plants. Thus, the method may be useful for detecting resistance factors that are not readily apparent in greenhouse inoculation trials or that are obscured in field nurseries by the presence of infections of different age and virulence.

Both receptivity and uredial size were affected by plant age. In the slow-rusting cultivars, uredia were larger on juvenile plants than on older plants. Changes in receptivity with plant age, however, varied with the cultivar; eg, receptivity of Thatcher and Sentry was high in juvenile plants and low in adult plants, whereas receptivity of Idaed 59 was low in juvenile plants and high in blades of adult plants. Whether characters for uredial size and receptivity were associated or inherited independently was not determined.

The low receptivity observed in Idaed 59, Thatcher, and Lee apparently had relatively simple inheritance. Low receptivity in Idaed 59 acted as a single dominant factor. Roelfs and McVey (*personal communication*) have identified *SrTt-1* in Idaed 59 by their method (10) of comparing seedling reactions to a number of diverse rust cultures. This gene is characterized by low infection type 0; with avirulent races such as 151-QSH and by high infection type 4, but with a few flecks also present, to all virulent races (such as 15B-2) that they examined. In our quantitative inoculation tests on seedlings in the greenhouse, the low receptivity is only slightly evident in that the number of uredia produced by the culture of 15B-2 on Idaed 59 is significantly (about 30%) lower than that produced on the fully susceptible line P5481C1. Since *SrTt-1* is associated with a chromosomal segment from *T. timopheevii* (9), the observed dominant character for low receptivity may be separate from but linked to this gene.

The two complementary recessive genes for the low receptivity of Thatcher resemble those observed by Koo and Ausemus (7) in their field tests of rust reaction of F_3 progenies from Timstein/Thatcher. The extremely low receptivity to infection by *P. graminis* f. sp. *tritici* observed in some progenies from crosses between Thatcher and Lee appears similar to the high resistance to wheat stripe rust produced by the cumulative effect of minor recessive genes observed by Sharp and Volin (13). Known specific genes for stem rust resistance in Thatcher are *Sr5, Sr12, Sr16* (8), and *Sr9g* (R. A. McIntosh, *personal communication*); in Lee, *Sr11* (6), *Sr9g*, and *Sr16* (R. A. McIntosh, *personal communication*); and in P5481C1, *Sr7b* and *Sr10* (D. V. McVey and A. P. Roelfs, *personal communication*). None of these resistances is effective against race 15B-2. The observed inheritance patterns for low receptivity among crosses between these lines do not fit models based on combinations of dominant genes for resistance. R. A. McIntosh (*personal communication*) stated that the resistance of *Sr12* acts as a recessive character with Australian rust cultures, and suggested that the observed resistances in Thatcher crosses may involve expressions of this gene. The general effectiveness of the distinctively low receptivity in some progenies from crosses between Thatcher and Lee is unknown at this time. The distinctively low receptivity of these 17 progeny lines, however, was effective in field tests with virulent cultures of races 15B-TNM, 15B-TDM, and 113-RKQ. Representatives of these lines have been submitted to the USDA International Spring Wheat Rust Nursery for tests against a wide diversity of races of the stem rust pathogen.

TABLE 3. Segregation of phenotypes for receptivity to infection with *Puccinia graminis* f. sp. *tritici* in field tests of F_2 families (in the F_3) from crosses between wheats of different receptivity

	Receptivity to infection							
	Observed ratios				Expected ratios			*P* (goodness of fit)
Parents	Low	High	:	All other	Low	High	:	All other	
Idaed 59, Purdue 5481C1		259	:	804		1	:	3[a]	> 0.50
Thatcher, Purdue 5481C1	53		:	983	1		:	15[b]	> 0.10
Idaed 59, Thatcher		138	:	585		11	:	53 [c]	> 0.10
Thatcher, Lee	160		:	936	10		:	54[d]	> 0.25
Thatcher, Lee	17[e]		:	1,079	1		:	63[f]	> 0.95

[a] Ratio if low receptivity is governed by a single dominant gene from Idaed 59.
[b] Ratio if low receptivity is governed by two complementary recessive genes from Thatcher.
[c] Ratio if the families that scored distinctively higher in receptivity than either parent included types that were homozygous recessive for the gene in Idaed 59 and (i) homozygous dominant for one or both of the complementary genes from Thatcher and (ii) those that were heterozygous for the two complementary genes from Thatcher, in which the family was a mixed population of 15 plants of distinctively high receptivity to one of low receptivity.
[d] Ratio if a single recessive gene for low receptivity from Lee is complementary with either of the two recessive genes from Thatcher.
[e] Families with distinctively lower receptivity than that of Thatcher.
[f] Ratio if families that scored distinctively lower in receptivity reflect the cumulative action of a recessive gene from Lee in types that are homozygous for the two complementary recessive genes from Thatcher.

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