Stripe Rust, Yield, and Plant Competition in Wheat Cultivar Mixtures

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ABSTRACT

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Mixtures of two, three, four, or five winter wheat (*Triticum aestivum*) cultivars and their component pure stands were either exposed to or protected from two stripe rust (*Puccinia striiformis*) races at three and two locations in 1986–1987 and 1987–1988, respectively. Disease severity and yield components per cultivar were determined for a subset of the mixtures and also for the pure stands. Disease severity in the mixtures compared to the mean of the components was reduced between 13 and 97%. Changes in disease severity could be separated into two effects. First, selection changed frequencies of the cultivars in the mixtures by up to 35% at harvest compared to the planted frequencies. Reductions in overall disease severity in mixtures due to selection for the more resistant cultivar were as high as 42%, and increases in overall disease severity due to selection for the more susceptible cultivar were as high as 11% over the mean disease severity in the pure stands. Second, disease severity on individual cultivars was reduced below that observed in pure stands because of the epidemiological effect of host diversity. Mixtures yielded between 0 and 5% more than the mean of the pure stands in the absence of disease. In the presence of disease, mixing increased yield between 8 and 13%. Location and year influenced the effects of disease on plant performance indirectly by affecting the competitive abilities of the cultivars.

Additional keywords: ecological combining ability, genetic diversity.

Intrafield diversification as a means of disease control was first promoted by Jensen (13) and Borlaug (5). Jensen (13) proposed selection of pure lines of oats that were similar in important agronomic traits, so they could be grown together, but that possessed genetic diversity for reactions to abiotic and biotic stresses, including disease. In contrast, Borlaug (5) promoted the development of backcrossed lines that differed in their reactions to rusts. More recently, attention has turned to the use of cultivar mixtures for disease control (34). There are several advantages to using cultivar mixtures rather than multilines, including ease of synthesis, additional disease control against the target disease through race nonspecific resistance, reduced selection for a super-race (a race virulent on all host components in the mixture), and protection from nontarget diseases and abiotic stresses (21,34). Some of the mechanisms by which host diversity might reduce disease severity include the dilution of host tissue susceptible to a given pathogen race, a barrier function of resistant hosts, and interactions among different pathogen genotypes (4,6,8,18,19,22, 32,34).

Mixtures have frequently been reported to increase yield (2,3,5,13,20,23,24,33,36). In an experiment with two-way mixtures of four different wheat cultivars, however, Klages (15) found that yields of mixtures were almost always lower than expected. Yielding ability of a cultivar in a mixture and in pure stand is not necessarily correlated. For example, the proportion of a barley (*Hordeum vulgare*) cultivar greatly declined in mixtures, despite its significantly better yield and leaf disease resistance record in pure stand than the other cultivars tested (30,31).

Such contrasting results indicate that interactions among plant genotypes in mixtures are complex. This was confirmed by Allard and Adams (3), who distinguished between neighborhood and competitive effects in mixtures and introduced the term ecological combining ability. Genotypes possess good ecological combining ability if they are both good competitors (yield higher when bordered by other genotypes than when bordered by themselves) and good neighbors (induce a mean increase in yield on a different, bordering genotype).

Few studies have addressed the reciprocal effects of disease and plant-to-plant interactions in mixtures (1), and little or no data that separate the contribution of disease control from other factors that influence the yield of mixtures are available. To understand the effects of disease on interactions among different plant genotypes and the effects of host genetic composition on disease severity, it is necessary to study the population dynamics of host mixtures in the absence and presence of disease.

Multilines or cultivar mixtures are usually composed of more than two components. These components are chosen because of good yielding ability in pure stands and for resistance to specific diseases. In agricultural production, these mixtures can be confronted with a mixture of pathogen races, each of which might affect one or more of the mixture components. On the other hand, most studies of disease effects on plant interactions have used a single race of one pathogen and only two host genotypes (1,7). In addition, host genotypes used in such studies are often not those that would be used in production agriculture.

To gain insight into the interactions between disease and host diversity in mixtures, it is necessary to study the effects of interactions among plant genotypes on host population composition, the influence of disease on interactions among different plant genotypes, and the effects of host genetic composition on disease severity.

Knott and Mundt (16) analyzed field trials of inoculated and uninoculated mixtures of five commercial wheat (*Triticum aestivum* L.) cultivars that were differentially susceptible to two races of stripe rust (*Puccinia striiformis* Westend. (=*P. glumarum* (Schm.) Jacob, Eriksson & Henn.). The mixing ability of cultivars with respect to yield and disease control was determined by combining ability analysis. An advantage of the analysis is that it does not require the physical separation of the mixture components for the evaluation of performance. However, it could not predict the end composition of a mixture at harvest. Therefore, no insight was provided into the interactive effects of disease and plant population dynamics in mixtures. In this paper, we provide an analysis of these effects by using data obtained from the experiments described by Knott and Mundt (16).

MATERIALS AND METHODS

The experiments were superimposed on a field trial designed for screening wheat cultivar mixtures for yield and disease.

Cultivars. Host genotypes were five soft, white, club-type winter wheat cultivars with different stripe rust resistances, heights, and chaff colors (Table 1). The cultivars differed up to a week in maturity. Our disease assessments revealed that the seed source of Faro consisted of two sister lines, one resistant and one susceptible to race 5. This finding was confirmed by R. E. Allan (Dept. of Crop Science, Washington State University, Pullman, *personal communication*).

Locations. Experiments were conducted at three locations in Oregon. Pendleton and Moro, located in the semiarid region of eastern Oregon, receive approximately 450 and 300 mm of annual precipitation, respectively. Corvallis is located in the Willamette Valley in western Oregon and receives approximately 1,000 mm of annual precipitation.

