Development of Crown Rust Epidemics in Genetically Diverse Oat Populations: Effect of Genotype Unit Area

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ABSTRACT

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Crown rust of oats was used as a model to test the effect of genotype unit area (the ground area occupied by an individual, independent unit of the host population that is genetically homogeneous) on the disease-reducing effectiveness of genetically diverse host populations. Multilines with differing genotype unit areas were obtained by arranging near-isogenic oat lines (isolines) into units of the same genotype and randomly positioning these units within plots, while keeping the proportions of isolines constant among multiline treatments. In 1980, mixtures of four isolines were used and disease progression was quantified by trapping uredospores over the plots with Rotorod spore samplers. In 1981, mixtures of an immune and a susceptible isoline were used and rust severity was estimated on the susceptible isoline at one point in time. Increasing genotype unit area from 0.003 to 0.84 and 0.58 m^2 in 1980 and 1981, respectively, had no significant effect on the efficacy of the multilines relative to a pure-line susceptible check.

Additional key words: *Avena sativa*, disease resistance, epidemiology, genetic diversity, *Puccinia coronata*.

With some crops, such as small grains, pure-line cultivars possessing single, race-specific genes for resistance to plant pathogens have been grown extensively (5,17). Such cultivars may initially provide immunity or a high level of resistance to most of a pathogen population. In some pathosystems, however, virulent genotypes increase rapidly in the pathogen population and, within a few years, render the resistance gene ineffective (4,5). For example, Kilpatrick (14) presented data indicating that the average life expectancy of race-specific genes for resistance to leaf rust (induced by *Puccinia recondita*), stem rust (induced by *P. graminis*), and stripe rust (induced by *P. striiformis* of wheat (*Triticum aestivum*) is about 5 yr.

Attempts have been made to increase the genetic diversity of crops to provide a more stable agroecosystem. Jensen (12) proposed the culture of multiline oat (*Avena sativa*) cultivars to buffer against biotic and abiotic sources of stress. Multilines, as Jensen proposed, would be mixtures of different genotypes that are phenotypically similar for important agronomic traits, but as genetically diverse as possible for all other traits, including disease resistance. Some multilines have been developed by mixing near-isogenic crop lines that possess different race-specific resistance genes (8,10). Wolfe and Barrett (30) have successfully used mixtures of different cultivars of barley (*Hordeum vulgare*) to manage powdery mildew (induced by *Erysiphe graminis*). Others have chosen diversification strategies intermediate between these two approaches (3,6,9).

Propagules that are retained on the same genotype on which they were produced will be unaffected by host mixtures (except for the effects of induced resistance and other competitive interactions among pathogen genotypes). Therefore, a low proportion of autoinfection sensu Robinson (23) has been hypothesized to increase the effectiveness of host mixtures for disease control (1,19). With small grains, plants are small and there may be a relatively low proportion of autoinfection. For example, the autoinfection rate of *P. graminis* on oats has been estimated to be 5–10% (18). McCartney and Bainbridge (20) calculated that only 1–2% of 20-μm particles produced on a barley plant would be deposited on the source plant. The epidemiological effectiveness of multilines and cultivar mixtures has been demonstrated for certain foliar diseases of small grains (4,11,30). With mixtures of crops with large plants, and with alternative gene management strategies such as intercropping and interfield diversity, however, one might expect a significant increase in the proportion of autoinfection and, therefore, a decrease in the effectiveness of the mixture. For example, it has been hypothesized that multilines will be most effective for crops with small plants (page 144 in Vanderplank [27]). Wolfe, in a discussion included with a paper by Wolfe and Barrett (29) stated, "... observation would suggest that even if you have alternate rows, certainly if you have different swaths of different varieties, then you lose a fair amount of this (the mixture) effect."

The purpose of our research was to use oat crown rust as a model determine the effect of genotype unit area on the disease-reducing effectiveness of genetically diverse host populations. In this paper, genotype unit area is considered to be the ground area occupied by an individual, independent unit of the host population that is genetically homogeneous. For example, in a random mixture of plants (as in a multiline or cultivar mixture), the genotype unit is a single plant and the genotype unit area is the ground area occupied by that plant. With interfield diversification, where plants within a field are of the same genotype but different genotypes are grown in different fields, the genotype unit area is the area of a field.

