Tolerance and Resistance to Plant Disease: An Epidemiological Study

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ABSTRACT

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Oat crown rust was used as a model for an epidemiological evaluation of concepts of tolerance and resistance to plant disease. The concepts included: "true tolerance," in which a cultivar has a susceptible infection type and supports the same amount of the pathogen as another cultivar but has significantly better yield and quality, or the same yield and quality as another cultivar but supports significantly more of the pathogen; "discriminatory resistance or susceptibility," in which the host rejects or favors certain components of the pathogen population; and "dilatory resistance," in which the host reduces the rate of pathogen development. We compared final cumulative spore counts of *Puccinia coronata* from large plots with host yield and kernel-weight ratios (rusted: healthy) from hill plots. Some cultivars had true tolerance relative to others; dilatory resistance, however, was responsible for the lower spore counts which result in higher yields compared to a susceptible check. For example, cultivar Otter was tolerant relative to Cherokee; both had nearly the same yield ratios (Otter, 0.58; Cherokee, 0.56) and kernel-weight ratios (Otter, 0.70; Cherokee, 0.67), but Otter produced more spores (177/100 liters of air) than Cherokee (90). Both had dilatory resistance compared with the susceptible check, which had the highest spore count (490) but low yield (0.32) and kernel-weight (0.55) ratios. In the greenhouse, we determined the numbers of pustules, spore yield, and pustule area on selected cultivars. Cultivars with lower spore counts in the field tended to have fewer pustules per leaf and less pustule area per leaf in the greenhouse. This may allow greenhouse selection of lines with dilatory resistance. More precise methods of pathogen assessment, such as spore collection, should be used with host yield and quality data to determine if a cultivar has tolerance or resistance relative to another; dilatory resistance may not be apparent by visual assessment.

Additional key words: *Avena sativa*, *Puccinia coronata*.

Controlling plant disease by use of host resistance and tolerance can make a major contribution toward world food production. These genetically conditioned phenomena are incompletely understood; therefore, we examined them conceptually, using epidemiological parameters.

Van der Plank (41) divided resistance into vertical and horizontal-terms that included both genetic and epidemiologic concepts of resistance. According to Robinson (31), however, there is not necessarily any relationship between the genetic and epidemiologic concepts of resistance. There are, in fact, enough exceptions to the seeming correlation between the type of genetic resistance and its epidemiological consequences that Browning et al. (3) proposed separate terms for genetic and epidemiologic concepts of resistance. For genetic concepts they suggest retaining the terms "specific resistance" and "general resistance." For epidemiologic concepts they proposed two new terms, "discriminatory resistance" and "dilatory resistance." Discriminatory means "to distinguish and treat differently" while dilatory means "to delay." Thus, "a population of host plants is defined as having discriminatory resistance or susceptibility if it affects the epidemic by discriminating among strains (i.e., by favoring or rejecting certain components of the pathogen population)" and "as having dilatory resistance if it affects the epidemic by reducing the rate of development of the pathogen population" (thus delaying the onset of the epidemic).

It is obvious that a cultivar displaying a resistant infection type is resistant. In many other instances, however, cultivars can be said to have some resistance even though they display a susceptible infection type if they support less pathogen development. This includes such phenomena as partial resistance (27, 28, 29), slow rusting (5, 17, 18, 22, 38, 42), quantitative resistance (26, 31), slow mildewing (34), moderate resistance (10), field resistance (8), and dilatory resistance (3).

Tolerance, a term that has been used in many different ways, also is used to describe a host plant's response to

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infection. The concept of tolerance suggests endurance and implies that "A" undergoes the same stress as "B" but withstands it better. In relation to plant diseases, a cultivar has "true tolerance" if it has a susceptible infection type and supports the same amount of the pathogen (i.e., the same number of spores) as another cultivar but has significantly better yield and quality (each relative to its disease-free check), or if it has the same yield and quality as another cultivar but supports significantly more of the pathogen (11, 13, 33, 35). A cultivar "A" with less disease is expected to yield more relative to its disease-free check than another cultivar "B" with more disease relative to its check; the pathogen would be using less of "A's" energy. With tolerance, however, one cultivar yields better than another while supporting the same amount of the pathogen. For example, Murphy et al. (24) found that several oat selections from a Markton × Rainbow cross produced higher yields and test weights than indicated by their crown rust coefficients (numerical equivalent of infection type multiplied by the percentage of infection) and thus may be suspected of having tolerance. From the literature on tolerance (4, 5, 9, 23, 35, 40), including that of oats (*Avena sativa* L.) to crown rust caused by *Puccinia coronata* Cda. var. *avenae* Fraser & Led., we concluded that some cultivars rated as tolerant actually had less rust than known susceptible cultivars even though the former had a susceptible infection type. For example, Caldwell et al. (4) considered cultivar Benton to be tolerant to crown rust and Clinton 59 to be susceptible. Clifford (5), however, subsequently found that Benton rusted at a slower rate than Clinton 59. Simons (35) found that "tolerance" (particularly as measured by kernel weight ratios) was correlated with the rust coefficient of infection. Thus, cultivars with less rust yielded better because of their resistance, not their tolerance. Torres and Browning (40) found that the "tolerant" oat cultivar Cherokee had a lower spore yield per uredium than did susceptible cultivars. Thus, Cherokee does not fit the definition of true tolerance. Similarly, Michel and Simons (23) found that "tolerant" cultivars had a somewhat lower percentage of leaf area covered by pustules than did susceptible ones. Thus, the better performance of these "tolerant" cultivars was due to resistance. Also, with wheat stem rust, Hayden (9) found that fewer lesions developed on "tolerant" than on nontolerant cultivars and that spread and severity of the stem rust fungus were limited in the tolerant cultivars. Again, equivalent disease was not present over the season.

