Slow Rusting in Oats Compared with the Logistic and Gompertz Models

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ABSTRACT

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Rates of crown rust development were estimated in oats that had different degrees of slow rusting. The rates were calculated with the logistic and Gompertz models for two distances from focal centers. When disease severity was low, small increases in disease caused great increases in the logistic rate (r) compared to the changes in the Gompertz rate (k). Less statistical variation existed for k values than for r values among replications, distances from infection foci, and rating periods. The logistic transformation caused considerable variation in rusting rates for individual cultivars. The Gompertz transformation was therefore more consistent at detecting degrees of slow rusting. Rates of disease progress were measured to determine the interdependence of slow rusting and late maturity. Red Rustproof, a late-maturing oat, rusted more slowly ($k = 0.03–0.07$) than Fulghum, an early-maturing oat ($k = 0.25–0.47$). Two oat selections that matured 8 days earlier than their late-maturing parent retained the slow-rusting quality ($k = 0.02–0.09$). Disease gradients and isopathic rates were calculated to differentiate various levels of slow rusting. No differences in the slopes of the disease gradients were observed, but the isopathic rate (1 m/day) of the susceptible cultivar (Fulghum) was significantly greater than that of the slow-rusting cultivars (0.2 m/day).

Additional key words: Avena sativa, Puccinia coronata, disease progress rates.

Some cultivars of oats (*Avena sativa* L.) become rusted at slower rates than others (3,5,7,10). The unusual ability of Red Rustproof oats to retard crown rust development is manifested in two ways. The first is by "late rusting" (8). Rust occurs later in the season on a late-rusting cultivar than on a susceptible type. The second is by low receptivity. When a given number of spores are applied, fewer pustules develop on cultivars with low receptivity than on susceptible types. In this article, we use the general term "slow rusting" to denote the combined effects of late rusting and low receptivity.

Slow-rusting cultivars of oats are useful because their resistance is more stable and longer lasting than race-specific resistance (8). Slow rusting in oats is associated with several undesirable characteristics, one of which is late maturity. When plants that matured earlier than the slow-rusting parents were selected from segregating populations, some of the slow rusting was lost (7). Consequently, the use of slow rusting to control crown rust is based on the choice of a level of resistance that satisfactorily retards the rate of disease development and also maintains the desired maturity date. The objectives of this study were to assess the effects of the date of maturity on slow rusting and to find a reliable procedure to make comparisons of rusting rates in cultivars with different degrees of slow rusting.

MATERIALS AND METHODS

Fulghum (CI 708), a fast-rusting cultivar, and three slow-rusting cultivars were used in these tests. The slow-rusting types were: Red Rustproof-14 (CI 4876), Q-827-7, and Q-827-9. The latter two cultivars were F_6 progeny, selected from a cross of Fulghum and Red Rustproof-14. The selections matured about 8 days earlier than their Red Rustproof parent. These four cultivars have been exposed to natural field infection for many years (7,8). The cultivars have also been inoculated with 12 races of *P. coronata* to

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which no specificity has been expressed. We therefore assume that none of the cultivars used in this study has any race-specific (vertical [11]) resistance.

The four cultivars were planted at different dates so that they would be in the same stage of growth at the onset of the epidemic. In 1979, Red Rustproof-14 was planted on 14 November, Q-827-7 and Q-827-9 on 27 November, and Fulghum on 5 December. Each plot was surrounded by alleys 4 m wide seeded with rye (*Secale cereale* L.) on 30 November. This test was repeated in 1980. The planting dates for Red Rustproof-14, the two selections, and Fulghum were: 6 November, 16 November, and 3 December, respectively. Rye was planted in the alleys on 7 November.

Seed of the four cultivars were planted at 3 g/m with a funnel seeder in rows 30.5 cm apart. The square plots measured 4 m on a side, and the plot design for cultivars was a 4 × 4 Latin square. Stakes were placed in all plots in transects oriented in four compass directions (NE, NW, SE, and SW) to mark data collection points. The marker stakes were 1 and 2 m from the plot center; therefore, each plot had eight data collection points.

