Effect of Host Genotype Unit Area on Development of Focal Epidemics of Bean Rust and Common Maize Rust in Mixtures of Resistant and Susceptible Plants

C. C. Mundt and K. J. Leonard

Former graduate research assistant and research plant pathologist, U.S. Department of Agriculture, Agricultural Research Service, Department of Plant Pathology, North Carolina State University, Raleigh 27695-7616.
Present address of first author: Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331-2902.
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ABSTRACT

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We studied the effect of host genotype unit area (ground area occupied by an independent, genetically homogeneous unit of a host population) on the effectiveness of host mixtures for controlling focal epidemics of common maize rust and bean rust. For both crops, mixtures of resistant and susceptible plants with four genotype unit areas were established by altering the spatial arrangement of host genotypes within plots. With maize, genotype unit area for a mixture of 1:3 susceptible/resistant plants was increased from 0.21 to 1.88 m^2. By the end of the epidemics, there were fewer than half as many pustules on susceptible plants in the mixtures as on plants in the pure-line susceptible plots. However, there was little difference in the amount of disease in the mixtures with the four genotype unit areas. With beans, genotype unit area was increased from 0.023 to 0.84 m^2 in mixtures of either 1:1 or 1:3 susceptible/resistant plants over 3 yr (1982–1984). There was always less disease on susceptible plants in mixtures with the smaller genotype unit areas than in the pure-line susceptible plots. In all 3 yr, the effectiveness of the mixture declined as the genotype unit area increased. However, the quantitative relationship between mixture efficacy and genotype unit area varied among years.

Additional key words: corn, cultivar mixtures, epidemiology, multilines, *Phaseolus vulgaris*, *Puccinia sorghi*, *Uromyces phaseoli*, *Zea mays*.

One strategy for the management of genetic resistance to plant disease is to grow mixtures of plants that possess different resistance genes (3,5,7,13). Most of the research with host mixtures, however, has been restricted to foliar pathogens of small grains. Because the effectiveness of host mixtures depends on inoculum spread among host genotypes, the mixture strategy may be less effective for crops with plants larger than those with small grains. In fact, Vanderplank (20) hypothesized that multiline cultivars will be most effective for crops with small plants and that horizontal resistance will have a "clear advantage" over multilines for the control of disease in crops with large plants, e.g., tree crops. Also, alternative cropping systems such as intercropping and interfield diversification may not provide optimal reduction of epidemic development.

A few studies have been conducted to determine the effect of plant size and host aggregation on the effectiveness of host mixtures for disease control. Barrett and Wolfe (2) altered the size of barley (*Hordeum vulgare* L.) plants in a three-component cultivar mixture by changing sowing rates and thus altering the number of tillers per plant. Their results suggested that the effectiveness of the mixture in controlling powdery mildew (induced by *Erysiphe graminis* DC. f. sp. *hordei* Marchal) increased with decreasing plant size (reduced number of tillers per plant). Mundt and Browning (12) altered the planting arrangement of near-isogenic oat (*Avena sativa* L.) lines to attain mixtures with different genotype unit areas (ground area occupied by an independent, genetically homogeneous unit of a host population). They found that increasing the genotype unit area from 0.003 to 0.84 m^2 had no significant effect on the effectiveness of the mixtures in controlling oat crown rust (induced by *Puccinia coronata* Cda. var. *avenae* Fraser & Ledingham). More recent studies with oat crown rust, however, suggest that the difference between Barrett and Wolfe's (2) results and those of Mundt and Browning (12) can be explained by differences in the spatial distribution of initial disease (15). In those studies (15), genotype unit area had less influence on the efficacy of an oat mixture in plots with a single initial disease focus than in plots where the initial disease was distributed uniformly or randomly. In addition, studies conducted with *Pythium irregulare* Buisman indicate an effect of host aggregation on epidemic development when initial inoculum is distributed randomly but not when epidemics begin from a single focus (4).