In the field, the level of resistance or the rate of disease development (41) on a given host genotype to a fungal pathogen may be due to the amount of penetration (8, 10, 17, 18), rate and amount of hyphal growth (8, 10, 15, 38), latent period (8, 25, 27, 28, 29), number of lesions (6, 15, 16, 25, 26, 34, 42), lesion size (6, 10, 16, 25, 34), and/or rate and amount of sporulation (6, 8, 10, 13, 15, 34, 38). Thus, even though a cultivar has a susceptible infection type, it can be considered to have some resistance. Therefore, we undertook this research to determine epidemiologically if so-called tolerant oat cultivars are really tolerant to *P. coronata* or if they yield better because they have dilatory resistance and support less pathogen development.

Many researchers, for economy of time and money, have sought techniques for early generation selection of field-resistant plants, preferably at a young stage in the greenhouse. Therefore, a second purpose of our research was to determine, for oat crown rust, if there was a correlation between characters measured in the field, such as grain and spore yield, and characters measured in the greenhouse, such as number of pustules, spore yield, and pustule area.

MATERIALS AND METHODS

Field experiments.—*Biological material.*—These experiments were conducted in the summer of 1975. Twelve oat cultivars were chosen to represent various types of resistance and tolerance, including a resistant check (Iowa isoline X421-I), a susceptible check (Iowa isoline C649), two multilines with population resistance (3), cultivar Portage with moderate resistance (10), and lines (particularly Cherokee and Nodaway 70) reported as being tolerant (23, 40).

Four races of *P. coronata* were used: 264B, 321, 326, and 264B Ascençao. All cultivars in our field experiments had susceptible-type pustules to all four races except Portage, which was resistant to race 321, and X421-I, which was resistant to all four.

Experimental design.—Each cultivar was planted in 15 × 21 m plots in three ranges, with each range being a replication. The ranges were oriented in an E-W direction to minimize interplot movement of spores from prevailing southwest winds. Plots were separated and surrounded by a buffer planting of isoline X421-I. Hill plots of the same 12 cultivars were planted in eight replications. Hills were 30 cm apart with 30 seeds per hill. Every other row of hills was planted to X122-12 (a susceptible midseason Iowa isoline) for the rusted treatment, and to the sister isoline X421-I for the nonrusted treatment.

Inoculation.—One day after the 15 × 21 m plots were planted, four clumps (approximately 10 seeds/clump) of X122-12 were planted in each corner of each plot. Near the end of May when the plants were in the 3- to 5-leaf stage, they were inoculated with uredospores suspended in a 0.5% emulsion of Tween-20 and water by using a hypodermic syringe. We used one race for each of the four clumps in each corner of each large plot. In the rusted hill-plot treatment, every other row of X122-12 was inoculated with inoculum of two of the races, and the other rows of X122-12 were inoculated with that of the other two. Two plants per hill or clump were injected with inoculum of each race.

Maintenance.—The nonrusted hill-plot treatment was sprayed with a fungicide (Dithane M-45) every 5-7 days after secondary infection was noticed. After inoculation, temperature, dew onset and duration (1), and precipitation were recorded.

Collection and counting of spores.—When secondary infection was found (approximately 20 days after inoculation) we began spore collection. Spores were collected 24 June-13 July 1975. Sampling was done from approximately 1300 to 1500 hours CDT with 12-volt battery-operated Rotorod spore samplers mounted approximately 15 cm above the plant canopy at the periphery of each plot and downwind from the plot's center. Rod exposure time was recorded to the nearest minute. The U-shaped rods, coated with a special rubber

cement, were rotated by a small electric motor at a nominal speed of 2,400 rpm (the Rotorods, rubber cement, and motors currently are available from Ted Brown Associates, 26338 Esperanza Drive, Los Altos Hills, CA 94022). Each motor was used with the same plot throughout the experiment. The rpm of each motor was determined at the beginning and end of the experiment by using a Type 1531-AB Strobotac (General Radio Co., Concord, MA 01742), and an average was used for the calculations in each plot.