Fulghum plants used to provide inoculum were grown in a greenhouse in clay pots 15.2 cm in diameter. Plants about 25 days old were uniformly inoculated in a settling tower and maintained in a dew chamber that provided 14 hr of dew. Numerous pustules were present on the Fulghum plants used to start the epidemic (source plants) when they were transplanted in the plots. The amount of disease on the source plants was approximately equal. One source plant was planted in the center of each plot on 8 March 1979 and 5 March 1980. These dates were considered as day 0.

Disease severity was assessed on individual plants at each data collection point. The same plants were evaluated on each assessment date. In the early part of the epidemic, the numbers of pustules were counted on the leaves of each plant and their areas were calculated. Average leaf areas for individual plants were also determined and used to calculate percent infection. In the latter part of the epidemic, the Horsfall-Barratt rating scale was used (4). This assessment procedure has resulted in a relatively smooth continuum along the disease progress curve (2). Disease assessments were begun 28 March 1979 (day 20) when the plants were in the late boot stage and continued at 6- or 7-day intervals until 24 April (day 47). In 1980, disease assessment on Fulghum was begun on 24 March (day 19) and continued at 5- or 7-day intervals until 18 April (day 44). Disease assessment on Red Rustproof and the two selections was begun 31 March (day 26) and continued at 5- or 7-day intervals until 18 April (day 44).

The rates of disease progress were calculated with the logistic model as used by Vanderplank (11), ie, $r = [\text{logit}(y_2) - \text{logit}(y_1)]/(t_2 - t_1)$, where $\text{logit}(y) = \log_e[y/(1-y)]$, and the Gompertz model as used by Berger (1), ie, $k = [\text{gompit}(y_2) - \text{gompit}(y_1)]/(t_2 - t_1)$, where $\text{gompit}\ y = -\log_e[-\log_e(y)]$. We used "y" rather than "x" to denote proportions of disease. Rates for both models were calculated by the two-point method. The late-rusting characteristic of Red Rustproof and the two selections delayed the onset of disease and reduced the number of disease assessments that could be made during the epidemic. Because of the few disease assessments for a time period common to all the cultivars, the calculation of rates by linear regression or a nonlinear least squares curve-fitting procedure would not have been valid. The most accurate estimates of epidemic variables are obtained when numerous estimates ($N \sim 20$) are available for analysis (1).

RESULTS

Disease severities and infection rates. Crown rust developed earliest and fastest in the susceptible cultivar, Fulghum (Table 1). The disease proportion was 0.28 (1979) and 0.14 (1980) on Fulghum before enough rust was present on the slow-rusting cultivars to make reliable estimates. Disease severities on Fulghum were significantly higher than on the three slow-rusting cultivars for all assessment dates. The disease severities were always higher in the two oat selections than in their slow-rusting parent (Red Rustproof-14) but not significantly so.

Infection rates (r) calculated with the logistic transformation were highest for the susceptible Fulghum, but the differences from the rates of the slow-rusting cultivars were not always significant for both distances and both years. The r values were quite variable among replicates, distances, and years. The less variable infection rates (k) calculated with the Gompertz model provided reliable identification of the slow-rusting cultivars. No significant differences in k values existed among the three slow-rusting cultivars, but all rates were significantly slower than for the susceptible Fulghum.

Comparison of the logistic and Gompertz transformations. The rates of disease progress on the most resistant (Red Rustproof) and the most susceptible (Fulghum) cultivars were not significantly different when the logistic transformation was used. The lack of statistical difference occurred in 1979 and 1980 at 1 and 2 m from plot centers. Conversely, a significant difference in the rates of disease progress was always found between the resistant and susceptible cultivars when the Gompertz transformation was used. The r and k values of selections Q-827-7 and Q-827-9 were not significantly different ($P=0.05$) under any of the conditions tested. The r values of the two selections were significantly less than those of the resistant and susceptible cultivars at 1 m from plot centers but not at 2 m from plot centers. The k values of the selections were never significantly different from their slow-rusting parent, Red Rustproof.