Results from studies on small-grain diseases such as oat crown rust (12,15) and barley powdery mildew (2) may not be representative of the effects of mixtures on epidemics in other crops. For example, pathogen dispersal gradients might differ for pathogens of crops that have different canopy structures. The purpose of our research was to determine if the effect of genotype unit area on the development of focal epidemics of common maize rust and bean rust in mixtures of resistant and susceptible plants is similar to that reported for oat crown rust (12,15).

MATERIALS AND METHODS

Field methods: common maize rust. Field plots in Clayton, NC, were arranged in a 5 × 5 Latin square. Each plot was 5.5 × 5.5 m with 4.0 or 5.9 m between adjacent plots.

Plots were planted 10–11 May 1984. Each plot was divided into 144 sections using wire with grids 0.46 × 0.46 m. Two maize (*Zea mays* L.) seeds were planted in the center of each grid. Plots were thinned to one plant per grid on 2–3 June, except for the center four

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grids, which were thinned after rust was established in the plots. Four rows of B37Ht × B14AHt maize (resistant to *Puccinia sorghi* Schw.) were planted between adjacent plots, with 1 m between rows. In addition, at least two rows of B37Ht × B14AHt were planted on each side of the experiment. Standard cultural practices were used, and plots were irrigated as necessary to maintain adequate growth of the crop and adequate moisture for rust development.

There were five treatments. One treatment was a pure stand of B37Ht × B632Ht, which is susceptible to the isolate of *P. sorghi* used in the experiment. The other four treatments were all mixtures of 25% B37Ht × A632Ht and 75% B37Ht × B14AHt (resistant) planted in groups of one, two, four, and nine grids of like genotype to provide genotype unit areas of 0.21, 0.42, 0.84, and 1.88 m^2, respectively (Fig. 1). Positions of genotype units within plots were ordered, but the starting position of the first susceptible genotype unit was chosen randomly for each column of the Latin square.

Inoculations were made on 2 June with a naturally occurring isolate of *P. sorghi* obtained from maize at Clayton, NC, in 1982 and maintained on maize in the greenhouse. Both plants in each of the four grids at the center of each plot were injected into the whorl below the uppermost node with 3 ml of a suspension of 2 mg of viable uredospores per milliliter of distilled water. Tween 20 was added to the suspension at a rate of two drops per 100 ml. After the first inoculation between 0830 and 1030 hours EDT, the same plants were inoculated again between 1830 and 2030 hours EDT with 1 mg of viable uredospores per milliliter because dry, warm winds during that day were suspected to have reduced the viability of the first inoculum. The four central grids were thinned to one plant per grid on 9 June, when pustules resulting from the artificial inoculation were first observed.

Disease progression was quantified by counting or estimating the number of new pustules on susceptible plants on 12 and 28–29 June and 6–7 and 15–16 July. The first assessment was conducted before secondary spread occurred, and the pustules were counted on the inoculated plants at the center of each plot. Pustules were not observed on plants that were not artificially inoculated, indicating that there was no interference from naturally occurring inoculum. In all subsequent assessments, susceptible plants were marked and the number of new pustules (pustules not present during the previous assessment) were counted or estimated for susceptible plants in each plot.

For mixtures, all susceptible plants in each plot were marked. In pure-line susceptible plots, plants in the same positions as susceptible plants in the mixture of 0.21-m^2 genotype units in the same column of the Latin square were marked. In plots of 0.21-m^2 genotype units, alternate marked plants were rated. In pure-line susceptible plots, rated plants were chosen in the same manner as for the mixture of 0.21-m^2 genotype units. In plots of 0.42- and 0.84-m^2 genotype units, half of the plants in each susceptible genotype unit were rated. In plots of 1.88-m^2 genotype units, five plants from each of the four groups of nine contiguous susceptible plants were rated.

In addition to the pustule counts described, the pustules on the second and third leaves above the ear leaves were counted from 31 July to 4 August. These counts were made because observations indicated a larger difference among treatments on the upper leaves than on whole plants. Pustules were counted on all susceptible plants in the mixture treatments and on one-fourth of the plants in the pure-line susceptible plots. In the pure-line susceptible plots, the plants sampled were in the same grid positions as the susceptible plants in the plot of 0.21-m^2 genotype units located in the same column of the Latin square. One column of plots in the Latin square was rated per day. Data were expressed as the mean number of pustules per susceptible leaf for each plot.

