Evaluation of Slow-Mildewing Resistance of Knox Wheat in the Field

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ABSTRACT

Because major gene, race-specific, resistance to powdery mildew in wheat is often short-lived, studies were undertaken on more stable types of "adult-plant" resistance. Mildew development was followed in field plots on wheat cultivars which were fully susceptible as seedlings, but which had various levels of adult-plant resistance. During grain filling, mildew severity was substantially lower on 'Knox' wheat and three of its progeny than on 'Vermillion' or 'Riley 67'. Infection rates, calculated from logit analyses, were lower on Knox and its progeny than on the two susceptible wheat cultivars. The resistance of Knox and 'Benhur' was effective regardless of row spacing or planting date. The resistance of experimental line Purdue 5724B3 was less effective in wheat plantings sown 15 September than in those sown 2 or 4 weeks later. The level of Knox's resistance, and its stability over the past 20 years, suggest that such resistance would provide practical, stable control of powdery mildew in the soft red winter wheat region of the USA.

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Triticum aestivum L. em. Thell 'Knox' appears to have a stable, adult-plant resistance to *Erysiphe graminis* DC. f. sp. *tritici* em. Marchal (14). Although Knox is fully susceptible to attack by *E. graminis* in the seedling stage, mature plants of that cultivar have never been as severely mildewed in breeding nurseries as have many other lines. Because the disease takes longer to develop on Knox, its resistance has been termed "slow-mildewing" (14). Colonies on Knox were slightly smaller and had fewer conidial chains than colonies on more susceptible lines.

Adult-plant resistance to powdery mildew has been reported for other wheat cultivars and for oats (5, 8, 11, 12, 13, 15, 16). In some cases it was phenotypically similar to moderate seedling resistance (11). In other cases, adult-plant resistance was recognized by less severe symptom expression, without reference to the infection type (5, 8, 15, 16). The plates of Jones & Hayes (8) indicate that the infection type on resistant 'Maldwyn' oats was as high as that on susceptible 'Milford' oats, although the amount of mildew was much less on the former. Some identify resistance as "field resistance" with no comment on its phenotypic expression (12, 13); others (8, 14, 15) suggest that adult-plant resistance is general (horizontal) (1, 19).

In 1970, I studied field resistance of Knox to powdery mildew. The progress of powdery mildew buildup was followed during the spring in plots of slow-mildewing and fast-mildewing wheat lines. Since sowing date and density of the canopy influence the severity of powdery mildew on cereals (7, 8, 10, 16, 17), the effect of these variables on slow-mildewing was examined.

MATERIALS AND METHODS.—All experiments were at the Purdue University Agronomy Farm in Tippecanoe County, Indiana. Six wheat cultivars or lines were used. 'Vermillion' (C.I. 13080) and 'Riley 67' (C.I. 14110) were chosen because of their susceptibility to mildew. 'Benhur' (C.I. 14054), 'Knox' (C.I. 12798), and experimental lines Purdue 5724A2 and Purdue 5724B3 were chosen as slow-mildewing wheats. Entries were sown in four-row plots 2.4-m long.

A time-of-planting experiment was conducted during 1969-70. Entries were sown 15 September, 30 September, and 17 October 1969. Treatments were replicated three times; rows were 30 cm apart. A split plot design was used, with planting date as the whole plot treatment.

In plant-density experiments entries were sown in rows 30 and 45 cm apart (1969-70 crop year) or 30 and 61 cm apart (1970-71 crop year). In 1969 the wheat was sown on 17 October with three replications; in 1970 wheat was sown 1 October with four replications. A split plot design with row spacing as the whole plot treatment was used.

In the 1969-70 experiments, natural infection of wheat by *E. graminis* occurred. In the 1970-71 experiment mildewed seedlings from the greenhouse were shaken in April over Riley 67 spreader rows planted in the aisles between replications.

During spring and summer mildew severity was recorded approximately every 10 days. In each plot five culms, selected at about equal intervals along each of the two center rows, were rated for mildew. Severity on each leaf, as percent of surface covered, was estimated using the Horsfall-Barratt scale (6). The average percent severity of mildew for each leaf on the culm for each plot was determined with the Elanco Conversion Tables® for the Horsfall-Barratt scale (Elanco Products Co., Indianapolis, Ind.). These 10-leaf averages were used for statistical analysis.