Spores were counted with an Ultropak incident-light attachment on a Leitz Labolux microscope at ×110 with a 5 × 5 or 10 × 10 square grid in the eyepiece. All spores in all grids on both leading edges of a rod were counted if there were fewer than an average of 10 spores/microscope field. Otherwise, at least 270 spores were counted, and the number of grids counted was recorded. The number of spores/100 liters of air then was calculated by the following formulas: Number of spores/100 liters of air = (number of spores on rod/volume of air sampled) × 100; number of spores on rod = number of spores counted × 112 grids/number of grids counted; and volume of air sampled = ASR × TEST, where ASR (air sampling rage) = rpm × 0.05 and TEST is total elapsed sampling time. After determing the number of spores/100 liters of air for each plot each day, we calculated a cumulative 3-day running average for each plot.

Fitting the cumulative 3-day running averages to a curve was done by the Modified Gauss-Newton method as described in TARSIER II (37) and applied by Jowett et al. (14) using the logistic equation, $Y = K/(1 + \beta e^{-\alpha t})$, where Y is the number of spores, K is the upper asymptote parameter at infinite time, β is a location parameter, and α is a parameter relating to the growth rate of the pathogen (7). These parameters were transformed to the more biologically meaningful parameters μ, M, and K, where μ (the time at which maximum growth occurs) = $\ln\beta/\alpha$, M (rate of growth at time μ) = $\alpha K/4$, and K (maximum attainable growth) = K. In terms more meaningful to plant pathologists, μ is the time when maximum spore release occurs, M is spore yield at time μ, and K is some measure of the total accumulated spore release during the course of the epidemic (or the asymptote). Because this procedure is iterative, it requires that initial guesses of the parameter values be provided, which are modified in subsequent iterations to converge on the values of best fit. We made initial guesses of α, β, and K as follows: We numbered the days (X) of spore collection beginning with 1 for the first day. From the daily data showing numbers of spores/100 liters of air, we chose μ to be the day when maximum spore release occurred. Because M is the rate of growth or slope at time μ, we let $M = \Delta Y/\Delta X$, where ΔY is the difference between the cumulative 3-day running average for the day following μ and the day preceding μ and $\Delta X = 2$ days. K was determined by drawing a graph of the cumulative 3-day running averages for each plot or cultivar and estimating the asymptote by sight or by adding a reasonable increment to the final cumulative spore count based on the last 3-day running average. Then we determined α and β by $\alpha = 4M/K$ and $\ln\beta = \mu\alpha$. After convergence was achieved for α, β, and K, we determined μ and M by $\mu = \ln\beta/\alpha$ and $M = \alpha K/4$. Analyses of variance were performed to determine the goodness of fit between the predicted curve and the observed cumulative spore counts for each cultivar.

Harvest.—Yield and kernel weight of 200 seeds from each hill plot were recorded. The ratio between the rusted and healthy plots for both yield and kernel weight was determined as follows: ratio = weight of each rusted plot/average weight of the sprayed plots of that cultivar (35).

Greenhouse experiments.—*Pustule numbers.*—For the data reported in this paper, four trials, two at the 1-wk stage and two at the 2-wk stage, were made with each oat cultivar. Ten seeds were planted per 10-cm pot in a circle with the embryo end down and the groove toward the pot center so that leaves would grow with the abaxial side out (30). Only the primary leaf was inoculated; for trials inoculated at the 2-wk stage, other leaves were removed. For each trial we removed one or more vials of uredospores of *P. coronata* races 264B or 321 from liquid nitrogen (20) and thawed them in a 45 C water bath (19). The uredospores were used at 1 mg of spores/ml of Soltrol-170, a nonphytotoxic mineral oil (Phillips Petroleum Co., Bartlesville, OK 74003) (32).

The pots were inoculated quantitatively in random order by using an aliquot inoculator attached to the side of a spore-settling turntable-tower (30). The plants were placed dry in a dew chamber set for a 12-hr 21 ± 0.5 C dew period followed by a gradual drying cycle (2). The plants were removed to a 21 C growth chamber (14-hr day) until pustules formed. Total number of pustules per leaf were counted on five leaves per pot, length of the infected area was measured, and number of pustules per 10 cm of leaf area was calculated. There was little difference in results from the two growth stages; therefore, they were combined in the analysis of each race with each trial being a replication.

Spore yield and pustule area.—Oat plants were grown singly in 15 cm polyvinyl chloride tubes with an inside diameter of 2.6 cm (12). Cotton plugs in the bottom of each tube secured soil.

Ten tubes of each of six cultivars were inoculated quantitatively 10 days after planting for each of three replications for *P. coronata* races 264B (1 mg of spores/ml of oil) and 321 (0.5 mg/ml); these were placed in the dew chamber and growth chamber as before. The tubes were secured in holes drilled through 2 × 14-cm boards. Ten holes in one side of one board accommodated the 10 tubes of one cultivar. The boards were placed on fiberglass cafeteria trays and the plants were subirrigated. Each board was attached to a wooden structure that supported two hinged aluminum frames. A strip of foil on the underside of each frame formed a spore-collecting tray (39).

About 5 days after inoculation, the primary leaves, adaxial side up, were secured with masking tape across the frame's 5-cm opening and secondary leaves were removed. Nine days after inoculation each leaf was numbered and the number of pustules over the opening were counted. Then spores were collected with a small cyclone spore collector from the adaxial side of the leaf over the opening and from the aluminum foil tray. Spores from each cultivar were collected and weighed. Seven collections were made on the same set of leaves at 2-day intervals.