Field methods: bean rust. Field plots were at Clayton, NC, in 1982 and 1983 and in Lewiston, NC, in 1984. A Latin square design was used, and each plot was 3.7 × 3.7 m with 2.4–3.7 m between adjacent plots.

Plots were planted in mid-July in 1982, mid-June in 1983, and late May in 1984. Each plot was divided into 144 sections using wire with grids 0.3 × 0.3 m. Four snap bean (*Phaseolus vulgaris* L.) seeds were planted in the center of each grid. Soybeans (*Glycine max* L.) were planted between adjacent plots and around the perimeter of the experiments. Standard cultural practices were used to grow the crops.

There were five treatments common to each of the 3 yr that the experiment was conducted. These five treatments included a pure stand of snap bean cultivar Bush Blue Lake (BBL) 47 (susceptible) and five 1:1 (1982) or 1:3 (1983 and 1984) mixtures of BBL 47/BBL 94 (resistant). In one mixture treatment, the appropriate percentages of seeds of the susceptible and resistant genotypes were mixed and planted in the center of each grid (genotype unit area = ground area occupied by a single bean plant = about 0.023 m^2). In all other mixture treatments, seeds planted within a grid were of the same genotype and genotypes were arranged in groups of one, four, and nine grids of like genotype to attain genotype unit areas of 0.093, 0.37, and 0.84 m^2, respectively. The positions of genotype units within plots were ordered as described for the maize experiment. The genotype assigned to the first planting unit was chosen randomly for each column of the Latin square. In 1982, there was also a second mixture treatment of 0.84-m^2 genotype units that differed only in the placement of the inoculum source.

In all 3 yr, plots were inoculated with collection 16 of *Uromyces phaseoli* (Reben) Wint., obtained from J. R. Stavely, Applied Plant Pathology Laboratory, Beltsville, MD, and was maintained on BBL 47 snap beans in the greenhouse. BBL 47 is very susceptible (pustules predominantly larger than 800 μm in diameter), and BBL 94 is highly resistant (necrotic spots with no sporulation) to this isolate of *U. phaseoli*.

In 1982 and 1983, infected BBL 47 plants were transplanted into the plots to provide initial inoculum for the epidemics. Plants were grown in 7.6-cm peat pots, one plant per pot, initially in the greenhouse, but later plants were placed outside to acclimate to field conditions. At 2–3 wk after planting, the beans were sprayed with a suspension of *U. phaseoli* uredospores. The plants were placed in a mist chamber overnight, maintained in the greenhouse for 1 day, and then placed outside.

Inoculated bean plants were transplanted into field plots when pustules were just beginning to open, 2–3 wk after the field plots