Severity of mildew after flowering and logit analysis (18) of disease progress curves were used to compare cultivars and treatments. Apparent infection rates were calculated by linear regression analysis.

RESULTS.—In all three experiments, there were substantial differences among cultivars in the final severity of powdery mildew. Differences in severity increased as the epidemics progressed because of differences in infection rates. Correlation coefficients for logits of mildew severity plotted against time were high (of 75 regression lines based on more than two points, 67 had correlation coefficients of 0.9 or greater; the lowest correlation coefficient was 0.788). Therefore, the apparent infection rates, which are the slopes of these regression lines (18), are useful parameters for comparing treatments.

Time-of-planting experiment.—Wheat in this experiment was naturally infected by *E. graminis* during the fall. On 30 October 1969, nine mildew colonies were found on Purdue 5724B3 and one colony was found on Knox, both sown 15 September. At this time plants had five to seven tillers. Wheat sown 30 September had two tillers per plant, and that sown 17 October was just emerging. Shortly after wheat had resumed growth in the spring (8 April 1970), powdery mildew was detected on

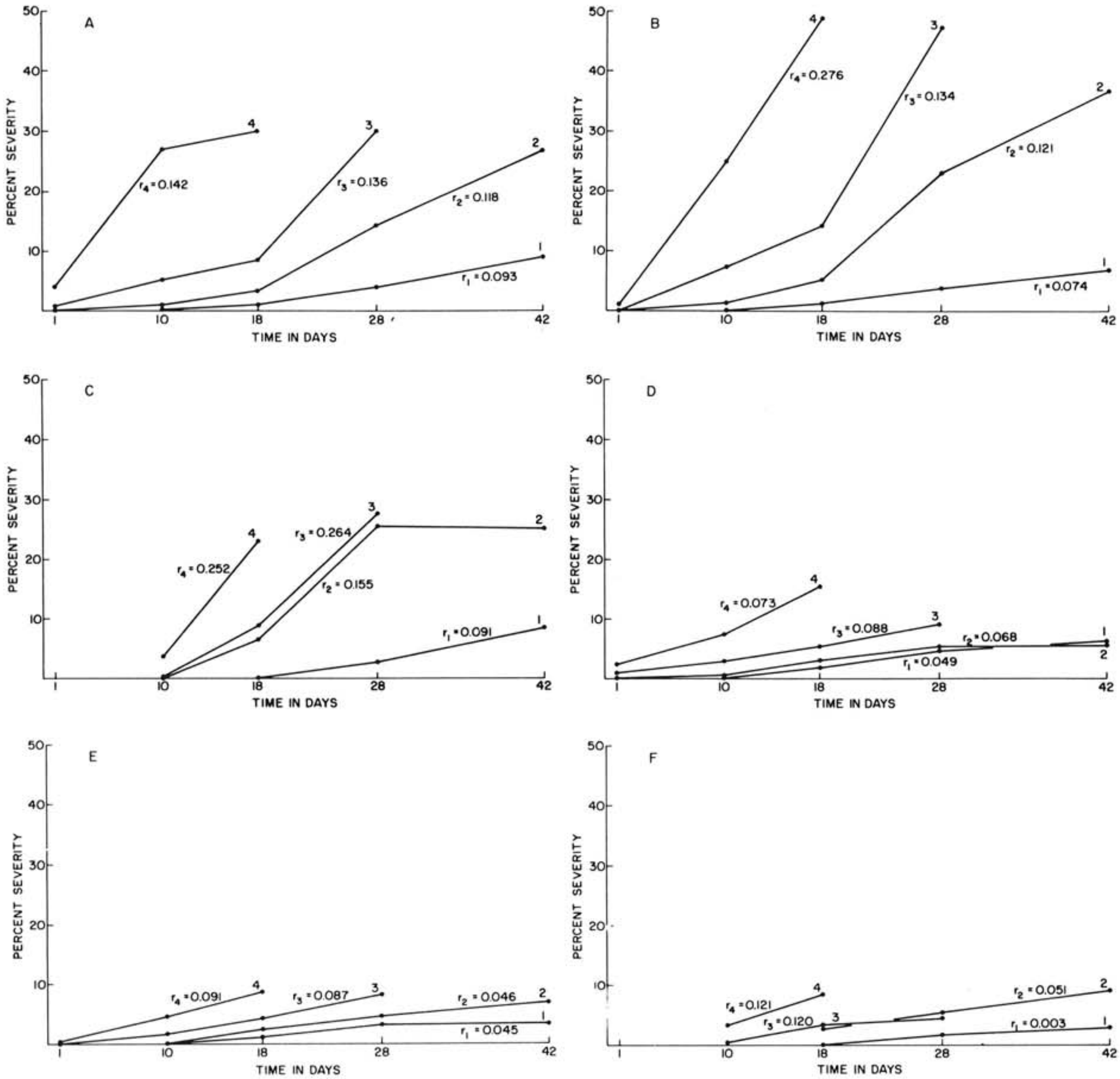

Fig. 1. Development of powdery mildew in the field on the upper four leaves of 'Vermillion' and 'Knox' wheat sown on three dates at the Purdue University Agronomy Farm in 1969-70. Leaf 1 is the uppermost (flag leaf). **A)** Vermillion, sown 15 September 1969; **B)** Vermillion, sown 30 September 1969; **C)** Vermillion, sown 17 October 1969; **D)** Knox, sown 15 September 1969; **E)** Knox, sown 30 September 1969; **F)** Knox, sown 17 October 1969. The apparent infection rate (r) for each curve was derived from linear regression analysis of logit severity on time.

wheat in all plots sown 15 September, in two plots sown 30 September, but in none of the plots sown 17 October. By 23 April, differences in severity among lines sown 15 September were evident. Severities of 4.0, 1.7, and 0.8% were recorded for Vermillion, Purdue 5724B3 and Knox, respectively. There were slight differences in severity among lines sown 30 September, but the level of mildew was less than 1% in the three lines.