Experimental design. All possible two-, three-, four-, and five-way combinations of equal numbers of germinable seeds of Faro, Jacmar, Moro, Tres, and Tyee, and their pure stands were planted in the fall of 1986. Plots were arranged in a randomized complete block design with four replications at each location. Plots were 1.5 by 4.5 m with four rows per plot (38 cm between rows) in Moro and six rows per plot (25 cm between rows) in Pendleton and Corvallis. Plots were adjacent in the narrow dimension and separated by 1.8 m of fallow ground in the long dimension. Seeding rates were those appropriate for commercial wheat production at each site and were 198, 316, and 395 seeds per square meter in Moro, Pendleton, and Corvallis, respectively. The plots were planted on 30 September and 5 and 8 October 1986 in Moro, Corvallis, and Pendleton, respectively. In the fall of 1987, six replications of all possible two-, three-, and four-way combinations of Faro, Jacmar, Tres, and Tyee, and their pure stands were planted at Pendleton and Moro in four-row plots, with 38 cm between rows. Planting dates were 9 and 15 October 1987 in Pendleton and Moro, respectively.

Two separate experiments were conducted in each location. In one experiment, plants were protected from stripe rust with triadimefon (as Bayleton 50 DF; Mobay Corp., St. Louis, MO) applications at 284 g a.i./ha; in the other experiment, plants were inoculated with stripe rust. The number of fungicide applications per season varied between locations and years from two to four, depending on the conduciveness of the weather to infection and on the time at which plants started to senesce. In both years, less than 0.1% infected total leaf area could be found in the fungicide-treated experiments. The inoculated experiment was located 12 m downwind from the fungicide-treated experiment at each site. The area between the experiments was planted to the resistant cultivar Stephens or to barley. Fertilizers and herbicides were applied according to standard practices for wheat in the respective regions.

Inoculation. Stripe rust races CDL 5 and CDL 27 (CDL race designations are those of the USDA Cereal Disease Laboratory, Washington State University, Pullman) were selected for the experiments. These races are present in the naturally occurring inoculum in the area. Because stripe rust incidence was low in commercial fields in 1987 and 1988, we assumed that external inoculum was not an important source for the disease in our experiments.

Peat pots (6 cm) containing 2- to 3-wk-old seedlings of the winter wheat cultivar Nugaines were inoculated with an equal mixture of uredospores of *P. striiformis* races CDL 5 and CDL 27. Inoculated plants were placed in a dew chamber for 12 h. Upon removal from the dew chamber, we placed plants outdoors so they would adapt to natural conditions until sporulation. At the onset of sporulation, one pot was transplanted into the center of each plot in the inoculated experiments. In 1986, inoculation was in late November to early December. Because disease occurrence was sporadic in Corvallis by spring, the inoculation was repeated in early April 1987. In fall 1987, inoculation in Pendleton took place on 28 November and was repeated on 28 March 1988. Because of a severe fall drought in Moro, the wheat did not emerge until late January 1988. Therefore, the plots were inoculated on 12 March 1988, when sufficient foliage was available, and again on 11 April.

Disease assessments. Assessments were made before disease had reached 90% severity on the F-1 leaf of the most susceptible cultivar. Assessment dates were 20–23 May 1987 and 30 May–1 June 1988 in Pendleton, 27–31 May 1987 and 12–16 June 1988 in Moro, and 3–6 June 1987 in Corvallis. Plants were heading (Feekes [17] stage 10.1–10.5) in all locations during the assessments in 1987 and at early (Feekes [17] stage 10.5.1) or full (Feekes [17] stage 10.5.2) anthesis in Moro and Pendleton in 1988, respectively. Subplots containing a minimum of 120 tillers were marked within each plot approximately midway between the inoculation point and the downwind end of the plot. The subplots included sections of equal length at the two center rows of the four-row plots and the four center rows of the six-row plots. Subplots were of uniform size within each experiment and location but varied in size among years and locations and ranged from 30 to 66 cm in length.

Plants usually started to senesce before significant disease reached the flag leaf. Therefore, disease was assessed by visually estimating the percentage (using an arithmetic scale from 1 to 100%) of the F-1 leaf area that was covered by stripe rust on each headbearing tiller in each subplot. A tag with an identification number was placed on each tiller that was assessed. The same person assessed all plants. To limit the duration of assessments to 4 days per location, we assessed only 19 of 31 treatments in 1987 and 12 of 16 treatments in 1988.

To determine if there was an effect of tagging on yield, we planted two plots of the common wheat cultivar Stephens in each block in 1986–1987; a duplicate plot of the mixture of Jacmar and Tres was the repeated treatment in 1987–1988. One of the repeated plots was left as an untagged control in each block in the inoculated experiments.

Harvest. With maturity, all tillers in each subplot of the inoculated and fungicide-treated experiments were cut with sickles and bagged. Plants were transported to the laboratory and separated by chaff color. The tag numbers were matched to disease notes taken in the field, so that mean disease severity could be calculated separately for the brown and white chaff components in the mixtures. Brown and white heads were counted to determine tiller frequencies and were threshed separately with a stationary thresher. Seed weight per plot and 1,000-seed weight were recorded.

Data analysis. Data were analyzed with SAS (27). Analyses of variance were performed for each experiment in each location. We used Fisher's unprotected LSD and linear contrasts to determine significance of treatment differences for disease and yield data. Variance*mean plots indicated homogeneous variances for the yield data. We eliminated nonhomogeneity of variances in the disease data by performing the analyses on log-transformed data. Thus, all of the reported disease data are the back-transformed least squares means.