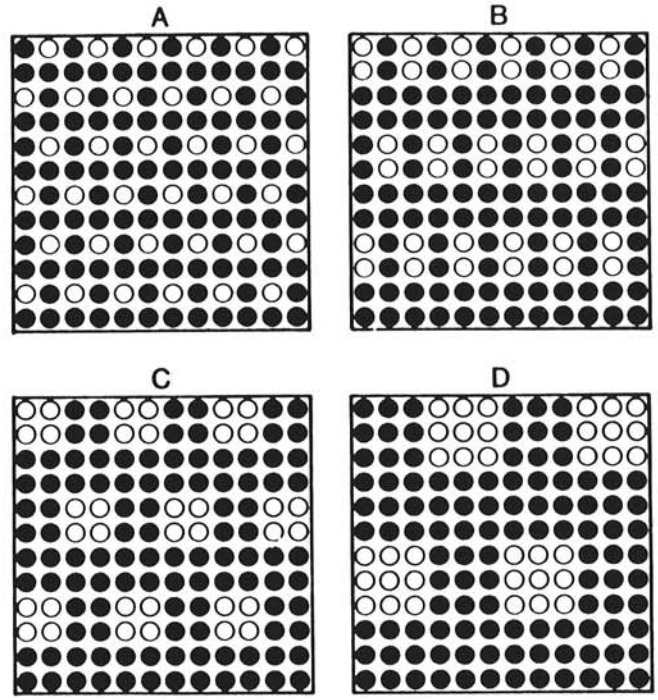

Fig. 1. Examples of planting arrangements used in the common maize rust experiment. Each circle represents one maize plant: open circles = susceptible plants and closed circles = resistant plants. **A,** Mixture of 0.21-m^2 genotype units, **B,** mixture of 0.42-m^2 genotype units, **C,** mixture of 0.84-m^2 genotype units, and **D,** mixture of 1.88-m^2 genotype units.

were planted. One plant was transplanted into the center of each plot, with the exception of one of the 0.84-m^2 mixture treatments in 1982. For this treatment, the source plant was placed near the center of a 0.84-m^2 unit of BBL 47 at the center of each plot. For all treatments, source plants were removed after rust was established in the plots.

In 1984, inoculations were performed by spraying a suspension of uredospores directly onto plots between 1915 and 2115 hours EDT on 13 June. Eight and two susceptible trifoliolate leaves were inoculated near the plot center for the pure-line susceptible and mixture treatments, respectively, to attain the same number of initial pustules per susceptible leaf for each treatment. Inoculum consisted of 0.5 mg of uredospores per 100 ml of distilled water, to which two drops of Tween 20 per 100 ml were added. The suspension was applied to the point of runoff on both leaf surfaces with a Chromist gas propellant, thin-layer chromatography sprayer (Gelman Sciences, Inc., Ann Arbor, MI). Inoculated plants were immediately covered with moistened plastic bags, which were removed between 0830 and 0900 hours EDT the following day.

In all 3 yr, disease progression was quantified by observing susceptible plants in each plot. Morphological differences between the resistant and susceptible genotypes allowed them to be distinguished from each other. In 1982, the percentage of rust severity in each plot was estimated on 15, 18, 21, and 25 August with standard area diagrams developed for bean rust (M. W. Imhoff, *unpublished*) as well as rust severity diagrams used for cereal rusts (17). In the first assessment, the percentage of rust severity of the susceptible genotype was visually averaged for the four quadrants of each plot. In all subsequent assessments, 32 susceptible leaflets spaced uniformly over each plot were rated. In the last three assessments, the Horsfall-Barratt (8) rating scale was used but modified to provide additional classes at the low end of the scale. For all assessment dates, data were expressed as the mean percentage of rust severity on the susceptible genotype for each plot.

In 1983, pustule counts were conducted on 18, 25, and 29–30 July. One susceptible plant was assessed in each of 18 planting grids, except 19 grids were sampled for the mixture with 0.84-m^2 genotype units. In the plots of 0.093-m^2 genotype units, alternate grids of susceptible plants were sampled. In the pure-line susceptible treatment and in plots of 0.023-m^2 genotype units, plants were sampled from grids in the same positions as in the plot