Beginning 28 April, detailed severity notes were taken on 10 culms in each plot. At this time, severity was less than 5% on the upper four leaves of all lines at all planting dates. During the next 6 weeks the disease progress curves of the three lines diverged (Fig. 1 & 2). Mildew severity increased rapidly on Vermillion, especially on the lower leaves. Severity was recorded for each leaf until senescence had progressed so far that the effect of mildew could no longer be distinguished from normal maturation. The three lower leaves of each plant all reached about the same final severity of mildew. The rate of disease development was slower on successively younger leaves, and is reflected in the values of the apparent infection rates on leaves four through one (Fig. 1 & 2). Apparent infection rates tended to be higher on successively lower leaves of Purdue 5724B3 and Knox, but not as consistently as on Vermillion.

The final severity of mildew on Vermillion was 20% greater for plots sown 30 September than for plots sown on the other two dates. Although the final severity was about equal on plants sown on the first and third dates, the rate of disease increase was greater on wheat sown 17 October than wheat sown 15 September. The final severities were about the same because the epidemic started later on the late-seeded wheat. Considerably more mildew developed on Purdue 5724B3 sown 15 September than on that sown later. Indeed, nearly as much mildew developed in the 15 September planting as developed on Vermillion sown at the same time. Planting date had little effect on the final severity of mildew on Knox. Severity was less than 10% in all cases except on leaf four of the 15 September planting.

All three wheat cultivars were "fully susceptible" to *E. graminis* in terms of infection type. That is, colonies of infection type 4, on the scale used by Cherewick (4), were present on all three wheats. There was variation in the size of colonies on individual leaves; on the average, colonies on Knox and Purdue 5724B3 were slightly smaller than those on Vermillion.

Row-spacing experiment, 1970.—Two suspected slow-mildewing lines, Benhur and Purdue 5724A2 were compared with the highly susceptible cultivars Vermillion and Riley 67. The wheat was sown 17 October 1969, late for that year. No infection by *E. graminis* was detected in the fall. No mildew was found in the plots on 22 April 1970, but by 4 May there was enough mildew to detect differences among lines. Severity on Vermillion was 2% whereas that on other lines ranged from 0 to 0.02%.

Differences in mildew severity at 30 cm and 45 cm row spacings were nonsignificant. Therefore, only cultivar means are presented here (Table 1). Riley 67 and Vermillion consistently had more mildew than Benhur and Purdue 5724A2. Apparent infection rates reflected these relationships. Statistical comparisons could not be made for leaf three because these rates were based on two points only. However, these rates followed the same pattern as those on leaves one and two.