Disease reduction in mixtures was first calculated relative to the mean of the disease severities on the pure stands:

TABLE 1. Chaff color, height, and reaction to two stripe rust races of wheat cultivars used in field experiments

Cultivar	USDA accession number	Chaff color	Relative height	Reaction[a] to *Puccinia striiformis* Race 5	Reaction[a] to *Puccinia striiformis* Race 27
Faro	CI 17590	Brown	Medium	VAR	R
Jacmar	NSL 95258	Brown	Short	S	R
Moro	CI 13740	Brown	Tall	S	R
Tres	CI 17917	White	Medium	MR	R
Tyee	CI 17773	White	Medium	R	S

[a] VAR, variable reaction (approximately one-half of the plants were resistant and one-half were susceptible, *personal observation*); R, resistant; S, susceptible; MR, moderately resistant.

$$1 - (S_X/S_M) = \text{total disease reduction} \quad (1)$$

in which S_X is disease severity of the mixture, and S_M is the mean disease severity of the mixture components grown in pure stands.

Equation 1 holds if the mixture to be analyzed is composed of equal proportions of its components. The proportions of mixture components were often unequal, however, because of different tillering and competitive abilities of cultivars. Therefore, we calculated the expected disease on the basis of the mean of the component pure stands weighted by the measured tiller frequencies of each cultivar in the mixtures (S_{MW}):

$$\sum_{i=1}^{n}([N_{ix}/N_x \times S_{iM}) = S_{MW} \quad (2)$$

in which N_{iX} denotes the number of tillers of component i in mixtures, N_X is the total number of tillers in mixtures, S_{iM} is the mean disease severity of component i in pure stands, and S_{MW} represents the weighted pure stand mean. The disease severity relative to the weighted pure stand mean represents the effect of mixing on epidemic development:

$$1 - (S_X/S_{MW}) = \text{epidemiological effect} \quad (3)$$

The difference between the total disease reduction in mixtures (Eq. 1) and the epidemiological effect (Eq. 3) is the effect on disease severity caused by selection for the more fit cultivar in the mixture:

$$\text{Total disease reduction} - \text{epidemiological effect} = \text{selection effect} \quad (4)$$

TABLE 2. Severity of stripe rust in wheat cultivar mixtures in subplots, on a per cultivar basis, and subdivision of percentage of disease reduction into selection and epidemiological effects in two-way mixtures in three and two locations in 1987 and 1988, respectively

Location and mixture	Disease severity[a] (%)			Selection effect[d]	Epidemiological effect[e]
		Cultivar			
	Subplot[b]	Brown[c]	White		
Corvallis 1987					
FJMR	1.2 (78)	1.1	0.1	...	...
FJMY	7.3 (69)	0.4	25.4	...	...
FJR	0.2 (97)** [f]	0.3	0.0	...	...
FJY	9.4 (67)	2.8	20.4	...	...
FMR	1.0 (36)	1.4	0.4	...	...
FMY	14.4 (41)*	2.5	34.0	...	...
JMR	0.6 (89)	0.7	0.2	...	...
JMY	16.3 (44)	6.8	28.9	...	...
FR	0.2 (85)	0.5	0.0	5	80
FY	13.8 (63)	1.3	28.8	5	58
JR	1.0 (81)	2.3	0.1	14	66
JY	33.6 (13)	19.9	45.1	−11	24
MR	0.5 (54)	1.0	0.1	7	46
MY	29.9 (19)**	1.7	53.4	−4	23
F	2.7	2.7		...	...
J	6.6	6.6		...	...
M	1.2	1.2		...	...
R	0.0		0.0	...	...
Y	71.6		71.6	...	...
Moro 1987					
FJMR	9.4 (56)	13.2	0.6	...	...
FJMY	26.9 (19)	31.1	8.3	...	...
FJR	14.2 (54)	25.6	0.8	...	...
FJY	17.1 (40)	21.4	2.5	...	...
FMR	2.9 (64)	5.8	0.4	...	...
FMY	6.7 (62)	7.8	2.3	...	...
JMR	6.0 (76)	10.0	0.9	...	...
JMY	16.7 (56)	23.6	4.6	...	...
FR	4.8 (29)	8.9	0.4	−5	34
FY	9.8 (51)	9.7	10.6	5	46
JR	6.6 (83)	20.0**	0.4	10	73
JY	19.1 (57)	25.7**	11.5	2	55
MR	1.1 (75)	1.2**	0.9	42	33
MY	8.4 (43)	3.8	15.6	6	37
F	14.1	14.1		...	...
J	79.8	79.8		...	...
M	8.6	8.6		...	...
R	0.3		0.3	...	...
Y	11.9		11.9	...	...

(*continued*)

[a] Percentage of F-1 leaf area covered with stripe rust. Disease per cultivar represents the average over all tagged tillers with a given chaff color (between 5 and 10% of the tags were lost in each plot; disease data from untagged tillers could be used to compute the mean disease severity in a plot, however, those data were ignored when the disease severity per cultivar was determined).

[b] Number in parentheses is the percentage of reduction relative to the mean of the pure stands of the mixture components.

[c] Brown and white refer to chaff colors. Faro (F), Jacmar (J), and Moro (M) are brown; Tres (R) and Tyee (Y) are white.

[d] Selection effect is the percentage of decrease or increase in disease severity in a mixture due to changes in frequencies of the mixture components.

[e] Epidemiological effect is the percentage of reduction in disease severity below the mean of the pure stands weighted by the harvested cultivar frequencies.

[f] *, **, ***, Disease severity on a cultivar was lower than on the same cultivar in pure stand at $P < 0.1$, $P < 0.05$, and $P < 0.01$, respectively (linear contrasts). No contrasts were performed on cultivar severities for mixtures that contained more than two components.