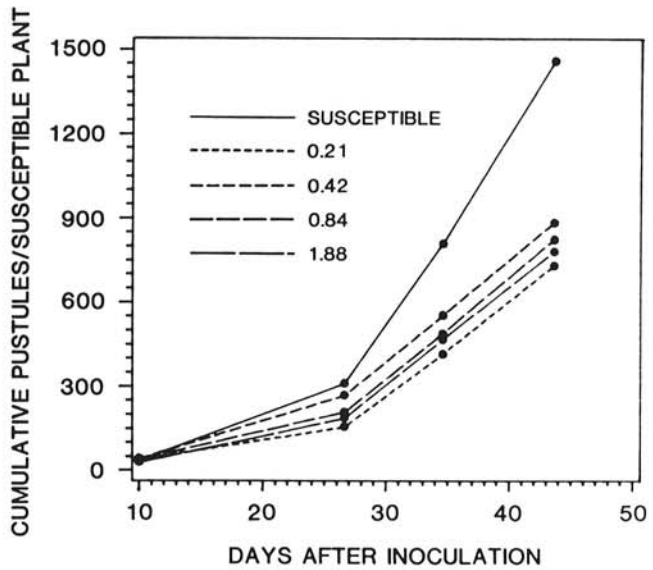

Fig. 2. Cumulative numbers of common maize rust pustules on susceptible plants in mixtures of 25% susceptible and 75% resistant plants and in pure stands of susceptible plants in field plots in 1984. S = pure-line susceptible population; 0.21, 0.42, 0.84, and 1.88 represent mixtures with genotype unit areas of 0.21, 0.42, 0.84, and 1.88 m^2, respectively (see Fig. 1). Each point is the mean of five replicates.

of 0.093-m^2 genotype units in the same column of the Latin square. In plots of 0.37-m^2 genotype units, two grids were sampled from each group of four contiguous susceptible grids. In plots of 0.84-m^2 genotype units, grids were sampled at the four corners and center of each group of nine contiguous grids of susceptible plants, except that the susceptible grid nearest to the plot center was not sampled. Grids adjacent to the source plant were not sampled in any of the plots.

For each sampled plant in 1983, the number of pustules was counted on three leaflets, one at each of the lower, middle, and upper parts of the canopy. It was sometimes necessary to choose leaflets from more than one plant if leaflets on the originally selected plant were missing or inadequate for counting. Data were expressed as the mean number of pustules per susceptible leaflet for each plot. The pustule counts from the lowest part of the canopy on 18 July were not used in calculating means because many of these leaflets abscised soon after the first assessment and could not be rated in subsequent assessments.

In 1984, the percentage of rust severity was assessed on 25 June and 3, 9–10, 13, and 18–19 July. For the first assessment, conducted before secondary spread occurred, the percentage of rust severity was recorded on the artificially inoculated plants. Rust was not observed on plants that were not artificially inoculated. Plant density and the number of expanded leaves per plant were recorded for the susceptible genotype in each plot so that severity ratings could be based on the total number of expanded, susceptible leaves in the plots. For the second assessment, 36 susceptible leaflets were rated in each plot. In the pure-line susceptible plots and in the mixture in which the two genotypes were mixed within grids, leaflets were sampled uniformly over plots. In the other treatments, one leaflet was chosen from each of the 36 grids of susceptible plants. In all subsequent assessments, the same sampling pattern was used, but rust severity was visually averaged over all susceptible plants in each of the 36 selected grids in each plot. Heavily rusted plants at the centers of plots were used as a guide to determine 100% severity. For all assessments, data were expressed as the mean rust severity for the susceptible genotype in each plot. No data were obtained from one plot of 0.84-m^2 genotype units because the inoculation failed.

Data analysis. For all experiments, the area under the disease progress curve (ADPC) was calculated for each plot as described by Shaner and Finney (19), except cumulative pustule counts were substituted for disease severity ratings for the maize rust experiment and pustule counts were substituted for disease severity ratings for the 1983 bean rust experiment. Analysis of variance was performed using PROC GLM of the Statistical Analysis System (18). Data from the 1983 bean rust experiment were log-transformed before being statistically analyzed so as to better satisfy the assumption of homogeneity of variance. Polynomial regression of ADPC on the square root of genotype unit area for the mixtures was used to determine the proportion of the sums of squares due to differences in genotype unit area among mixtures. Linear contrasts were used to compare the pure-line check with the mixture of smallest genotype units and to compare the pure-line check with the mixture of largest genotype units in each experiment. For the 1982 bean rust experiment, an additional linear contrast was used to compare the two mixtures of 0.84-m^2 genotype units. For the purpose of comparison among experiments, the relative ADPC was calculated by dividing the ADPC for each treatment by the ADPC for the pure-line susceptible check.

The same statistical analyses were applied to the pustule counts made on 31 July to 4 August from upper leaves in the maize experiment.