Row-spacing experiment, 1971.—Mildew severity

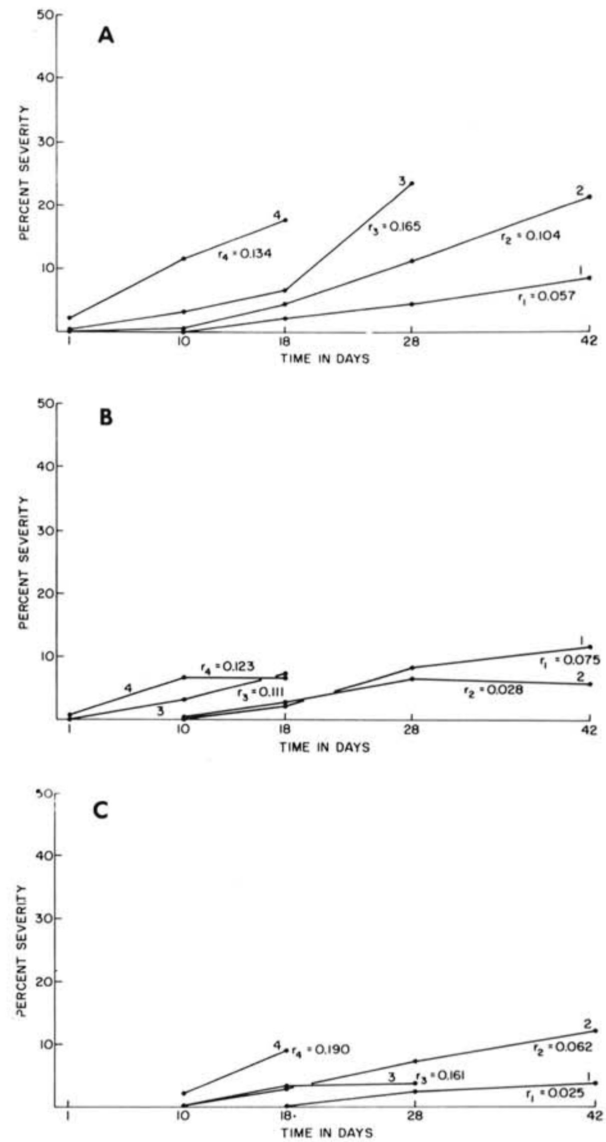

Fig. 2. Development of powdery mildew in the field on the upper four leaves of Purdue 5724B3 wheat sown on three dates at the Purdue University Agronomy Farm in 1969-70. Leaf 1 is uppermost (flag leaf). **A)** Wheat sown 15 September 1969; **B)** Wheat sown 30 September 1969; **C)** Wheat sown 17 October 1969. The apparent infection rate (r) for each curve was derived from linear regression analysis of logit severity on time.

was estimated five times, at weekly intervals, on the upper four leaves. The relative performance of Vermillion, Riley 67 and Benhur was the same as in 1970 (Table 2). Riley 67 and Vermillion had about the same level of mildew in all cases, which was significantly more than that on Knox and, except for leaf two on 31 May, Benhur.

Row spacing had a significant effect on mildew severity only on leaf two on 31 May. Interactions were nonsignificant; all cultivars had more mildew on this leaf at the wider row spacing. Since in the remaining seven comparisons (Table 2), row spacing had no significant effect, the data for each cultivar were pooled before calculating apparent infection rates. Despite the general lack of a significant effect of row spacing, Vermillion at 61 cm consistently had more mildew than Vermillion at 30 cm for leaves one, two, and three.

The apparent infection rates were greatest for Riley 67, but the disease started later in that cultivar than in Vermillion. The rate on Knox was consistently less than the rates on Riley 67 and Vermillion. Except for leaf one, the rate on Benhur was likewise less than the rates on Riley 67 and Vermillion. The relative performance of cultivars was the same for each leaf. On all cultivars, highest apparent infection rates were on leaf three, and lowest rates were on leaf two.

In this experiment, mildew severity on leaf sheaths was also measured. Severity was greater on sheath four than on sheath three for all cultivars; no mildew developed on sheaths of leaves one and two. Knox and Benhur had about 3% and 12% mildew on sheaths three and four, respectively. Corresponding values for Vermillion were 15% and 35% and for Riley 67 were 4% and 21%. There was a greater difference between Riley 67 and Vermillion in the amount of mildew on sheaths than in the amount of mildew on blades.