MATERIALS AND METHODS

Experiment in 1980. The experiment was located 8 km southwest of Ames, IA. The field plots were arranged in three blocks in a randomized complete block design with 40 m between blocks. Each plot was 6.4 × 6.4 m with 15.2 m between plots. The blocks were oriented in an east-west direction to minimize interplot interference within blocks due to predominant southerly winds. The areas

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between plots and an area 6 m to the north and south of the blocks were planted to soybeans (*Glycine max*) which, because no weed control practices were used, became a dense stand of weeds. The remaining areas between blocks were planted to sunflowers (*Helianthus annuus*).

The plots were planted on 14 and 15 April 1980. Seeds were planted in hills of eight seeds per hill on a 15.2-cm equidistant spacing. The field received 101 and 67 kg/ha of P_2O_5 and K_2O, respectively, in the autumn of 1979. No additional fertilizer was applied. Propachlor herbicide was applied at the rate of 2.8 kg a.i./ha before emergence of the oats. The plots were hoe-cultivated to provide additional weed control.

There were seven treatments. Treatment 1 was of a pure stand of C649 (C.I. 7555, the recurrent parent of the Iowa M-series multilines) (7). Treatments 2–6 were all 1:1:1:1 mixtures of four near-isogenic lines (isolines) of the Iowa M-series multilines (7) (X104c-7, X424, X422-III, and X449-I) planted in spatial arrangements to give five genotype unit areas. Treatment 2 consisted of plots in which seeds of the four isolines were mixed before being packaged for planting (genotype unit area = the ground area occupied by a single oat plant = ~ 0.003 m^2). In treatments 3–6, all seeds within a hill were of the same isoline, and the hills were arranged in groups of 1, 2, 9, and 36 hills of like genotype to attain genotype unit areas of 0.023, 0.046, 0.21, and 84 m^2, respectively. The locations of these genotype units within plots were random as determined by a computer program of the Iowa State University Statistical Computing Laboratory. Treatment 7 was of a pure stand of isoline X421 (7), which is immune from all crown rust (*Puccinia coronata*) races used in the experiment.

TABLE 1. Reactions of near-isogenic oat lines to races of *Puccinia coronata* used in the 1980 experiment

Isoline	Races of *Puccinia coronata*			
	264B-Ascençao	290	294	326
C649	S[a]	S	S	S
X421	R	R	R	R
C104c-7	MR	R	MS	MS
X422-III	S	MR	S	S
X424	MS	R	R	R
X449-I	MS	MS	S	MS

[a] S = susceptible, R = resistant, and M = moderately.

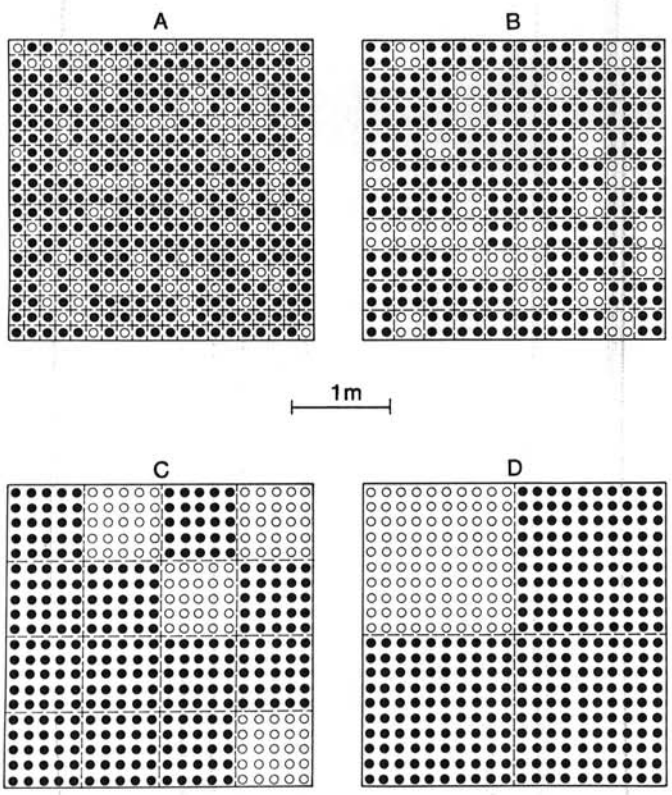

Fig. 1. Examples of hill arrangements used in the 1981 oat crown rust epidemiology experiment. Each circle represents one hill of eight oat plants. Open circles = C649 (susceptible); closed circles = X421 (immune). **A,** treatment 3, multiline (genotype unit area = 0.023 m^2); **B,** treatment 4, multiline (genotype unit area = 0.093 m^2); **C,** treatment 5, multiline (genotype unit area = 0.581 m^2); and **D,** treatment 6, quadrants (genotype unit area = 2.322 m^2).