[g] +, Disease severity on Tres was higher than in its pure stand at $P < 0.1$ (linear contrast).

Positive selection effects indicate that increased survival and/or tiller production of the more resistant components of the mixtures contributed to disease reduction. Negative selection effects indicate that disease severity in the mixtures was increased through selection for the more susceptible cultivar.

RESULTS

There was no significant effect ($0.16 < P < 0.86$ in the different experiments) of tagging tillers on yield per plot or 1,000-seed weight in either season or location.

Disease severity. Because of variable inoculation success, disease severity on Faro, Jacmar, and Moro, caused by race 5, was very variable in Corvallis 1987. For example, the severity on Jacmar ranged from 0.2 to 44.0% among replications. Similarly, in Moro 1987, disease severity on Tyee caused by race 27 ranged from 3.4 to 72.5%. Data from one replication in Moro 1987 were not used because of heavy weed infestation. Also contributing to variability was the reaction of Faro to stripe rust race 5. Disease severity on individual Faro tillers was either very high or less than 1%, suggesting that Faro consisted of two differential lines. On average, 53% of the tillers exhibited a resistant reaction.

Overall disease severity in all mixtures that were assessed was lower than the mean of the respective components grown in pure stands (Table 2). However, disease reductions were statistically significant in only 20 of 58 mixtures.

For the individual mixture components in two-way mixtures, disease reduction was greater on the cultivars that had higher disease severities in pure stands in a given year and location (Table 2). Although disease severity on Tres was often higher in mixtures than in pure stands, the increases were small.

Yield and yield components of the pure stands. Pure stands of Faro, Jacmar, Tres, and Tyee did not differ significantly in yield in the fungicide-treated experiments in either year, except in Pendleton 1988 where the yield of Faro was significantly higher than the yield of Jacmar and Tres (9). Moro yielded significantly less than the other cultivars in all three locations in 1987. Faro consistently produced more heads than the other cultivars; this was rarely statistically significant, however. The higher tillering of Faro was counteracted by either a low seed weight or a low number of seeds per head compared to the other cultivars. Differences between inoculated and fungicide-treated plots were usually smaller for Faro, Moro, and Tres than for Jacmar and Tyee. Yield was not always higher in the fungicide-treated plots of Faro, Moro, and Tres. There was little difference between number of heads produced in stripe-rust-inoculated and fungicide-treated

TABLE 2. *Continued*

Location and mixture	Disease severity[a] (%)			Selection effect[d]	Epidemiological effect[e]
		Cultivar			
	Subplot[b]	Brown[c]	White		
Pendleton 1987					
FJMR	19.7 (38)	27.9	2.3	...	...
FJMY	29.9 (30)	35.2	9.6	...	...
FJR	15.9 (48)	25.9	4.0	...	...
FJY	26.7 (41)	28.8	18.6	...	...
FMR	10.3 (47)	16.5	1.6	...	...
FMY	9.8 (70)***	9.8	8.1	...	...
JMR	11.4 (67)*	17.8	1.7	...	...
JMY	20.3 (57)***	20.9	14.9	...	...
FR	5.5 (55)	9.8*	1.7	7	47
FY	17.7 (48)**	14.1	10.2	4	43
JR	13.6 (60)	45.2	1.6	35	25
JY	28.9 (48)**	38.1	22.3***	1	47
MR	4.2 (67)***	7.6***	2.1	9	67
MY	17.2 (56)***	8.6***	27.1**	1	55
F	20.1	20.1		...	...
J	65.6	65.6		...	...
M	32.3	32.3		...	...
R	2.2		2.2	...	...
Y	42.9		42.9	...	...
Moro 1988					
FJR	15.6 (44)	19.5	6.2	...	...
FJY	25.6 (38)**	26.9	19.3	...	...
FRY	12.0 (53)*	9.8	12.7	...	...
JRY	17.8 (53)*	35.8	10.6	...	...
FR	8.2 (38)	10.2	5.8	−2	40
FY	19.7 (47)**	13.4	28.9	8	40
JR	23.2 (24)*	44.5	7.6	14	9
JY	33.4 (38)**	38.4	26.5	0	38
F	19.3	19.3		...	...
J	53.7	53.7		...	...
R	4.7		4.7	...	...
Y	52.2		52.2	...	...
Pendleton 1988					
FJR	4.6 (72)**	6.5	1.0	...	...
FJY	12.0 (56)***	8.1	20.6	...	...
FRY	8.5 (47)	3.0	11.2	...	...
JRY	13.2 (49)*	8.9	13.7	...	...
FR	3.1 (31)	4.4	1.4+ [g]	−6	37
FY	12.7 (46)	4.6*	22.2***	5	42
JR	4.0 (78)**	10.6***	1.7+	20	57
JY	26.4 (32)	8.7***	37.2	0	32
F	7.7	7.7		...	...
J	35.3	35.3		...	...
R	0.7		0.7	...	...
Y	39.2		39.2	...	...

