# Tolerance to Leaf Rust in Susceptible Wheat Cultivars

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## ABSTRACT

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Studies of leaf rust tolerance were conducted under controlled conditions in the greenhouse using ten cultivars of winter wheat (*Triticum aestivum*) and races 76 and 82 of *Puccinia recondita*. Split-plot trials were used, subjecting one plant of each pair of plants of each cultivar in each replication to a massive inoculation of urediniospores to ensure severe, reasonably uniform infection. Cultivars were inoculated at the same stage of growth. Comparisons were made of the effect of leaf rust on grain yield, numbers and weights of kernels, and stem or leaf elongation. The greatest total mean loss over all cultivars (56%) occurred when inoculations were made before plants headed. Mean losses were about 15% when plants were inoculated after heading. These greenhouse studies confirmed field observations that cultivars of apparently equal susceptibility to leaf rust differ significantly in the magnitude of yield losses sustained. Fulhard, the most tolerant cultivar, had a high level of protection against yield losses due to rust. The tolerance of Kanqueen, although less than that of Fulhard, may still be of importance. Butler was tolerant when inoculated after heading, but not when inoculated before heading. Seneca was just the opposite, tolerant when inoculated before heading, but not when inoculated after heading. Riley and Purdue Sel 45 were consistently intolerant, regardless of growth stage when inoculated. Tolerant cultivars, but not intolerant ones, were markedly stunted by rust. This was also demonstrated in the seedling stage, but no inheritance information was found in tests of $F_1$ or $F_2$ generation materials. The data support a hypothesis that the relative tolerance of a cultivar may vary with maturity of the plant or tiller inoculated. The levels of tolerance demonstrated in these studies are of potential economic importance, but practical breeding methods for transferring tolerance to superior new cultivars must still be developed.

*Additional key words*: germ plasm, maturity, yield reduction.

Leaf rust (caused by *Puccinia recondita* Rob. ex. Desm.) of wheat (*Triticum aestivum* L. em Thell) has been recognized for many years as a cereal disease of major economic importance. Efforts to reduce losses have been directed primarily towards developing rust-resistant wheat cultivars and germ plasm that utilize specific resistance. Such cultivars eventually succumb to new races of *P. recondita* and provide only ephemeral protection. Cultivars of oats and wheat have been found to differ significantly in losses sustained from crown rust and leaf rust attacks of apparent equal severity under field conditions. The ability of a host cultivar to endure heavy rust infection without sustaining severe yield losses would provide valuable protection through tolerance to the disease. Theoretically, such tolerance should offer a more permanent type of protection against losses from disease, because it would not impose selective pressure on the pathogen population (3).

There are few reports of true cereal rust tolerance in the literature. Cobb (5) used the term "rust-enduring" to describe "a type of wheat, which although infected by the rusts, produced a fair crop of grain." He also stated that such wheats were "uncommonly rare." Bolley and Pritchard (1) suggested selecting plump seed from badly rusted wheat to provide wheats capable of "rust-endurance." Caldwell et al (2) reported that although severely rusted, the cultivar Fulhard suffered no yield loss. Other wheats in their study suffered up to 28% yield reduction due to rust. Caldwell et al (3) reported that the spring oat cultivar Benton was more tolerant to crown rust than Clinton 59. Simons (7) reported Cherokee to be a crown rust tolerant spring oat cultivar. Clark (4) demonstrated tolerance to stem rust, crown rust, and *Septoria avenae* in duplicated and replicated trials studying yields of oats under light and heavy attack by the three diseases. In his review of tolerance, Schafer (6) pointed out that there have been few studies investigating true tolerance to the cereal rusts and that often there are confusing reports mistaking low infectibility for tolerance.

These studies were conducted to evaluate tolerance to leaf rust in susceptible wheat cultivars.

## MATERIALS AND METHODS

Three main experiments, similar in design and materials, were conducted in the same greenhouse to evaluate tolerance to leaf rust in wheat. Two of the 10 cultivars that were used (Fulhard CI 8527 and Kanqueen CI 12762) were hard red winter wheats. Butler CI 12527 and Seneca CI 12529 were soft winter wheats from Ohio. Monon CI 12367, Riley CI 13702, Purdue 579C8, and Sel 45 were soft wheats from Indiana. These eight cultivars were used in all three main experiments. Two additional soft wheats, Ill 53-818 and Ill 59-884 (= CI 14023) were added for the third experiment.

Cultures of *P. recondita* with the required virulences were chosen and were maintained and increased on mildew-resistant seedling stock plants.