To determine pustule area, we photographed four

leaves of each cultivar alongside a metric scale immediately after collecting spores. Two slides, representing two consecutive collection days, were projected simultaneously on separate screens at a magnification of ×10. Ten pustules on each cultivar were selected from the first collection day and traced onto white paper as original infection sites. Each pustule selected and traced in the first slide was traced on subsequent slides of the sequence.

Area was determined by dropping a plastic grid marked in square inches, containing 100 dots/square inch, on top of the pustule tracing. This was done three times. The number of dots that fell within the pustule tracing was converted to real area in square millimeters. Total pustule area per leaf was the product of the average number of pustules per leaf and the average area per pustule for each race-cultivar combination.

RESULTS

Field experiments.—*Spore counts.*—Predicted disease progress curves for each cultivar, as an average of three replications fitted to the logistic equation, are shown in Fig. 1. Analyses of variance to test goodness of fit for each curve showed good agreement between observed and predicted cumulative spore counts as indicated by the small F-values of the residual mean squares (authors, *unpublished*).

We were unable to fit the cumulative spore counts for three cultivars in one replication to the logistic equation, so we used our original estimates of μ, M, and K for those three cultivars in that replication to determine the means and do an analysis of variance. The mean computer estimates of μ, M, and K as well as the final cumulative spore counts for each cultivar are presented in Table 1. There was a significant difference at $P = 0.05$ for μ and at $P = 0.01$ for M, K, and the final cumulative spore counts. The susceptible check isoline C649 had the most spores, both in terms of K and final cumulative spore counts/100 liters of air, while the resistant check isoline X421-I had the least. The spores from X421-I represented spores from the spreader clumps and stray spores from other plots. The cultivar rankings for final cumulative spore counts, K, and M are nearly identical. The data on μ did not show any meaningful trend.

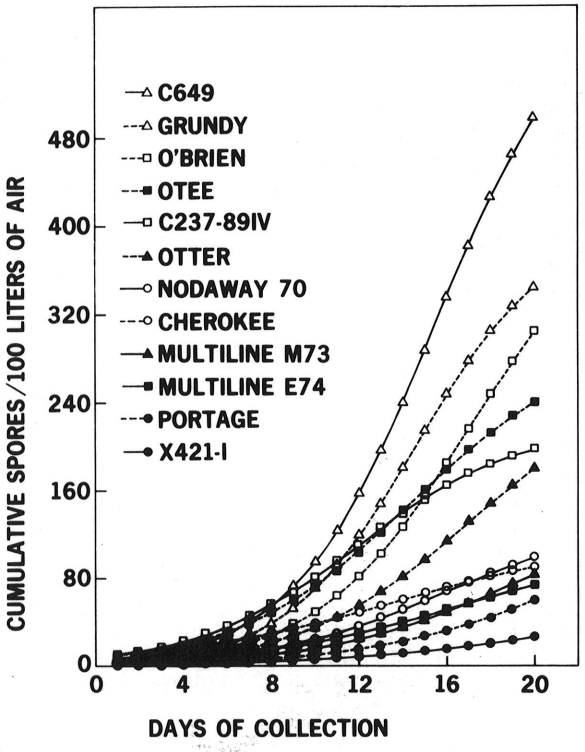

Fig. 1. Predicted disease progress curves of *Puccinia coronata* increase on each of the 12 oat cultivars in the 1975 field experiments. Cumulative spore counts per 100 liters of air are an average of three replications fitted to the logistic equation.

TABLE 1. Mean final cumulative *Puccinia coronata* spore counts (spores/100 liters of air), and mean predicted estimates of K (asymptote of total accumulated spore release), M (spore yield at time μ), and μ (time of maximum spore release) for the 12 oat cultivars in the 1975 field experiments[a]

Cultivar	Final cumulative spore count[b]	Predicted		
		K[c]	M[d]	μ[e]
C649	490	629	49	16
Grundy	348	408	34	15
O'Brien	302	402	32	16
Otee	237	285	20	14
C237-89IV	198	229	15	12
Otter	177	300	19	19
Nodaway 70	99	141	9	17
Cherokee	90	106	7	11
Multiline M73	81	101	8	16
Multiline E74	72	99	6	16
Portage	59	94	8	19
X421-I	25	36	3	16

[a]Data are averages of three replications.
[b]Standard error of the mean = 70.
[c]Spores/100 liters of air; standard error of the mean = 88.
[d]Spores/100 liters of air; standard error of the mean = 7.
[e]Days; standard error of the mean = 1.

TABLE 2. Yield and kernel-weight ratios from rusted and healthy hill plots for the 12 oat cultivars in the 1975 field experiments[a]

Cultivar	Yield ratio[b] (mean)	Kernel-weight ratio[c] (mean)
X421-I	0.85	0.89
Multiline M73	0.68	0.76
Multiline E74	0.66	0.74
Nodaway 70	0.64	0.72
Portage	0.58	0.75
Otter	0.58	0.70
O'Brien	0.58	0.61
Cherokee	0.56	0.67
Otee	0.48	0.62
C237-89IV	0.47	0.58
Grundy	0.36	0.53
C649	0.32	0.55

[a]Data are averages of eight replications.
[b]Standard error of the mean = 0.12.
[c]Standard error of the mean = 0.09.