TABLE 3. Yield of wheat cultivar mixtures relative to the mean of the mixture components in pure stands, and number of heads, number of seeds per head, and 1,000-seed weight of mixtures and pure stands in the presence and absence of stripe rust in three locations in 1987 and in two locations in 1988

Year and mixture	Location					
	Moro		Pendleton		Corvallis	
	Fungicide-treated[a]	Inoculated[b]	Fungicide-treated	Inoculated	Fungicide-treated	Inoculated
1987 Relative yield per subplot						
FJMRY[c]	1.06	1.00	1.01	1.04	0.99	1.15
FJMR	1.03	1.15	1.16*	1.04	0.98	1.16
FJMY	1.01	1.04	1.14	1.11	1.14*	1.21**
FJRY	0.97	1.28**	1.09	1.16*	0.88	1.06
FMRY	1.12*[d]	1.36**	1.05	0.98	1.01	1.25**
JMRY	0.96	1.21	0.97	1.13	1.06	1.12
FJM	0.90	1.01	1.10	1.02	0.99	0.98
FJR	1.07	1.00	1.05	1.08	1.03	1.09
FJY	1.08	0.90	1.04	1.17*	0.85*	1.37***
FMR	1.14*	0.98	0.97	1.24**	1.01	1.04
FMY	1.04	1.11	1.03	1.17	1.07	1.25**
FRY	1.12*	1.03	0.94	1.04	1.04	1.03
JMR	1.04	1.09	1.06	1.08	0.99	1.07
JMY	1.16**	1.34**	0.95	1.26*	1.04	1.20*
JRY	1.02	1.06	0.97	1.15	0.99	1.19*
MRY	1.11	1.10	1.04	1.15	0.95	1.40***
FJ	1.03	0.81	1.03	1.00	1.04	0.93
FM	1.17**	1.00	1.16*	0.91	0.95	0.88
FR	0.98	1.10	1.01	1.18*	0.83**	1.19*
FY	0.98	0.92	1.06	1.08	0.90	1.26**
JM	1.03	1.09	0.87	0.88	1.10	0.97
JR	1.03	1.14	1.03	1.19*	0.92	0.98
JY	0.92	1.19	1.07	1.17*	1.12	1.10
MR	0.97	1.21	1.18**	1.11	1.10	1.06
MY	1.03	1.15	0.89	0.94	1.12	1.27**
RY	1.05	1.09	0.88	1.13	0.97	1.29**
Mean	1.04	1.09	1.03	1.09++[e]	1.00	1.13+++
Number of heads per subplot						
Mixtures[f]	141.99	142.13	126.50	126.13	143.02	131.38++
Pure stands	136.60	135.47	119.95	124.45	143.50	125.20
Number of seeds per head						
Mixtures	36.59++	32.44	30.32++	30.39	31.94	29.05
Pure stands	38.06	31.69	31.75	29.93	33.19	28.32
1,000-Seed weight (g)						
Mixtures	26.92	21.08	30.41	28.47++	32.77	33.48+
Pure stands	26.17	20.85	29.76	26.83	32.05	32.23
1988 Relative yield per subplot						
FJRY	1.05	1.11	1.08	1.11		
FJR	1.07	1.02	1.20++	1.09		
FJY	0.96	1.15*	1.04	1.22*		
FRY	1.17**	1.10	1.06	1.03		
JRY	1.05	1.15	1.04	1.10		
FJ	1.00	0.99	1.00	1.06		
FR	0.98	1.04	1.01	0.98		
FY	1.20**	1.01	1.03	1.05		
JR	0.98	1.13	1.05	1.26		
JY	1.13	1.10	1.07	1.18		
RY	1.08	1.07	0.97	1.01		
Mean	1.05	1.08+	1.05+	1.10+		
Number of heads per subplot						
Mixtures	138.09	141.11	119.05+	113.61		
Pure stands	134.04	139.83	113.46	109.58		
Number of seeds per head						
Mixtures	46.99	42.04+	42.11	36.33		
Pure stands	46.63	40.52	41.28	35.30		
1,000-Seed weight (g)						
Mixtures	28.63	26.43+	30.23++	27.65+++		
Pure stands	28.36	25.38	31.06	26.30		

[a] Plots treated with fungicide.
[b] Plots inoculated with stripe rust.
[c] F = Faro; J = Jacmar, M = Moro, R = Tres, Y = Tyee.
[d] *, **, ***, Mixture yield is significantly different from the mean of the pure stands at $P < 0.1$, $P < 0.05$, and $P < 0.01$, respectively (linear contrasts).
[e] +, ++, +++, Mean of mixtures was different from the mean of the pure stands at $P < 0.1$, $P < 0.05$, and $P < 0.01$, respectively (linear contrasts).
[f] Means of all mixtures and of all pure stands are reported, respectively.

plots. However, the 1,000-seed weight and number of seeds per head were smaller in the inoculated experiments.

Yield and yield components of mixtures. In 1987, 64% of the mixtures in the fungicide-treated plots and 79% of the mixtures in the inoculated plots had higher yields than the corresponding components in pure stands (Table 3). Similarly, in 1988, 77% of the fungicide-treated mixtures and 91% of the inoculated mixtures yielded higher than the mean of their pure stands. However, few of these yield increases were statistically significant.

The mean number of heads and the range of number of heads in mixtures were approximately the same as the mean of the component pure stands in both years, but the 1,000-seed weight was usually increased in mixtures (Table 3). No single mixture had a significantly lower seed weight than the mean of the component pure stands. In 1987, 83% of the fungicide-treated mixtures had fewer seeds per head than the corresponding pure stands. The differences in number of seeds per head between mixtures and pure stands were significant at $P < 0.05$ in Moro and Pendleton and at $P = 0.11$ in Corvallis (Table 3). In contrast, the number of seeds per head was lower than the pure stand mean in only 23% of the inoculated mixtures. In 1988, the differences in seeds per head between mixtures and pure stands were much smaller in both locations and inoculation treatments.