Clintford oats, growing in a nearby field, were transplanted to plastic pots (4–10 plants per pot). Plants in each pot were inoculated quantitatively on 23 May with one of the following races of *P. coronata*: 264B-Ascençao, 290, 294, or 326. After the onset of flecking, leaves were trimmed to obtain approximately equal numbers of pustules/pot /race. Four pots of plants, each inoculated with one of the four races, were placed in the center of the southern edge of each plot on 30 May. They were watered daily until 7 June, when flecks were observed that indicated secondary spread in the plots and the spreader plants were removed. The reactions of the oat isolines to the four rust races used in the experiment are given in Table 1.

Disease progression was measured by trapping uredospores over each plot with a Rotorod spore sampler (Ted Brown Associates, 26338 Esperanza Drive, Los Altos Hills, CA) fitted with U-shaped impaction rods coated with rubber cement. The 21 samplers were operated ~15 cm above the oat canopy on the downwind edge of each plot on alternate days for ~2 hr (1200-1400 CDT) from 16 June-8 July. The sampling time for each plot was recorded to the nearest minute. The number of uredospores trapped/100 L of air was calculated for each plot on each sampling day as described by Politowski and Browning (22). Two-sampling-day running averages of the spore counts were calculated to reduce fluctuations in the data due to environmental differences among sampling days. The running averages were cumulated over time and produced sigmoid spore-count curves. The area under the curve (AUC) was calculated for each plot as described by Shaner and Finney (24), except that the cumulative spore count was substituted for the disease severity rating.

The statistical significances of differences in the AUC among treatments were determined by analysis of variance. Linear contrasts were used to determine the significance levels for differences between C649 and X421, C649 and the mean of the multilines, and between X421 and the mean of the multilines. Polynomial regression of AUC on the square root of genotype unit area was used to determine the proportion of the treatment sums of squares due to genotype unit area among multiline treatments. All analyses were performed with the Statistical Analysis System (25).

Experiment in 1981. The experiment was located 5 km northeast of Ames, IA. The field plots were arranged in a 6 × 6 Latin square. Each plot was 3.0 × 3.0 m with 3.0 m between plots within rows and columns of the Latin square. The areas between plots and an area ~4 m around the perimeter of the experiment were planted to isoline X421 (immune from all races of *P. coronata* used on the experimental farm in 1981).

The plots were planted on 10 April 1981 as described for the 1980 experiment. Before planting, all seeds were treated with carboxin (Vitavax 200F) at the rate of 0.9 g a.i./kg of seeds. The entire experimental area received 28.0 kg/ha each of N, P_2O_5, and K_2O at planting. The plots received two additional fertilizer applications consisting of 16.8 kg/ha each of N, P_2O_5, and K_2O at the time of jointing and 11.2 kg/ha each of N, P_2O_5, and K_2O at heading. Propachlor herbicide was applied before oat emergence at the rate of 3.4 kg a.i./ha. Bentazon was applied as a postemergence herbicide treatment at the rate of 1.1 kg a.i./ha. The plots were hoe-cultivated for additional weed control. The experiment was overhead irrigated as necessary to sustain adequate oat growth. In addition, the experiment was overhead irrigated for ~30 min at dusk each evening from 16 May to 12 June to ensure adequate leaf wetness for uredospore germination.

There were six treatments. Treatment 1 was of a pure stand of C649 (susceptible). Treatments 2-6 consisted of 25% C649 and 75%

X421 (immune). Treatment 2 consisted of plots in which seeds of the two isolines were mixed before being packaged for planting. In treatments 3-6, all seeds within a hill were of the same isoline, and the hills were arranged in groups of 1, 4, 25, and 100 hills of like genotype (Fig. 1). Locations of these groups within plots were determined as described for the 1980 experiment. In treatment 6, aggregation of genotypes was taken to the extreme; the susceptible isoline occupied one quadrant of the plots and the immune isoline occupied the other three quadrants. Thus, this treatment differed from the multiline treatments because the susceptible and immune genotypes were not intermixed.

Hills of field-grown C649 oats (15 plants per hill) were transplanted to plastic pots. Plants in each pot were inoculated quantitatively on 9 May with race 264B of *P. coronata*. On 16 May, when the inoculated plants were heavily flecked, they were transplanted, one pot per plot, into the centers of the field plots. Plants of approximately equal vigor and degree of infection were used. The transplants were removed after rust was established in the plots.