Yield and kernel weight.—Yield and kernel-weight ratios for the 12 cultivars are presented in Table 2. Because our hill plots were lost from herbicide carryover, we used the 1975 yield and kernel-weight data from similar plots of M. D. Simons. There was a significant difference ($P = 0.01$) for yield and kernel-weight ratios. As might be expected, X421-I had the highest ratios, indicating least damage by rust. There were significant correlations between final cumulative spore counts and yield ratios (−0.85), between final cumulative spore counts and kernel-weight ratios (−0.85), and between yield ratios and kernel-weight ratios (0.93).

Greenhouse experiments.—*Numbers of pustules.*—Data on numbers of pustules per leaf and pustules per 10 cm of leaf area for races 264B and 321 are presented in Tables 3 and 4, respectively. There was a significant difference ($P = 0.01$) for numbers of pustules per leaf of both races and pustules per 10 cm of leaf area for race 264B, and ($P = 0.05$) for pustules per 10 cm of leaf area for race 321. Of the cultivars tested, Cherokee always had the fewest pustules per leaf and pustules per 10 cm of leaf area, and Portage was nearly the same with race 264B (Portage is resistant to race 321). Bonkee, a Cherokee derivative, acted similarly to Cherokee with race 264B. Isoline C649, the susceptible check in our field experiments, ranked near the top with both races. Nodaway 70, which had a relatively low spore count in the field, also ranked low with both races (data not shown for race 264B). There were significant correlations between final cumulative spore counts in field experiments and pustules per leaf with both races 264B (0.94) and 321 (0.89), but not between final cumulative spore counts and pustules per 10 cm of leaf area.

Spore yield and pustule area.—Cumulative spore yield (milligrams per 10 leaves) of race 264B for each cultivar is shown in Fig. 2-A. There was a significant difference ($P = 0.01$) among cultivars for 9 days after inoculation and at $P = 0.05$ for 11 and 13 days. For 9, 11, 13, and 15 days, C649 had the highest cumulative spore yield per leaf, and for 17, 19, and 21 days, Grundy was the highest. Portage was the lowest for all dates. Cherokee started relatively low but increased toward the end. For final cumulative spore yield per leaf, Grundy yielded highest, Cherokee and C649 second, Red Rustproof-14 third, Markton fourth, and Portage last.

Cumulative spore yield (μg/pustule) of race 264B for each cultivar is shown in Fig. 2-B. There was a significant difference ($P = 0.05$ or $P = 0.01$) among cultivars for all collection times. Isoline C649 had the highest cumulative spore yield per pustule for 9 days after inoculation but Grundy had the highest for subsequent days. Portage yielded the smallest amount of spores per pustule for 9, 11, 13, and 15 days, and isoline C649 yielded the least for 17, 19, and 21 days. Portage started relatively low but increased toward the end, and C649 started relatively high and then decreased. For final cumulative spore yield per pustule, Grundy yielded highest, Cherokee second, Portage third, Markton and Red Rustproof-14 fourth, and C649 last.

Cumulative spore yield (milligrams per 10 leaves) of race 321 for each cultivar is shown in Fig. 2-C. There was a significant difference ($P = 0.05$ or $P = 0.01$) among cultivars for all collection times. Isoline C649 had the highest cumulative spore yield per leaf each time. The lowest was Red Rustproof-14 for 9 days, Otter for 11 days, and Grundy for the other days. For final cumulative spore yield per leaf, isoline C649 yielded highest; Markton second; Cherokee, Red Rustproof-14, and Otter third; and Grundy last.

Cumulative spore yield (μg/pustule) of race 321 for each cultivar is shown in Fig. 2-D. There was a significant difference ($P = 0.05$ or $P = 0.01$) among cultivars for all collection times. Isoline C649 had the highest cumulative spore yield per pustule for 9 and 11 days, Cherokee for 13 and 15 days, and Red Rustproof-14 for 17, 19, and 21 days. Grundy was always lowest or tied for lowest. Otter started relatively low and increased, and C649 started relatively high and decreased. For final cumulative spore yield per pustule, Red Rustproof-14 yielded highest, Markton and Cherokee second, Otter third, and C649 and Grundy last.

The numbers of pustules per leaf, area per pustule, and total pustule area per leaf of races 264B and 321 are

TABLE 3. Pustules per leaf and pustules per 10 cm of leaf on primary leaves of 12 oat cultivars inoculated quantitatively with *Puccinia coronata* race 264B[a]

Cultivar	Pustules/leaf[b] (mean no.)	Pustules/10 cm[c] (mean no.)
C237-89III	58	62
C649	58	59
X122-12	55	58
Clinton	53	64
Markton	52	57
Red Rustproof-14	50	51
Otee	49	58
Grundy	47	54
Stout	46	51
Bonkee	43	48
Portage	40	50
Cherokee	40	44

[a]Data are averages of four replications, two inoculated at the 1-wk stage and two at the 2-wk stage.
[b]Standard error of the mean = 4.
[c]Standard error of the mean = 3.