Competitive interactions among cultivars in mixtures. The relative yield of Tres in mixtures was always significantly higher than the relative yield of Tyee, except in the inoculated experiment in Corvallis 1987 (Table 4). Correspondingly, in the presence of Tres, the relative yield of Faro, Jacmar, and Moro was significantly lower than in the presence of Tyee in all experiments in both seasons. Except in Moro 1988 in the fungicide-treated experiment, the average relative yield of Faro was greater than the relative yield of Jacmar (Table 4), and the relative yield of Tres and Tyee was lower in the presence of Faro than in the presence of Jacmar. The relative number of heads, seed weight, and number of seeds per head in the mixtures followed similar trends, although the effects were not always statistically significant (data not shown).

A more detailed analysis has been performed on the two-way mixtures containing one brown-chaffed and one white-chaffed cultivar (9). The number of heads produced by a cultivar in mixture relative to its pure stand provided an estimate of interference between cultivars during early development, whereas relative yield per head reflected cultivar interactions after tillering rather than effects of density on yield. Relative yield per cultivar provided a cumulative measure of interference effects throughout the season. The effects of competition on the different cultivars did not always remain constant over time. For example, number of heads and yield per head of Jacmar were affected similarly by competition. In contrast, the relative yield per head could not be predicted from the relative number of heads for the other four cultivars.

Figure 1 gives an overview of the relative performance of the cultivars in two-way mixtures. Mixtures that fall above the expected line, which is the majority of the mixtures, yielded more than the mean of their component pure stands. Most mixtures fall in the lower right quadrants, indicating that Tres and Tyee were good competitors. Mixtures containing Tres usually fall further to the right than mixtures containing Tyee, indicating that Tres was a stronger competitor than Tyee. Similarly, mixtures with Jacmar fall lower than mixtures with Faro and Moro.

Although neither the slopes nor the intercepts of the regression lines in Figure 1 were significantly different from the expected lines, some distinct trends were discernible. Except for the fungicide-treated experiments in 1988, distance between the regression lines and the expected lines increased with the improvement of the performance of the white cultivars (right quadrants in Fig. 1), indicating that the corresponding decrease in relative yield of the brown cultivars was not as strong as the increase in relative yield of the white cultivars. On the other hand, in cases in which Faro, Jacmar, and Moro were the better competitors (top quadrants in Fig. 1), the yield decrease of Tres and Tyee was somewhat stronger than the corresponding increase of Faro, Jacmar, and Moro. In only a few mixtures, both cultivars had higher yields than expected (Fig. 1, upper right quadrants). All of these mixtures contained Tyee. Also, the majority of the mixtures that contain Tyee fall above the regression lines, whereas the majority of the

TABLE 4. Relative yield[a] of the wheat cultivars Faro, Jacmar, Moro, Tres, and Tyee grown in mixtures[b] in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust

	Location					
	Moro		Pendleton		Corvallis	
Mixture	Brown[c]	White	Brown	White	Brown	White
1987 Fungicide-treated						
Mix + Tres[d]	0.73***[e]	1.52**	0.81***	1.50***	0.60***	1.60***
Mix + Tyee[f]	1.03	1.08	1.14	0.91	0.95	1.18
Mix + Faro[g]	0.97***	1.06**	1.02***	1.01***	0.72***	1.08***
Mix + Jacmar[h]	0.66	1.30	0.67	1.32	0.43	1.49
1987 Inoculated						
Mix + Tres	0.70***	1.66**	0.70***	1.68	0.70***	1.65
Mix + Tyee	1.09	1.09	1.17	1.04	0.99	1.74
Mix + Faro	0.93**	1.10**	1.04***	1.12***	0.84***	1.44
Mix + Jacmar	0.69	1.50	0.53	1.56	0.43	1.63
1988 Fungicide-treated						
Mix + Tres	0.94***	1.08*	0.73***	1.59***		
Mix + Tyee	1.11	0.99	0.91	1.21		
Mix + Faro	0.97***	1.06*	1.03***	1.05***		
Mix + Jacmar	1.08	1.01	0.51	1.47		
1988 Inoculated						
Mix + Tres	0.95***	1.14*	0.83***	1.25***		
Mix + Tyee	1.21	0.90	1.20	1.03		
Mix + Faro	1.08	1.01*	1.15***	0.90***		
Mix + Jacmar	0.95	1.18	0.74	1.34		

[a] Yield (total seed weight) relative to the pure stands.
[b] Mixtures in which at least one cultivar could be separated by chaff color are included.
[c] Brown-chaffed cultivars were Faro (F), Jacmar (J), and Moro (M); white-chaffed cultivars were Tres (R) and Tyee (Y).
[d] Mixtures containing Tres were FJMR, FJR, FMR, FR, JR, MR.
[e] *, **, ***, Yield of mixture was different from that of mixture in line below at $P < 0.1$, $P < 0.05$, and $P < 0.01$, respectively.
[f] Mixtures containing Tyee were FJMY, FJY, FMY, FY, JY, MY.
[g] Mixtures containing Faro were FRY, FR, FY.
[h] Mixtures containing Jacmar were JRY, JR, JY.

mixtures that contain Tres fall below. Thus, Tyee was usually a less aggressive neighbor than Tres.

Effects of plant competition on disease. In most of the mixtures that were evaluated for selection effects, the cultivar that produced more tillers (9) was also the more resistant cultivar; this resulted in positive selection effects ranging from 1 to 42% (Table 2). In cases in which selection favored the more susceptible cultivar, disease was increased between 2 and 11%. The highest selection effects were usually observed in the Jacmar-Tres mixtures because of the great differences in competitiveness between the two cultivars. In the Faro-Tres mixture, selection effects were sometimes positive and sometimes negative but overall not very strong, indicating the similarity in competitiveness of Faro and Tres.