Disease gradients and isopaths. Disease gradients and isopathic rates (spread per unit of time) were calculated as described

TABLE 1. Disease proportions and progress rates of crown rust (*Puccinia coronata*) on oat cultivars with different degrees of slow-rusting resistance[a]

		Distance from inoculum sources (m)							
		1				2			
		Proportion[b]		Rate		Proportion[b]		Rate	
Year	Cultivar	y_{min}	y_{max}	r[c]	k[d]	y_{min}	y_{max}	r[c]	k[d]
1979	Fulghum	0.5700 a	0.980 a	0.52 a	0.47 a	0.2400 a	0.940 a	0.56 a	0.45 a
	Red Rustproof	0.0017 b	0.017 b	0.31 a	0.06 b	0.0004 b	0.011 b	0.47 a	0.08 b
	Q-827-7	0.0080 b	0.018 b	0.12 b	0.03 b	0.0024 b	0.031 b	0.40 a	0.08 b
	Q-827-9	0.0068 b	0.019 b	0.14 b	0.03 b	0.0023 b	0.021 b	0.34 a	0.06 b
1980	Fulghum	0.2800 a	0.910 a	0.30 a	0.24 a	0.1400 a	0.880 a	0.35 a	0.25 a
	Red Rustproof	0.0003 b	0.005 b	0.26 a	0.04 b	0.0001 b	0.002 b	0.27 a	0.03 b
	Q-827-7	0.0034 b	0.013 b	0.13 b	0.02 b	0.0009 b	0.006 b	0.14 b	0.03 b
	Q-827-9	0.0049 b	0.022 b	0.14 b	0.03 b	0.0008 b	0.011 b	0.24 a	0.04 b

[a] Numbers in each column for each year followed by a common letter are not significantly different ($P=0.05$), according to the Duncan's multiple range test.

[b] Proportion of disease observed at the beginning (y_{min}) and the end (y_{max}) of the rating period. Each value is the average of 16 observations (four data points × four replications).

[c] Rates of disease progress using logistic transformation: $r = [\text{logit}(y_{max}) - \text{logit}(y_{min})]/(t_2 - t_1)$, in which $\text{logit} = \ln[y/(1-y)]$, and $(t_2 - t_1) = 7$ days in 1979 and 11 days in 1980.

[d] Rates of disease progress using Gompertz transformation: $k = [\text{gompit}(y_{max}) - \text{gompit}(y_{min})]/(t_2 - t_1)$, in which $\text{gompit} = -\ln[-\ln(y)]$.

previously (2). No difference in the slopes of the disease gradients for the four cultivars was observed (data not presented). The gradients did not flatten over time even when final disease severities (y_{max}) were high. The slow rusting of Red Rustproof, Q-827-7, and Q-827-9 was also expressed in the rate of isopathic movement. For these three cultivars, isopaths (moving annuli of disease of equal intensity [2]) moved peripherally at the rate of 0.1–0.2 m/day, whereas for the fast-rusting Fulghum, the rate was about 1 m/day.

DISCUSSION

Slow rusting in oats is frequently associated with late maturity (7,8). Selections that matured 8 days earlier than the slow-rusting parent had a higher disease severity than the slow-rusting parent but retained enough of their resistance to be useful in the control of crown rust. Disease progress rates of the slow-rusting parent and the earlier-maturing selections were quite similar when the data were properly transformed. In another study (7), selections that matured 12–14 days earlier than the slow-rusting parent did not have an adequate degree of slow rusting.

Kranz (6) warned plant pathologists about the uncritical selection of a transformation model without first examining the underlying distribution. Because the daily increase of disease is commonly skewed to the right, the choice of the logistic equation for linearization may be inappropriate (1). This skewness is more noticeable at disease proportions less than 0.05 (1). The fast increase of rust in our plots and the low number of common time periods of assessment among cultivars precluded us from obtaining sufficient disease comparisons to make reliable statistical estimates of linearization. However, we obtained consistent results with the Gompertz transformation for each cultivar over years, distances, and replications. The results for the logistic transformation were quite variable. The y_{max} for the slow-rusting cultivars were all 0.03 or less. This is in the range in which Berger (1) considered the logistic transformation to provide inadequate linearization. With the Gompertz transformation, cultivars with low final disease (slow rusting) were found to have rates of disease increase significantly slower than those of the fast-rusting Fulghum for both distances in both years. Such a distinction in rates between cultivars could not always be made with the logistic model.