TABLE 4. Pustules per leaf and pustules per 10 cm of leaf on primary leaves of 11 oat cultivars inoculated quantitatively with *Puccinia coronata* race 321[a]

Cultivar	Pustules/leaf[b] (mean no.)	Pustules/10 cm[c] (mean no.)
C649	79	72
X122-12	76	71
C237-89III	75	70
Markton	69	64
C237-89IV	63	72
Grundy	63	63
O'Brien	60	58
Red Rustproof-14	59	60
Otter	59	66
Nodaway 70	56	62
Cherokee	56	51

[a]Data are averages of four replications, two inoculated at the 1-wk stage and two at the 2-wk stage.
[b]Standard error of the mean = 5.
[c]Standard error of the mean = 4.

presented in Tables 5 and 6, respectively. There was no significant difference among cultivars for the number of pustules per leaf of race 264B, but there was a significant difference at $P = 0.01$ for area per pustule. Isoline C649 had the most and Cherokee the largest pustules, Grundy and Portage had the fewest, and Portage the smallest pustules. There was a significant difference ($P = 0.01$) among cultivars for the number of pustules per leaf of race 321 and at $P = 0.05$ for area per pustule. Isoline C649 had the most and Red Rustproof-14 the largest pustules, whereas Red Rustproof-14 had the fewest, and Otter and Grundy the smallest pustules. Isoline C649 had the most total pustule area per leaf of both races 264B and 321. Portage had the least pustule area per leaf of race 264B, whereas Otter and Grundy had the least of race 321.

With race 264B, there were significant correlations between area per pustule and total pustule area per leaf (0.85), and between pustules per leaf and final cumulative spore yield per pustule (−0.86). Cultivars with more pustules per leaf also tended to have more total pustule area per leaf and higher final cumulative spore counts in field experiments.

With race 321, cultivars with more pustules per leaf tended to have a lower final cumulative spore yield per pustule (due to crowding of the pustules), more total pustule area per leaf, and higher final cumlative spore counts. Cultivars with more total pustule area per leaf tended to have a higher final cumulative spore yield per leaf and higher final cumulative spore counts. Also, cultivars with a higher final cumulative spore yield per pustule (due to fewer pustules) tended to have lower final cumulative spore counts.

DISCUSSION

One goal of our epidemiological study was to determine if so-called tolerant oat cultivars really are tolerant to *P. coronata* or if they yield better than nontolerant cultivars because they support less pathogen development. A cultivar has "true tolerance" if it has a susceptible infection type and supports the same amount of the pathogen as another cultivar but has significantly better yield and quality (each relative to its disease-free check), or it has the same yield and quality as another cultivar but supports significantly more of the pathogen. Thus, cultivar "A" can be said to have tolerance when compared with "B", but to have moderate resistance or slow rusting compared with "C", as in the work of Clifford (5). In the strictest sense, a cultivar with true tolerance does not necessarily have a susceptible infection type as long as it endures the same amount of the pathogen as another cultivar but has better yield and quality. For practical purposes, however, one need not test a plant for tolerance if it has a resistant infection type, even if there is some reproduction of the pathogen, because the cultivar will be useful in a breeding program on the basis of its visible resistance. Of course, if a cultivar with a susceptible infection type has a greatly reduced number of lesions, which is visually discernible, one probably can say that the cultivar has moderate resistance without subjecting it to yield and quality tests to determine ratios between diseased and healthy plots. In situations where the moderate resistance is not so apparent visually, tests of host yield and quality and pathogen yield must be made to determine whether the cultivar has resistance or tolerance.

Characterization of the cultivars we studied indicates that Otter has tolerance compared with Cherokee; both had essentially the same yield and kernel-weight ratios (Table 2), but Otter had a higher final cumulative spore count than Cherokee (Table 1). Otee, compared with C237-89IV, has some tolerance because it produced more spores but had higher ratios. Portage, Otter, and O'Brien each had yield ratios of 0.58 although they had different final cumulative spore counts. On this basis alone, O'Brien could be considered the most tolerant of the three because it produced the most spores. This trend, however, is not evident when one considers kernel-weight ratios; O'Brien, the cultivar with the most spores, had the lowest kernel-weight ratio of the three, while Portage, the cultivar with the fewest spores, had the highest kernel-weight ratio. Kernel weight is the main yield component affected by crown rust in the Midwest (36), and we found that, in general, cultivars with more rust have lower kernel-weight ratios.

Even though some cultivars had some true tolerance compared with other cultivars, resistance, not tolerance, was responsible for the lower spore counts which result in higher yields when compared to the susceptible check. We conclude that cultivars with the lower spore counts in our field experiments, except X421-I (none of the races used can reproduce on it), have slow rusting or moderate resistance.