Vernalized plants of each cultivar were selected for uniformity of size, tillering, and maturity and placed in a split-plot arrangement on the greenhouse bench with 16 replications. Each replication consisted of a pair of plants of each cultivar, one to be infected, and one to serve as a healthy control. The cultivars were separated into groups by relative maturity to facilitate inoculation at approximately the same stage of development. In the first experiment (experiment I), inoculations were made from 3 to 6 days before heading, at growth stages 43–45 (9). In experiment II, they were made from 6 to 10 days after heading, growth stages 65–68, and in experiment III, from 2 to 5 days after heading, growth stages 61–64. The plants were thoroughly dusted with fresh urediniospores from stock inoculum on seedling plants, moistened with a fine spray of water and incubated under a tent of water-soaked muslin for 15 hr. The uninoculated control plants were shifted from their original positions to eliminate confounding by unequal root establishment in the greenhouse bench, but were not given a moist treatment.

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When the leaf rust reached maximum development (15 days after inoculation), estimated percentages of infection, based on the modified Cobb scale, were recorded for each plant. The heights to the base of the basal spikelet of the primary stem and the first two tillers on each plant were also recorded. For ease of discussion, the terms first, second, and third tiller will be used after this to designate the primary stem and first two tillers in order of maturity. Grain yields were determined at maturity for each plant in experiment I and separately for each tiller in experiments II and III.

Three other split-plot trials comparing rusted and nonrusted seedlings of Fulhard, Kanqueen, Riley, and Monon were conducted to compare various levels of seedling tolerance under severe rust infection. Seedlings at growth stage 11 were subjected to a saturation inoculation with *P. recondita* just as the second leaf was emerging. Subsequent growth was measured through the four leaf stage. To evaluate the usefulness of seedling tests in a program to develop rust-tolerant wheat germ plasm, similar experiments were conducted using $F_1$ and $F_2$ populations from crosses of cultivars differing in tolerance.

Analyses of variance of data from the factorial design were performed using the method of partitioning degrees of freedom and error terms for cultivar means as described by Steel and Torrie (8). Regression analyses were run to evaluate leaf rust infection severity and yield loss. These were done both by experiment and by cultivar.

## RESULTS

Leaf rust severity was above 70% on both the flag and lower leaves of most cultivars in each experiment. Most lower leaves (below penultimate) were dead or dying 12–14 days after inoculation.

The effect of leaf rust on yield varied in the three experiments. The mean loss due to rust for all cultivars inoculated 3–6 days before heading was 56% in experiment I. In experiments II and III, when inoculations were delayed until 6–10 days or 2–5 days after heading, losses averaged 13% for the first tiller to 19% for the third tiller.

All cultivars in experiment I suffered a significant reduction in grain yield due to rust (Table 1). The cultivar × treatment interaction for grain yield and the cultivar effect were both significant based upon the analysis of variance. This indicates significant differences in tolerance of cultivars that are equally susceptible to leaf rust. Kanqueen and Seneca suffered the least yield loss. These losses were significantly less than those of Butler and Riley. It should be noted that the estimated severity of rust infection was somewhat lower on Kanqueen and Seneca than on Butler and Riley. Fulhard, however, having equally severe infection, showed significantly more tolerance than the most severely damaged cultivars, as it did in subsequent studies. Butler was extremely sensitive to rust in this trial.

In experiment II, in which plants were inoculated at the oldest stage of growth, there were no significant cultivar × treatment interactions for yield reductions due to rust for any of the three tillers. Butler was one of the least affected cultivars. It suffered no loss in yield due to rust for the first and third tiller, and only a 10% loss on the second tiller. Losses due to rust on the first and third tillers of Sel 45 were 21 and 26%, respectively. For the comparable tillers on Riley, losses were 26 and 28%. This was consistent with their substantial losses in the other experiments, indicating intolerance. Fulhard appeared to be tolerant in this trial also, sustaining only minor losses.

In experiment III, there were significant cultivar × treatment interactions for yield reduction for all tillers for both yield and percentage loss. Cultivar Fulhard was the least affected, with no reduction in yield on tiller one or three (Tables 2 and 3) and less than 5% loss on tiller two (Table 4). Fulhard suffered significantly less yield reduction than Riley, Seneca, Monon, and Sel 45. Similar comparisons show that Kanqueen and Butler also possess some tolerance.

None of the regression analyses showed any significant relationship between yield loss and the severity of infection. This was true for within-cultivar and within-experiment analyses. Therefore, tests for significance of deviation from the regression line were not conducted.