TABLE 1. Powdery mildew development in the field on four wheat cultivars in the 1970 row-spacing experiment

Leaf[a]	Riley 67	Vermillion	Benhur	Purdue 5724A2
	Apparent infection rate[b] (r), per unit per day			
1	0.204 a	0.178 ab	0.054 b	0.055 b
2	0.127 a	0.105 b	0.057 c	0.030 d
3	0.130	0.119	0.039	0.016
	Percent severity[b] on 1 June			
1	4.3 a	4.2 a	2.5 b	2.6 b
2	10.5 a	16.5 b	3.9 c	3.5 c
3	20.8 a	21.5 a	3.7 b	3.2 b
	Percent severity[b] on 10 June			
1	10.1 a	7.5 a	3.1 b	2.8 b
2	27.0 a	32.4 a	6.2 b	4.1 b

[a] Leaf 1 is uppermost (flag).

[b] Values followed by different letters are significantly different at the 5% level (Duncan's multiple range test). Separate comparisons were made among cultivars for each leaf. Apparent infection rates were calculated from linear regression analysis of the logit of the average severity of six plots vs. time. There were three observation dates for leaves one and two, and two observation dates for leaf three.

TABLE 2. Powdery mildew development in the field on four wheat cultivars in the 1971 row-spacing experiment

Leaf[a]	Riley 67	Vermillion	Benhur	Knox
	Apparent infection rate[b] (r), per unit per day			
1	0.190 a	0.159 ab	0.132 ab	0.089 b
2	0.166 a	0.140 b	0.086 c	0.074 c
3	0.268 a	0.188 b	0.148 c	0.126 c
4	0.198 a	0.154 b	0.118 c	0.072 d
	Percent severity on 31 May			
1	2.8 a	2.7 a	1.8 b	0.9 c
2	5.7 a	6.4 a	4.4 ab	3.0 b
3	20.0 b	25.4 a	7.8 c	4.8 c
4	42.2 a	45.3 a	12.6 b	6.9 b
	Percent severity on 7 June			
1	11.1 a	11.2 a	3.5 b	1.3 b
2	24.6 a	23.8 a	7.5 b	4.6 b
3	48.1 a	55.7 a	14.8 b	8.6 b
4	61.7 a	64.1 a		15.6 b

[a] Leaf 1 is uppermost (flag).

[b] Values followed by different letters are significantly different at the 5% level (Duncan's multiple range test). Separate comparisons were made among cultivars for each leaf. Apparent infection rates were calculated from linear regression analysis of the logit of the average severity of eight plots vs. time. There were three observation dates for leaf one; four observation dates for leaf two, and five observation dates for leaves three and four.

Relative performance of Vermillion and Knox.—Van der Plank (19, eq. 10.4) expresses the relationship between the apparent infection rate (r) and the basic infection rate (R) as:

$$r = R\,(e^{-pr} - e^{-(i+p)r}).$$

In this equation, p is the latent period and i is the infectious period. R measures the rate of disease increase based only on infectious tissue. This equation is only valid in the early stages of an epidemic when the amount of diseased tissue is small compared to the amount of healthy tissue. If r remains constant throughout an epidemic, R will steadily decrease. Anything that reduces the amount of inoculum, or the proportion of inoculum that will produce infection, will affect R in that proportion. By working in the other direction it should be possible to predict the cumulative effect of all such factors for resistance by comparing the values of R for Knox and Vermillion.

The apparent infection rates for Knox and Vermillion calculated from the 1971 row-spacing experiment were used to calculate R. The latent period, p, was taken as 12 days, based on observations of adult plants of Knox and Vermillion in the greenhouse. The value of i was taken as 13 days, also based on greenhouse observations. Values of R and the ratios of R for Vermillion and R for Knox were calculated (Table 3). The combined effects of the frequency of colony formation and rate of spore production are 2 to 5 times greater in Vermillion than in Knox.

DISCUSSION.—Wheat cultivars and breeding lines developing type 4 seedling infections to all mildew races tested during the past 4 years were evaluated for slow-mildewing type resistance. Slow-mildewing reactions were indicated since some of them consistently showed less powdery mildew in the field than others. These observations have been verified by the experiments reported here. As the season progressed, differences in severity among wheat cultivars became greater because of different rates of disease increase. Mildew consistently developed more slowly on Knox, Benhur, Purdue 5724B3, and Purdue 5724A2 than on Vermillion and Riley 67. The slow-mildewing of Benhur, Purdue 5724B3, and 5724A2 was probably derived from Knox, a parent in the cross giving rise to these lines. All four lines behaved similarly to mildew; however, Knox's resistance was often slightly superior. Vermillion and Riley 67 are not closely related. Although both were quite susceptible to mildew, the disease tended to begin later and build up faster on Riley 67 than on Vermillion. As a result, disease severity at the end of the season was approximately the same on the two cultivars.