TABLE 5. Pustules per leaf, mean area per pustule, and total pustule area per leaf on primary leaves of six oat cultivars inoculated quantitatively with *Puccinia coronata* race 264B[a]

Cultivar	Pustules/leaf[b] (mean no.)	Area/pustule[c] (mm^2)	Total pustule area/leaf (mm^2)
C649	32	0.26	8.32
Red Rustproof-14	27	0.25	6.75
Markton	26	0.24	6.24
Cherokee	24	0.31	7.44
Grundy	23	0.23	5.29
Portage	23	0.17	3.91

[a]Data are averages of three replications.
[b]Standard error of the mean = 2.
[c]Standard error of the mean = 0.03.

TABLE 6. Pustules, per leaf, mean area per pustule, and total pustule area per leaf on primary leaves of six oat cultivars inoculated quantitatively with *Puccinia coronata* race 321[a]

Cultivar	Pustules/leaf[b] (mean no.)	Area/pustule[c] (mm^2)	Total pustule area/leaf (mm^2)
C649	29	0.28	8.12
Markton	20	0.20	4.00
Grundy	20	0.14	2.80
Otter	19	0.15	2.85
Cherokee	15	0.24	3.60
Red Rustproof-14	14	0.31	4.34

[a]Data are averages of three replications.
[b]Standard error of the mean = 4.
[c]Standard error of the mean = 0.05.

Because the term "slow rusting" should be used only for rust diseases, it would be helpful to have another term that could describe this phenomenon for all diseases. Browning et al. (3) proposed separate terms for genetic (specific and general) and epidemiologic (discriminatory and dilatory) concepts of resistance. Because our study

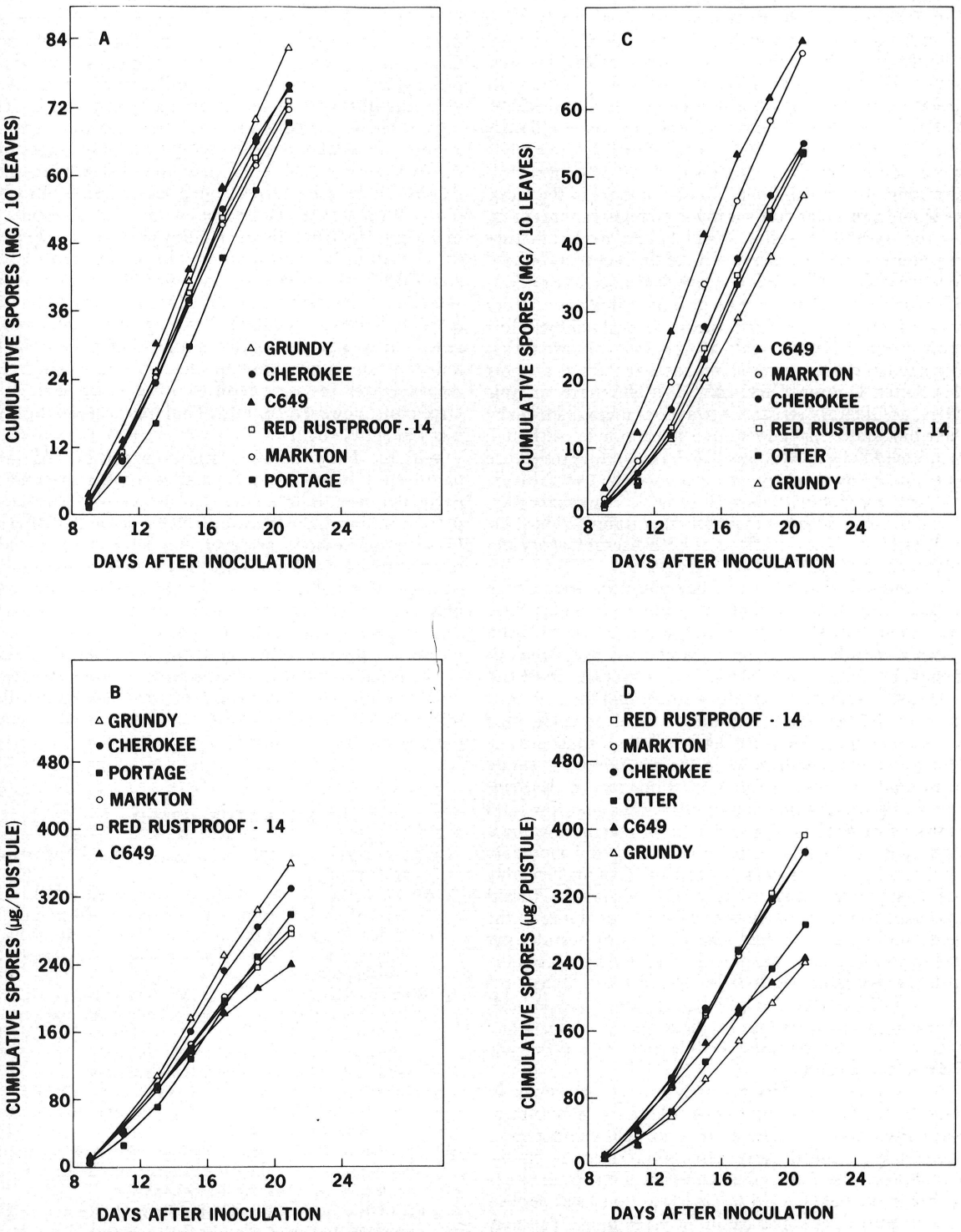

Fig. 2-(A to D). Cumulative spore yield of *Puccinia coronata* on primary leaves of six oat cultivars for different days after inoculation: **A)** milligrams of spores of race 264B from 10 leaves; **B)** micrograms of spores of race 264B per pustule; **C)** milligrams of spores of race 321 from 10 leaves; and **D)** micrograms of spores of race 321 per pustule.