Greater yield losses tended to occur in the younger tillers of the intolerant cultivars such as Riley and Sel 45 in contrast to tolerant cultivars such as Fulhard, Kanqueen, and the partially tolerant Butler for which this difference was generally not observed. Yield losses in all experiments were due to a combination of reduction in kernel number and a reduction in weight per kernel. The earliest

TABLE 1. Effect of leaf rust on grain yield, experiment I

| Cultivar | Severity on flag leaf (%) | Mean yield per plant[a] Rusted[b] (gm) | Nonrusted (gm) | Loss[c] (%) |
|---|---|---|---|---|
| Kanqueen | 81 | 1.72* | 3.27 | 47.4 ab |
| 579C8 | 80 | 1.85* | 3.81 | 51.3 abc |
| Seneca | 66 | 3.09* | 5.52 | 44.0 a |
| Monon | 61 | 2.03* | 4.90 | 58.6 abcd |
| Sel 45 | 97 | 1.84* | 4.57 | 59.9 d |
| Fulhard | 94 | 1.84* | 3.83 | 51.8 abc |
| Butler | 94 | 1.28* | 4.83 | 75.5 e |
| Riley | 91 | 2.34* | 5.71 | 59.1 cd |

[a]Means of 14 replications.
[b]Asterisks (*) indicate means significantly different from nonrusted check of the same cultivar, LSD ($P = 0.05$) = 0.39 gm.
[c]Losses followed by the same letter are not considered significantly different, $P = 0.05$, according to Duncan's new multiple range test.

TABLE 2. Effect of leaf rust on grain yield of the first tiller, experiment III

| Cultivar | Severity on flag leaf (%) | Mean yield of first tiller[a] Rusted[b] (gm) | Nonrusted (gm) | Loss[c] (%) |
|---|---|---|---|---|
| 579C8 | 60 | 1.18* | 1.31 | 9.9 ab |
| Ill 53-818 | 32 | 1.08* | 1.27 | 10.9 ab |
| Ill 59-884 | 95 | 1.15* | 1.45 | 20.7 b |
| Monon | 72 | 1.15* | 1.35 | 14.8 ab |
| Kanqueen | 88 | 1.12* | 1.26 | 11.1 ab |
| Sel 45 | 92 | 1.26* | 1.47 | 14.3 ab |
| Fulhard | 89 | 0.73 | 0.69 | + 5.8 a |
| Riley | 78 | 1.07* | 1.49 | 28.2 c |
| Seneca | 83 | 1.48* | 1.95 | 24.1 b |
| Butler | 74 | 1.55* | 1.74 | 10.9 ab |

[a]Means of 16 replications.
[b]Asterisks (*) indicate means significantly different from nonrusted check of the same cultivar, LSD ($P = 0.05$) = 0.12.
[c]Losses followed by the same letter are not considered significantly different, $P = 0.05$, according to Duncan's new multiple range test. Figures preceded by + represent a gain.

TABLE 3. Effect of leaf rust on grain yield of the third tiller, experiment III

| Cultivar | Severity on flag leaf (%) | Mean yield of third tiller[a] Rusted[b] (gm) | Nonrusted (gm) | Loss[c] (%) |
|---|---|---|---|---|
| 579C8 | 57 | 0.87 | 0.94 | 7.4 ab |
| Ill 53-818 | 32 | 0.76* | 0.97 | 21.7 ab |
| Ill 59-884 | 94 | 0.79* | 1.02 | 22.5 ab |
| Monon | 74 | 0.69* | 1.03 | 33.0 bc |
| Kanqueen | 83 | 0.81 | 0.89 | 9.0 ab |
| Sel 45 | 89 | 0.89* | 1.18 | 24.6 bc |
| Fulhard | 87 | 0.63 | 0.60 | + 5.0 a |
| Riley | 73 | 0.67* | 1.06 | 36.8 c |
| Seneca | 86 | 1.08* | 1.41 | 23.4 b |
| Butler | 68 | 1.10* | 1.24 | 11.3 ab |

[a]Means of 16 replications.
[b]Asterisks (*) indicate means significantly different from nonrusted check of the same cultivar, LSD ($P = 0.05$) = 0.14.
[c]Losses followed by the same letter are not considered significantly different, $P = 0.05$, according to Duncan's new multiple range test. Figures preceded by + represent a gain.