Throughout the season, there was a gradient of mildew severity down the stem, the lowest leaves being most severely attacked. Such gradients are common (9) because mildew begins early in the spring and spreads up the plant as it grows. There was also an indication that mildew increased more slowly on upper leaves; i.e., upper leaves were more resistant (Vermillion, planting time experiment); however, the trend was not consistent. Since the apparent infection rates were estimated over different time intervals, a progressive decrease in the apparent infection rate going up the plant may reflect a deterioration of environmental conditions for mildew increase as the season progressed. In greenhouse experiments, however, gradients were found in the severity of mildew on oats (8) where neither length of exposure to infection, nor microenvironment, were factors. Resistance was related to the age of the leaf, diminishing as the leaf grew older. The resistance reported here for wheat fits the general scheme presented by Jones & Hayes (8). At any given time, differences between lines tended to be greater the lower the leaf. Likewise, differences between lines, for the same leaf, increased with time.

Time of planting affected mildew development. The resistance of Purdue 5724B3 was not as effective when the wheat was sown 15 September as when it was sown 2 or 4 weeks later. Knox's resistance was effective at all three planting dates. Row spacing generally had little effect on mildew and certainly did not alter the relative performance of cultivars. The tendency of mildew to be slightly more severe on Vermillion grown in wider rows is in contrast to reports of mildew being less severe on plants that were widely spaced (7, 10, 16). In my experiments the more vigorous growth of plants in wider rows (cultivars yielded from 14 to 44% more when grown in wider rows) may have compensated for any decrease in favorability of microclimate for mildew development as a result of greater air circulation and insolation in the canopy.

TABLE 3. A comparison of basic infection rate of powdery mildew development on Vermillion and Knox from the row-spacing experiment of 1970-71

	Leaf 1	Leaf 2	Leaf 3	Leaf 4
R_V[a]	1.130	0.911	1.903	1.149
R_K	0.378	0.291	0.352	0.579
R_V/R_K	2.99	3.13	5.40	1.98

[a] R_V and R_K are the basic infection rates for Vermillion and Knox, respectively (van der Plank, J. E. 1968. Disease resistance in plants. Academic Press, N.Y. 206 p).

The resistance of Knox, Benhur, Purdue 5724B3, and Purdue 5724A2 is characteristic of general (horizontal) resistance as described by Van der Plank (19). It is expressed by lower values of r compared to more susceptible cultivars. The individual colony does not differ greatly in appearance among cultivars. On all cultivars there is variation in size of colonies, but on Knox, Benhur, Purdue 5724B3 and Purdue 5724A2 there appear to be a greater proportion of smaller colonies than on Vermillion and Riley 67. Smaller colonies producing fewer spores for each successful infection, would slow the rate of disease development (19). Evidence accumulated over many years has indicated that Knox has no specific (hypersensitive) resistance to *E. graminis*. Yet it can never be formally "proved" that Knox's resistance is general. One need only show that at least one race of the pathogen will overcome resistance to show that it is specific. Thus, it is a logical impossibility to show that a type of resistance is general (horizontal) as defined by Van der Plank (19), since this amounts to showing that there are no races, and that there never will be, races capable of overcoming the resistance. Caldwell (1) offers a more practical criterion of general (horizontal) resistance. It is "resistance that experience and adequate testing in nature have shown to confer an enduring and stable protection against a pathogen or disease". To this extent Knox's resistance may be regarded as general. Knox and its similar derivative Knox 62 were grown on more than 0.7 million hectares (1.73 million acres) annually from 1954 to 1969 (14). Knox maintained its resistance to mildew while other cultivars, such as Riley (3) and Monon (2) which were regarded as moderately resistant when they were released, became highly susceptible to *E. graminis*. The resistance of Knox, expressed as reduced disease development (slow-mildewing), should provide practical disease control of a stable nature if incorporated into newer wheat cultivars.

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