was an epidemiological one, we will characterize the cultivars we used only in terms of epidemiologic concepts of resistance. Of course, all cultivars, except X421-I, have some dilatory resistance compared to C649.

Thus, from our field experiments with four races of *P. coronata*, isoline C649 lacks discriminatory resistance to all four races; it had a high 1975 final cumulative spore count. Grundy has dilatory resistance to at least one race but discriminatory susceptibility to the others because its spore count was high, but not as high as that of C649. Nodaway 70 and Cherokee probably have dilatory resistance to all four races because of their relatively low spore counts. If either Nodaway 70 or Cherokee had discriminatory susceptibility to one or more of the races, we would expect the cultivar to have a higher spore count, as for Grundy. Isoline X421-I has discriminatory resistance to all four races; none of the races reproduced on it. Portage has discriminatory resistance to race 321; this race did not reproduce on it. It probably has dilatory resistance to the other three races as measured by its low spore count. Heagle and Moore (10) reported that Portage has moderate resistance, and our results support this. Otter, O'Brien, Otee, and C237-89IV have varying degrees of dilatory resistance to all four races as shown by their moderate final cumulative spore counts. Although Multiline M73 and Multiline E74 have dilatory resistance as indicated by their low spore counts, the two cultivars are synthetic populations with some races increasing on some isolines and some races on other isolines. Thus, the multilines combine the effects of both discriminatory and dilatory resistance.

Greenhouse data also can be helpful in determining whether a cultivar has dilatory resistance to a particular race even though there is not a perfect correlation between greenhouse and field characters. Thus, from our greenhouse experiments with *P. coronata* races 264B and 321, C649 (with discriminatory susceptibility to all four races in the field) had high numbers of pustules, high cumulative spore yield per leaf, and high total pustule area per leaf of both races in the greenhouse. Grundy (with dilatory resistance to at least one race in the field) had a low spore yield, small pustule size, and low total pustule area per leaf of race 321 in the greenhouse, but a high spore yield, moderate pustule size, and moderate total pustule area per leaf for race 264B; Grundy probably has dilatory resistance to race 321. Nodaway 70 and Cherokee (both probably with dilatory resistance in the field to all four races) had low numbers of pustules per leaf for both races in the greenhouse. Portage (probably with dilatory resistance to three races in the field) had low numbers of pustules, low cumulative spore yield per leaf, moderate cumulative spore yield per pustule, small pustule size, and low total pustule area per leaf for race 264B in the greenhouse.

Another goal of this research was to determine if, relative to dilatory resistance, there is a sufficient correlation between greenhouse and field characters to conduct economical early generation selection in the greenhouse. We found that cultivars with lower spore counts in the field tended to have fewer pustules per leaf and less pustule area per leaf in the greenhouse. This may allow greenhouse selection of lines with dilatory resistance. However, one should not expect all characteristics of resistance to be found on a single plant or cultivar. Resistance may be manifested in different ways by different genotypes, and it may be possible to combine these into one genotype by breeding (3, 8).

Therefore, it is obvious that cultivars can have some resistance even if they have a susceptible infection type as long as there is a significant reduction in pathogen development on the host plant. This reduction could be in terms of fewer lesions, smaller lesions, or fewer propagules, *even if this cannot be detected visually*. Host yield and quality data would give an indication of it. The high negative correlation between final cumulative spore counts and yield and kernel-weight ratios indicates that field selection of cultivars with dilatory resistance should be possible by using ratios from diseased and healthy hill plots. With visual assessment, it may be necessary to make more than one disease reading per season to find the time when differences among cultivars are most easily seen (21). This is especially true for hill plots in which a susceptible spreader is inoculated artificially and there is an abundance of inoculum. Readings made later in the season may not reveal differences that were visually apparent earlier because later the resistant cultivar may seem to reach the same level of rust development. With large plots, however, the rate of buildup is not so rapid on less susceptible cultivars.

Without fairly precise measurements of host and pathogen yield, it is not possible to say whether a particular host is tolerant or resistant to a particular pathogen when there is an appreciable amount of disease. Less precise methods, however, may cause a cultivar to be rated as tolerant when it is not. This would be the interim concept of tolerance (33) because later measurements may show that the cultivar is resistant. Indeed, it would be safer to assume that a cultivar is resistant if it has less yield reduction than another cultivar until more precise methods show that it is tolerant; true tolerance seems to be a rare phenomenon. Much of what has been called tolerance is dilatory resistance, but there is need to retain the concept of true tolerance.

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