RESULTS

Common maize rust. There were no clear differences among treatments until about 30 days after inoculation (Fig. 2). By 35 days after inoculation, there was considerably more rust in the pure-line check than on susceptible plants in the mixtures. There was little

difference, however, among disease progress curves for the four mixture treatments. For mixtures with genotype unit areas of 0.21, 0.42, 0.84, and 1.88 m^2, the relative ADPCs were 0.52, 0.70, 0.61, and 0.57, respectively. In the regression of the ADPC on the square root of genotype unit area for the mixtures, probability levels (probability of committing a type I error) for linear and quadratic terms were 0.92 and 0.29, respectively, indicating no significant effect of genotype unit area on the effectiveness of the mixtures. Differences between the pure-line check and the mixture of 0.21-m^2 genotype units and between the pure-line check and the mixture of 1.88-m^2 genotype units were highly significant ($P = 0.001$ and 0.002, respectively).

At the final disease assessment in 1984 in which only upper leaves were observed, there was a larger difference between the pure-line check and the mixtures than there had been in earlier assessments when whole plants were rated (Table 1). The mean number of pustules per susceptible leaf in the mixtures was only about one-fourth as great as that in the pure-line check. Although mixture treatments with larger genotype unit areas had slightly more pustules per susceptible leaf than those with smaller areas, this increase was not significant (regression of numbers of pustules per susceptible leaf on the square root of genotype unit area showed that probability levels for the linear and quadratic terms were 0.46 and 0.69, respectively). Differences between the pure-line check and the mixture of 0.21-m^2 genotype units and between the pure-line check and the mixture of 1.88-m^2 genotype units were both highly significant ($P < 0.0001$).

Bean rust. There was considerable variability in the growth of bean plants because the cultivars used were not well adapted to North Carolina and were rather susceptible to soilborne plant pathogens. In all 3 yr, *Rhizoctonia* sp. and other pathogens caused damping-off and reduction of plant vigor. Damage caused by soilborne plant pathogens seemed to be least in 1982, greatest in 1983, and intermediate in 1984. Also, at Clayton (1982 and 1983 experiments), the two bean genotypes seemed to be equally damaged by soilborne pathogens. At Lewiston (1984 experiment), the rust-resistant cultivar was much more heavily damaged than was the rust-susceptible cultivar. In all three experiments, the susceptible bean genotype grew taller and had a denser canopy than the resistant genotype.

In 1982, bean rust increased more slowly on susceptible plants in mixtures with the two smallest genotype unit areas than in the pure-line susceptible check. The ADPC for susceptible plants was about 25% less for these two mixtures than for the pure-line check (Table 2). Mixtures with 0.37- and 0.84-m^2 genotype unit areas had little effect on the rate of increase of rust on susceptible plants. When the ADPC was regressed on the square root of genotype unit area for the four mixtures, probability levels for the linear and quadratic terms were 0.02 and 0.10, respectively, indicating a significant effect of genotype unit area on mixture efficacy. The use of contrasts indicated that the difference between the pure-line check and the mixture of 0.023-m^2 genotype units was highly significant ($P = 0.005$), but the difference between the pure-line check and the mixture of 0.84-m^2 genotype units was not ($P = 0.26$). For plots in which source plants were placed near the center of a 0.84-m^2, susceptible genotype unit, the ADPC was slightly larger than that for the same mixture in which source plants were placed at the center of each plot (Table 2), but this difference was not significant ($P = 0.47$).

Results from 1983 were qualitatively similar to those from 1982. ADPCs for mixtures with 0.023- and 0.093-m^2 genotype units were smaller than those for mixtures with 0.37- and 0.84-m^2 genotype units (Table 2). However, variability in plant stand and vigor caused by heterogeneous soil and damping-off reduced the statistical significances of treatment differences. Regression of ADPC on the square root of genotype unit area for the mixtures indicated that the effect of genotype unit area on mixture efficacy was not very significant (probability levels for the linear and quadratic terms were 0.21 and 0.53, respectively). Differences between the pure-line check and the mixture of 0.023-m^2 genotype units and between the pure-line check and the mixture of 0.84-m^2 genotype units were not significant ($P = 0.50$ and 0.91, respectively).