DISCUSSION

Diversity for stripe rust resistance within wheat populations reduced disease severity below the mean of the component pure stands for all of the mixtures. The overall positive effects of the mixtures on disease that were reported by Knott and Mundt (16) were confirmed by our studies. Although the plots were adjacent and interplot interference may have increased overall disease severity, differences among the mixtures were considerable and reflected differences in host composition. Low success of the inoculations with race 5 in Corvallis 1987 and race 27 in Moro 1987 resulted in great variability in disease severity and accounted for the frequent nonsignificance of the reductions in that year.

Selection effects and epidemiological effects influenced stripe rust severity in the mixtures. If selection favors the more resistant cultivar, then disease severity in a mixture can be reduced below the mean of the pure stands of its components even if disease on the more susceptible cultivar is not reduced in the mixture. Selection can only affect disease if mixture components are differentially susceptible. In 1988, for example, the harvested tiller frequencies of Jacmar in the mixtures of Jacmar and Tyee were 0.37 and 0.60 in Pendleton and Moro, respectively, in contrast to the planted proportions of 0.50 (9). Nevertheless, selection effects were zero (Table 2), because the disease severity on the two cultivars in pure stand was almost the same. Although in most cases the epidemiological effect contributed most to disease control, selection effects played a major role in some of the mixtures. The differences in competitiveness were usually small when

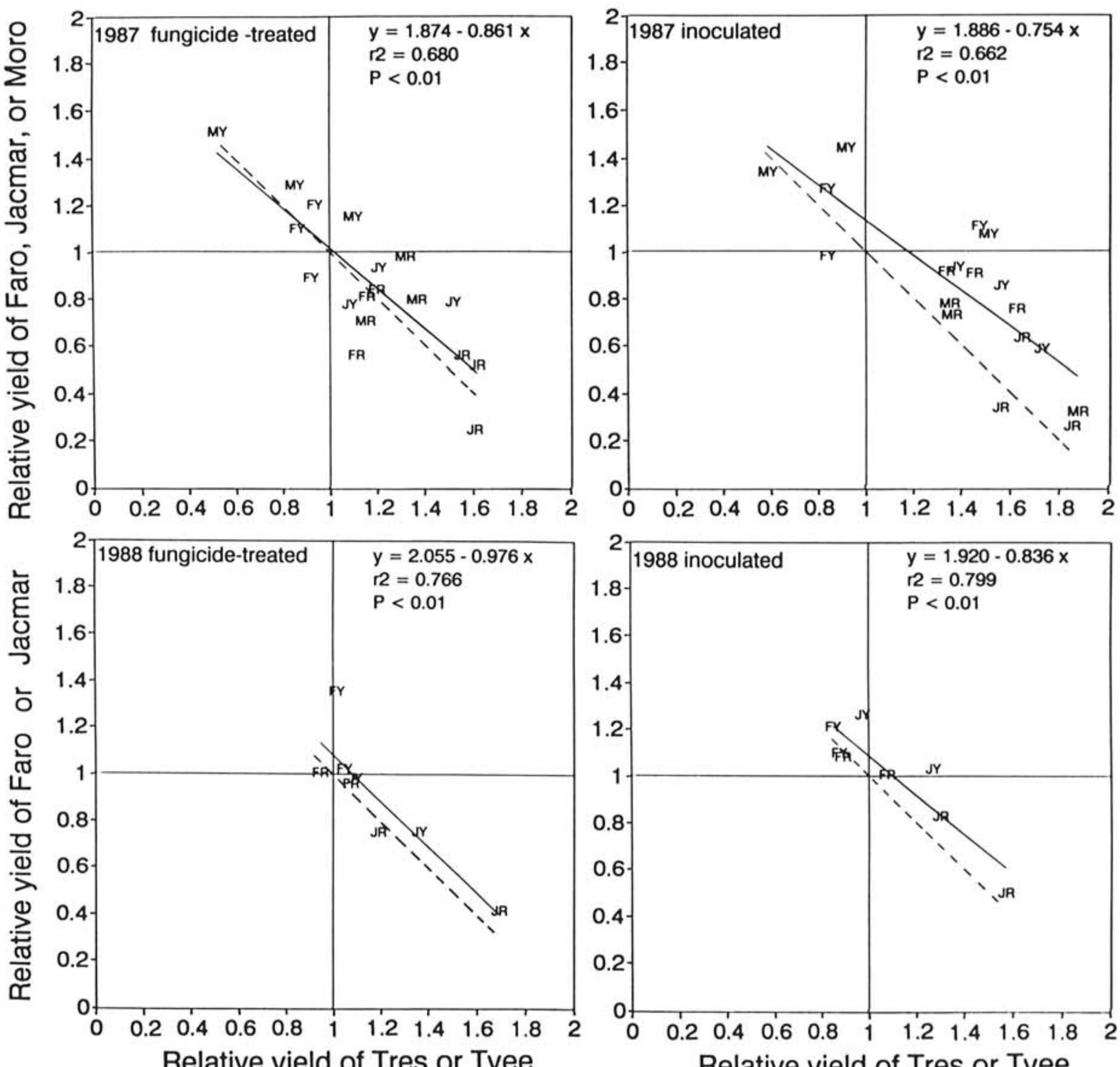

Fig. 1. Correlation of the yield relative to pure stands of the wheat cultivars Faro (F), Jacmar (J), Moro (M), Tres (R), and Tyee (Y) when grown in two-way mixtures in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust. The dashed line (- - -) represents the expected correlation between brown and white cultivar yield, if an increase in yield in one mixture component were compensated for by an equal decrease in yield of the other component. The solid line (—) is the actual regression line. The graph is divided into quadrants in which either none (lower left), one (upper left or lower right), or both (upper right) components yielded higher than expected. Mixtures falling above the expected correlation yielded more than the mean of their pure stands.

selection was for the more susceptible cultivar and greater when selection favored the more resistant cultivar. Thus, overall selection effects added to disease control in our experiments. However, this result can not be generalized. For example, in Corvallis 1987, Tyee was much more heavily infected than Jacmar and was the stronger competitor (Tyee frequency = 0.57); this resulted in a negative selection effect almost half the size of the epidemiological effect (Table 2). The outcome of our experiments might have been dramatically different had we used a stripe rust race that attacks Tres instead of one that attacks Tyee.