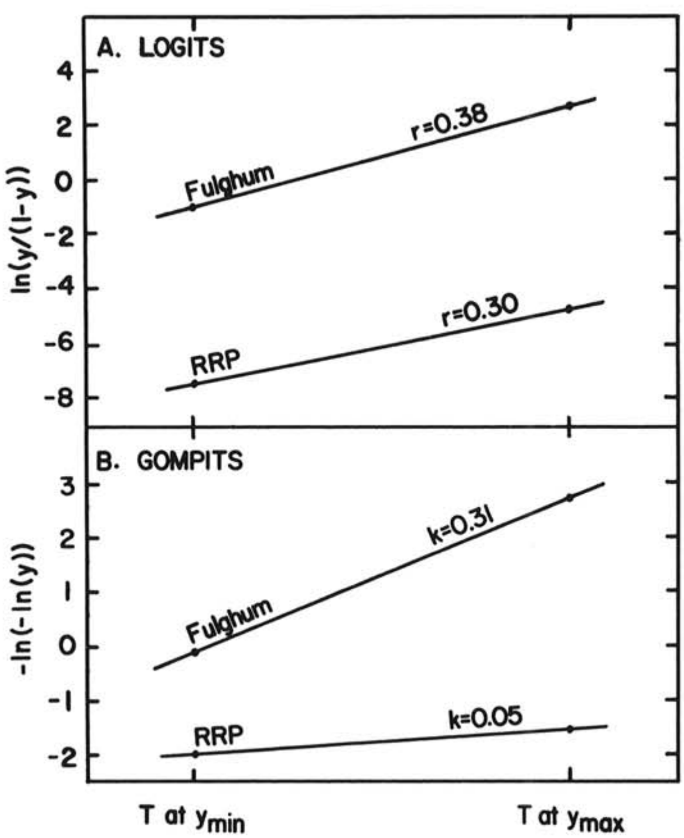

Fig. 1. Infection rates of *Puccinia coronata* on Fulghum and Red Rustproof (RRP) oats calculated with the logistic **(A)** and Gompertz **(B)** models. The rates were averaged over two distances (1 and 2 m) from the focal source, four replicates, and 2 years. The time (T) between the first disease estimate (y_{min}) and last estimate (y_{max}) common to both cultivars was 7 days in 1979 and 11 days in 1980.

The logistic transformation allows misinterpretation of epidemic rate when low disease proportions are encountered. For example, a significant difference in the infection rate existed between Red Rustproof and Q-827-7 at 1 m in 1979 even though y_{max} were virtually identical. The significant difference in infection rate was caused by the large differences in logit values (−6.38 and −4.82) for the small differences in actual disease at initial reading (0.0017 and 0.008). The logistically transformed values change markedly for slight differences in disease proportions whether these are real differences or errors in disease estimation. Such slight differences in disease proportions at low severities are not amplified when the Gompertz transformation is used (Fig. 1). No significant differences in rates were obtained when the Gompertz equation was used to calculate the same values (Red Rustproof and Q-827-7 at 1 m in 1979).

We also could have used y_{max} as a measure of slow rusting, as is typically done by plant breeders. Final disease severities are more variable among years, distances, and varieties than rates of progress. Y_{max} ratings are subject to misinterpretation if disease develops nonuniformly in the plot area. A variety that has juvenile, adult, or late-rusting resistance may be incorrectly assigned to resistance classes if ranking is based solely on final disease severity. Plant breeders should assess disease more than once during the season, using the slow-rusting characteristic. Careful examination of rusting rates should then provide a more reliable evaluation of a cultivar's potential resistance.

The isopathic rates we observed for Red Rustproof (0.2 m/day) and Fulghum (1 m/day) compare favorably with the rates reported previously (2) for these two cultivars (0.3 and 0.9 m/day, respectively). Thus, isopathic rate is another method that may be used to compare cultivars for degree of slow rusting. Apparently, disease gradients do not offer a reliable means to differentiate cultivar resistance, as MacKenzie (9) hypothesized but was unable to prove conclusively. Berger and Luke (2) also could not differentiate cultivar resistances by disease gradients. We also observed that gradients did not flatten over time even at high y_{max}. Thus, cultivars with slow rusting may be defined by a decrease in the infection rate and by the slowing of horizontal spread (isopathic rate).

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