In 1984, there was a smaller effect of genotype unit area on the efficacy of the mixtures than in 1982 or 1983 (Table 2). ADPCs for mixtures with the three smallest genotype unit areas all were about 43% less than that for the pure-line check, whereas the ADPC for the mixture with 0.84-m^2 genotype units was 28% less. Regression of ADPC on the square root of genotype unit area for the mixtures indicated that the effect of genotype unit area on mixture efficacy was marginally significant (probability levels for the linear and quadratic terms were 0.05 and 0.14, respectively). Differences between the pure-line check and the mixture of 0.023-m^2 genotype units and between the pure-line check and the mixture of 0.84-m^2 genotype units were both highly significant ($P < 0.0001$ and 0.001, respectively).

Within each year of the experiment, shapes of disease progress curves for all treatments were similar (disease progress curves for 1984 are shown in Fig. 3), indicating that the ADPC was an appropriate parameter for comparing treatments.

DISCUSSION

With common maize rust, there was a much larger difference in the amount of disease between the pure-line check and the mixtures when only upper leaves were rated than when whole plants were rated. There seemed to be little or no disease increase between the time when the last whole-plant rating was made and when upper leaves were rated. Pustules on upper leaves could only have occurred from infections at later stages of the epidemics because upper leaves had not yet emerged from the whorl at the beginning of the epidemics. This result is consistent with theoretical studies (1,9–11) indicating that a difference in the amount of disease between a pure-line susceptible population and a mixture of resistant and susceptible plants should increase with

TABLE 1. Effect of spatial arrangement of susceptible and resistant maize on the increase of common maize rust in mixtures of 25% susceptible and 75% resistant plants and in pure stands of susceptible plants in field plots in 1984

Treatment	Genotype unit area (m^2)	Pustules per susceptible leaf[a]
Pure-line susceptible	30.14	135
Mixture	0.21	27
	0.42	32
	0.84	36
	1.88	37

[a] Mean number of pustules on second and third leaves above ear leaves for the susceptible genotype. Pustules were counted 59–63 days after inoculation.

TABLE 2. Effect of spatial arrangement of susceptible and resistant snap beans on the increase of bean rust in mixtures of susceptible and resistant plants and in pure stands of susceptible plants in field plots

Treatment	Genotype unit area (m^2)	Relative ADPC[a]		
		1982[b]	1983[c]	1984[c]
Pure-line susceptible	13.400	1.00	1.00 (1.00)[d]	1.00
Mixture	0.023	0.73	0.42 (0.74)	0.57
	0.093	0.76	0.29 (0.53)	0.58
	0.372	0.99	0.71 (1.35)	0.56
	0.836	0.90	1.31 (0.95)	0.72
Mixture-alternate[e]	0.836	0.96	... ...	...

[a] The area under the disease progress curve (ADPC) for each treatment divided by the ADPC for the pure-line susceptible treatment.
[b] Mixture treatments consisted of 50% susceptible and 50% resistant plants.
[c] Mixture treatments consisted of 25% susceptible and 75% resistant plants.
[d] Values in parentheses were calculated from geometric means of the ADPC for treatments in 1983.
[e] Mixture in which the inoculum source was placed within one of the susceptible genotype units rather than at the plot center.

increasing numbers of generations of the pathogen, at least until disease in the pure-line approaches the maximum.

Because of variability in plant stand and vigor, results from the bean rust experiments should be interpreted cautiously. Different results might be obtained using well-adapted cultivars with more normal canopy structures. In addition, morphological differences between the resistant and susceptible cultivars could have caused some microclimatological differences between the pure-line check and the mixtures and among mixture treatments.

With focal epidemics of oat crown rust (12,15), oat multilines reduced epidemic development relative to a pure-line check, but there was little or no effect of genotype unit area on the effectiveness of the mixtures. This lack of effect of genotype unit area was also observed in our maize rust epidemics but not in the bean rust epidemics. Initially, we thought that dispersal gradients for bean rust might differ from those for common maize rust and oat crown rust and that this might account for differences in the performance of host mixtures among the three diseases. Results from field experiments, however, suggest that dispersal gradients for bean rust and common maize rust may be more similar to each other than are gradients for oat crown rust and common maize rust (14).