The plots were sampled destructively on 23–28 June to estimate rust severity. By using standard area diagrams (21), the percentage severity was estimated for each susceptible hill in the plots. Only the penultimate leaves (the first leaves below the flag leaves) were rated, and the percentage severity was averaged visually over all plants within a hill. Rust severity ratings were based on sporulating pustules; flecking was ignored. In treatment 2, in which C649 and X421 plants were mixed within hills, only infected plants were rated, infection being the only detectable indication of the susceptible isoline. One column of plots in the Latin square was rated per day. There was little increase in the number of pustules observed in the plots during the six-day rating period. Data were expressed as the mean rust severity on susceptible plants for each plot. Two values were eliminated from the data, one because of extremely poor growth of a plot and the other because of a suspected error in disease assessment.

The statistical significances of differences in rust severity among treatments were determined by analysis of variance. Linear contrasts were used to determine significance levels for differences between C649 and the quadrants treatment, C649 and the mean of the multilines, and between the quadrants treatment and the mean of the multilines. Polynomial regression of rust severity on the square root of genotype unit area was used to determine the proportion of the treatment sums of squares due to genotype unit area among multiline treatments. All statistical analyses were performed with the Statistical Analysis System (25).

RESULTS

Experiment in 1981. Few spores were trapped over the X421 (pure-line immune) plots relative to the other treatments (Fig. 2). The AUC for the X421 treatment was only 1.3 and 8.1% of the AUC for C649 (pure-line susceptible) and the mean of the multiline treatments, respectively. Analysis of variance indicated that the AUC of X421 was different from that of C649 and the mean of the multiline treatments at significance levels of <0.0001 and 0.02, respectively. Thus, interplot interference probably did not contribute significantly to the numbers of spores trapped over the plots.

Cumulative spore count curves for the five multilines were similar (Fig. 2), and their AUCs ranged from 11 to 22% of that for C649. The AUC for the mean of the multiline treatments was different from that of C649 at a significance level of <0.0001. When the AUC was regressed on the square root of genotype unit area for the multiline treatments, the linear and quadratic components of the polynomial model were significant only at $P = 0.78$ and 0.24, respectively.

Experiment in 1981. Genotype unit area had little effect on rust severity in the multilines. Rust severity on the susceptible isoline increased from 9.9 to only 11.3% over a 200-fold increase in genotype unit area (Table 2.). When the AUC was regressed on the square root of genotype unit area for the multiline treatments, the linear and quadratic components of the polynomial model were significant only at $P = 0.31$ and 0.67, respectively. The mean rust severities for pure-line C649, the quadrants treatment, and the mean of the multiline treatments were 20.0, 14.0, and 10.5%, respectively (Table 2). Differences among these three groups of treatments were all significant at $P = 0.02$ or less.

TABLE 2. Effect of spatial arrangement of susceptible (C649) and immune (X421) oats on the increase of crown rust in multilines consisting of 25% susceptible and 75% resistant plants and in pure stands of susceptible plants in 1981

Treatment	Genotype unit area (m^2)	Rust severity[b] (%)
Pure-line C649	9.290	20.0
Multiline	0.003	9.9
Multiline	0.023	9.9
Multiline	0.093	11.0
Multiline	0.581	11.3
Quadrants[a]	2.322	14.0

[a] Plots of 25% C649 and 75% X421 in which all susceptible plants were contained within one quadrant of the plots and all immune plants were contained within the other three quadrants.

[b] Mean percentage rust severity on penultimate leaves (first leaves below the flag leaves) of C649. Each value is the mean of six replicates.

DISCUSSION

Results from experiments in both 1980 and 1981 indicate that, over the range tested, crown rust development in multilines was insensitive to changes in genotype unit area and was appreciably reduced relative to a pure-line check even when the genotype unit areas were relatively large (up to 0.84 and 0.58 m^2 in 1980 and 1981, respectively). Barrett and Wolfe (2) gave a brief report regarding a field experiment designed to determine the effect of genotype unit