TABLE 4. Effect of leaf rust on grain yield of the second tiller, experiment III

| Cultivar | Severity on flag leaf (%) | Mean yield of second tiller[a] | | |
|---|---|---|---|---|
| | | Rusted[b] (gm) | Nonrusted (gm) | Loss[c] (%) |
| 579C8 | 52 | 0.95 | 1.08 | 12.0 a |
| Ill 53-818 | 28 | 0.86* | 1.11 | 22.5 ab |
| Ill 59-884 | 92 | 0.88* | 1.19 | 26.1 ab |
| Monon | 72 | 0.80* | 1.11 | 27.9 b |
| Kanqueen | 85 | 0.97 | 1.06 | 8.5 a |
| Sel 45 | 91 | 1.03* | 1.31 | 21.4 ab |
| Fulhard | 84 | 0.61 | 0.64 | 4.7 a |
| Riley | 77 | 0.75* | 1.14 | 34.2 b |
| Seneca | 86 | 1.18* | 1.61 | 26.7 ab |
| Butler | 64 | 1.26 | 1.39 | 9.4 a |

[a] Means of 16 replications.
[b] Asterisks (*) indicate means significantly different from nonrusted check of the same cultivar, LSD ($P = 0.05$) = 0.17.
[c] Losses followed by the same letter are not considered significantly different, $P = 0.05$, according to Duncan's new multiple range test.

inoculation time resulted in the most drastic reduction in kernel number and also caused severe stunting in some of the plants. Fulhard and Kanqueen were drastically stunted by rust when inoculated before heading, whereas Riley, Monon, and Sel 45 were not significantly stunted. When inoculations were delayed until after heading, no differences in growth were observed.

The same relationship was observed in the three experiments that evaluated the effect of leaf rust on seedling growth of tolerant and intolerant cultivars. Seedlings of tolerant cultivars infected by *P. recondita* were severely stunted, while seedlings of intolerant cultivars were not (Table 5). In the two experiments to determine the feasibility of using this seedling characteristic to transfer tolerance to advanced germ plasm, neither $F_1$ plants from crosses of tolerant × intolerant cultivars nor the succeeding $F_2$ populations yielded any significant information. The parents were stunted or normal as in previous experiments, but none of the hybrid material showed sufficient differences for selection.

## DISCUSSION

Proof of leaf rust tolerance is based upon the comparison of cultivars that differ in relative responses to rust in yield or other characters while showing equally severe symptoms of infection. Such comparisons require a level of inoculation severe enough to overcome differences in infectibility that might exist between otherwise susceptible cultivars. In greenhouse tests, controlled inoculations with massive numbers of spores overcame such cultivar differences.

Originally, only cultivars that had approximately equal rust infection were directly compared. Although Kanqueen and Seneca were the cultivars suffering the least loss in yield due to rust in the first experiment, their slightly lower rust infection percentages could have been at least partly responsible. The regressions of leaf rust severity on yield loss indicate that the levels of loss were unrelated to the ranges of severity in these experiments. This indicates that our inoculations were adequate to provide the desired severity levels. It was a surprise to find no major differences in losses due to leaf rust at ranges in severity from 50 to 100%. Kanqueen was tolerant in the next two tests, and behaved much like Fulhard when inoculated in the seedling stage. Fulhard was

TABLE 5. Effect of leaf rust on seedling growth of tolerant and intolerant wheat

| Cultivar | Elongation of the fourth seedling leaf | | |
|---|---|---|---|
| | Rust[a] (cm) | Nonrusted (cm) | Percent of nonrusted |
| Kanqueen | 118.3** | 179.9 | 66 |
| Fulhard | 115.0* | 153.6 | 75 |
| Riley | 137.2 | 133.5 | 103 |
| Monon | 143.4 | 156.9 | 91 |

[a] Asterisks (* and **) indicate significant difference $P = 0.05$ and $P = 0.01$, respectively.

tolerant in all experiments regardless of the time inoculated. This substantiates previous findings in field studies by Caldwell et al (2). Some cultivars varied in the relative degree of tolerance in the different experiments. Seneca, although appearing relatively tolerant when inoculated before heading, was intolerant when inoculated after heading. Butler, which was highly intolerant when inoculated before heading, was somewhat tolerant when inoculated after heading.

In the more tolerant cultivars there was no general trend for losses to be greater on the younger tillers. The younger tillers of the intolerant cultivars, Riley and Sel 45, suffered greater losses due to rust than the first tillers. These relationships suggest that tolerance is a very complex characteristic and perhaps not highly stable.

The level of tolerance demonstrated in these studies is high enough to be of practical importance. However, there appears to be no promising method for economically recognizing tolerance in early generation progeny of crosses in breeding programs. The stunting reaction of the tolerant cultivar's seedlings appeared encouraging and may be exploited as additional information becomes available. The stunting reaction may also be confounded by hybrid vigor in the seedling tests of $F_1$ plants. The likelihood that the character is under complex genetic control is high. The relative rarity of the character may also be related to its complexity. Tolerance may best be utilized in combination with other forms of protection from leaf rust loss such as specific resistance or slow rusting.

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