Experiments conducted with oats have shown that increasing genotype unit area can greatly reduce the efficacy of host mixtures for crown rust control if initial disease is distributed uniformly or randomly rather than in a single focus (15). The stronger effect of genotype unit area on mixture efficacy for bean rust in 1982 and 1983 than in 1984 could have been caused by differences in the spatial distribution of early infections. In 1982 and 1983, source plants with sporulating pustules were placed in plots early in the growing season (17 and 14 days after planting in 1982 and 1983, respectively). Epidemics resulting from these inoculations seemed to begin slowly, perhaps because the crop canopy was relatively sparse, and early secondary spread resulted in a small number of pustules scattered throughout the plots when the crop canopy "closed over" and microclimatological conditions became favorable for more rapid disease increase. In 1984, a uredospore suspension was applied to plants at the centers of plots later in the growing season (23 days after planting), and a minimum of an additional 8 days passed before the first pustules began to produce spores. Therefore, in 1984, the epidemics were more focal at the stage when the crop canopy was sufficiently developed to support rapid epidemics.

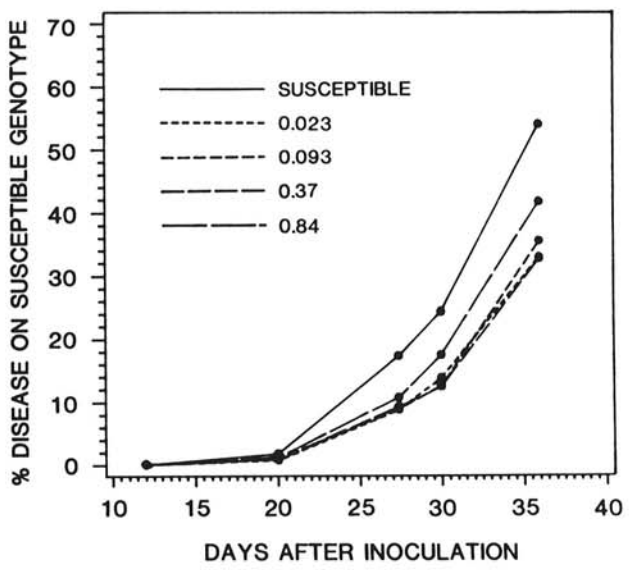

Fig. 3. Percentage of bean rust severity on susceptible plants in mixtures of 25% susceptible and 75% resistant plants and in pure stands of susceptible plants in field plots in 1984. S = pure-line susceptible population; 0.023, 0.093, 0.37, and 0.84 represent mixtures with genotype unit areas of 0.023, 0.093, 0.37, and 0.84 m^2 that were obtained by planting seeds in groups of 1, 4, 16, and 36 seeds of like genotype, respectively. Each point is the mean of five replicates.

We have conducted computerized simulation studies (16) on the effects of genotype unit area, the spatial distribution of initial disease, the steepness of pathogen dispersal gradients, the rate of disease increase, and the percentage of susceptible host plants on the effectiveness of mixtures of immune and susceptible host plants for the control of foliar disease. Results from the simulations suggest that the reduction of the proportion of susceptible plants from 50% in 1982 to 25% in 1983 and 1984 or possible differences in rates of disease increase or dispersal gradients cannot explain the decreased effect of genotype unit area that was found in 1984. The only factor that resulted in a decreased sensitivity to genotype unit area that was consistent with field observations was the spatial distribution of initial disease. In the simulations, genotype unit area had much less of an effect on mixture efficacy when initial infections were confined to a single focus than when initial infections were distributed uniformly within the simulated field plots.

Our results indicate that mixtures provide significant rust control for crops with larger plants and different canopy structures than small grains. For both common maize rust and bean rust, mixtures of resistant and susceptible plants reduced disease severity on the susceptible genotype by about 25–50% relative to the pure-line susceptible check. However, the level of disease control attained with the maize and bean mixtures was less than the 40–70% reductions reported for rusts and powdery mildews in small-grain mixtures with 25–50% susceptible plants (6,11,12,15).

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