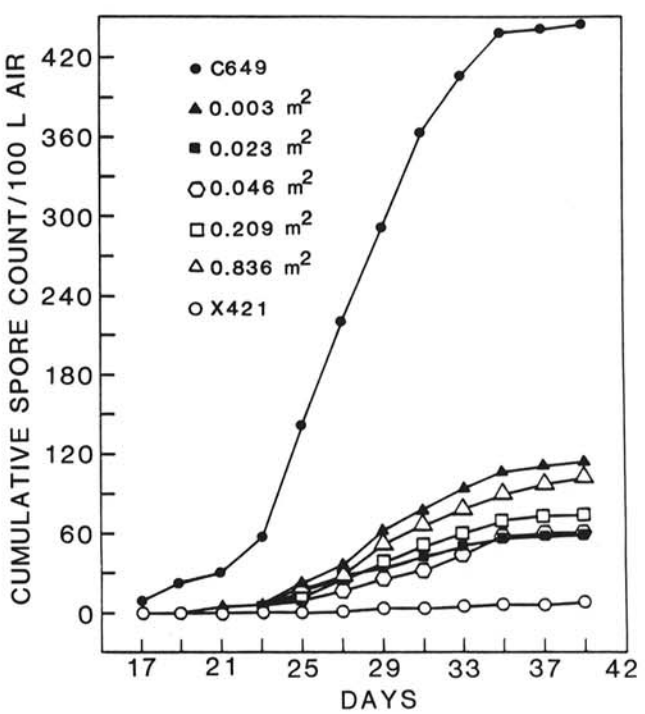

Fig. 2. Cumulative counts of uredospores of *Puccinia coronata* per 100 L of air over field plots of oats in 1980 versus days after appearance of pustules resulting from artificial inoculation. C649 = pure-line susceptible population; X421 = pure-line immune population; all other treatments were multilines consisting of equal percentages of four near-isogenic oat lines in which seeds were arranged within plots to attain genotype unit areas of 0.003, 0.023, 0.046, 0.209, and 0.836 m^2 (see text for details). Each data point is a two-sampling-day running average and is the mean of three replications.

area on epidemic development of powdery mildew in a three-component barley cultivar mixture. Their experimental approach was based on the assumption that, with barley, there is a small increase in the number of tillers per unit area but a large decrease in the number of tillers per plant as sowing density is increased. Thus, they expected that with increasing sowing density there would be a decrease in plant size. They found that the relative spore output for the mixture was 30, 21, and 6 at sowing densities of 80, 160, and 240 kg/ha, respectively, compared with 48 for the mean of the components sown in pure stand at 160 kg/ha. The authors stated that the effect of sowing density was "... in addition to the slowing of the epidemic due to the closing of the canopy and possible reduction of nutrients in individual tillers in the denser stands." Thus, the results of Barrett and Wolfe (2) suggest that the effectiveness of barley cultivar mixtures in reducing epidemic development of powdery mildew decreases substantially as genotype unit area is increased. The difference between the results of Barrett and Wolfe (2) and the results reported in this paper could be due to differences in the environment, disease, or experimental approach between their study and ours.

Our results suggest that host mixtures may contribute significantly to disease control in crops and cropping systems where the genotype unit area is large. There are several factors, however, that may interact with genotype unit area to determine the efficacy of host mixtures for disease control. For example, mathematical models suggest that the steepness of the spore dispersal gradient will affect the efficacy of host mixtures (15,16). Using EPIMUL, (13) a computer simulation model, Zadoks and Kampmeijer (31) addressed the small-field versus large-field controversy that was discussed earlier by Vanderplank (26) and Waggoner (28). Their results suggested that the relative effectiveness of small versus large fields for the control of plant disease will depend on several factors including the frequency, size, and distribution of susceptible fields; the number, position, and size of inoculum sources; the steepness of the dispersal gradient; and the predominant wind. We expect that the effect of genotype unit area on the efficacy of host mixtures will depend on similar factors. In fact, field and computer simulation studies suggest that increasing genotype unit area will greatly reduce the efficacy of oat mixtures for rust control if initial inoculum is distributed uniformly or randomly, but not if it is concentrated in widely dispersed foci (C. C. Mundt and K. J. Leonard, *unpublished*).

We cannot be certain that the differences in epidemic development between the pure-line susceptible check and the multilines in 1980 were due totally to the effects of mixing isolines because the components of the mixtures were not tested in pure stand. There may have been differences in the levels of rate-reducing resistance between C649 and the multiline components. In fact, two components were not rated as fully susceptible to any of the four races used in the experiment (Table 1). In 1981, the same susceptible isoline (C649) was used in the pure-line susceptible treatment as was used in the multilines. Thus, in 1981, the differences in rust severity on C649 plants between the pure-line susceptible check and the multilines should be due totally to mixture effects.

A comparison of the pure-line C649 treatment with the quadrants treatment in 1981 indicates that reducing the proportion of susceptible plants within plots had a significant effect on epidemic development even when the immune and susceptible isolines were not mixed. The difference between these two treatments may be due to a larger amount of spore loss from the smaller blocks of susceptible plants in the quadrants treatment as compared with the pure-line C649 treatment. Quantitatively different results may be obtained if the same comparison is made with a different plot size than we used in our experiment.

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