The magnitude of the yield increases in our mixtures over the mean of the pure stands was similar to increases that were observed by others (3,20,23,35). Although only a few mixtures yielded higher than the highest yielding pure stand in a given location and year, no mixture yielded less than the lowest yielding pure stand. Our data support the view of Wolfe and Barrett (35) and Mahmood et al (20) that cultivar mixtures should help reduce risks involved in choosing cultivars, because it is usually impossible to predict the best yielding cultivar before planting.

Like others (30,31), we found that the performance of a cultivar in pure stand was not always indicative of its performance in mixtures. The poor performance of Jacmar in the mixtures could be due to its shortness. No height measurements were taken in 1987, but the pure stands of Jacmar and Moro could be identified without difficulty as the smallest and tallest stands, respectively. In Pendleton 1988, Jacmar was between 11 and 26 cm shorter than the other cultivars, and in Moro 1988 it was between 7 and 16 cm shorter. Poor performance of a cultivar in rice cultivar mixtures has been ascribed to its shortness relative to other mixture components (12). However, Moro was by far the tallest cultivar, but its performance was not always improved by mixing.

The experiments precluded a formal competition analysis as proposed by others (11,14,28,29), because no yield-density function was determined for the cultivars. Nevertheless, differences in competitive abilities of the cultivars were evident. Variable competitiveness of the cultivars among locations and years might be partially explained by climatic conditions. For example, at the Moro site under the drought conditions in 1988, which kept the taller cultivars almost as short as Jacmar, the yield of Jacmar relative to its pure stand when mixed with Tres was 0.75 and 0.83 in 1988 in the absence and presence of disease, respectively. In 1987 in the same mixtures, the yield of Jacmar was 0.52 and 0.63, respectively. The relative yield of Tres when mixed with Jacmar in Moro 1988 was 1.30 and 1.19 in the presence and absence of disease, respectively, and 1.64 and 1.61 in the same mixtures in 1987 (9). An increase or decrease in competition for resources might also directly alter the response of plants to disease. Such effects could have acted on Jacmar. When mixed with Tres, the disease severity on Jacmar was 44% in 1988 and 20% in 1987 (Table 2), but it still performed relatively better in 1988. This counter-intuitive result could be explained by a decrease in competitive pressure from Tres, due to climatic conditions, that rendered Jacmar more tolerant to disease. In subsequent experiments, we found that disease severity on cultivars in mixtures was affected not only by selection and epidemiological effects, but also depended on the genotype of the companion cultivar (10).

The effects of disease on the competitive abilities of the cultivars could not be analyzed statistically. Nevertheless, it is interesting to note that the resistant cultivar Tres usually had higher relative yields in the inoculated experiments than in the fungicide-treated experiments (9). This could be due to the effects of disease on the competitive abilities of Faro, Jacmar, and Moro. Effects of disease on the competitive ability of plants in mixtures have been reported in other host-pathogen systems (7,25,26). However, the yield of Faro and Jacmar relative to their pure stands was often very similar in the diseased and the nondiseased mixtures and sometimes even higher in the presence of disease. This may be because cultivar performance in mixtures was determined relative to the performance of the cultivar in the pure stand. Such a comparison is direct in nondiseased mixtures. However, we compared the performance of cultivars in diseased mixtures with their pure stands, which were more heavily diseased. For example, in Moro 1987, disease severity on Jacmar in mixtures with Tres was reduced from an average of 80% in pure stands to an average of 20%. However, the disease reduction on Jacmar was not reflected in its performance. The relative yield of Jacmar was 0.52 in the absence of disease and 0.63 in the presence of disease, which corresponds to 81 and 57 g of total yield of Jacmar per plot. This might indicate the stronger competitive effects of Tres on diseased Jacmar plants than on healthy plants.

Only a few cultivar combinations possessed good ecological combining ability sensu Allard and Adams (3), that is, both components responded with a yield increase in mixtures (Fig. 1, upper right quadrants). This is consistent with the work of Allard and Adams (3), who found that good ecological combining ability was common in mixtures of barley lines that had coevolved for many generations, but it was very rare among cultivars that had been selected as pure lines. Our results indicate that different degrees of competitiveness and neighborhood effects can produce similar effects on the total yield in mixtures. For example, in mixtures that contained Tres, yield increased despite the negative neighborhood effects of Tres on the other cultivars, and the increase was mainly because of the competitive ability of Tres. On the other hand, in mixtures with Tyee, yield increases were due to a combination of less negative and sometimes positive neighborhood effects of Tyee and its good competitive ability.

The performance of cultivars in mixtures containing more than two cultivars cannot be predicted on the basis of our results, because not all of the mixtures could be separated into their components on the basis of chaff color. However, experiments with the four-way mixture of Faro, Jacmar, Tres, and Tyee, in which all the mixture components were separated, suggested that the overall performance of the four cultivars relative to each other was similar in the four-way mixtures and in the two-way mixtures (9).

Our study shows that disease reduction in mixtures can be partitioned into selection and epidemiological effects. Differences in disease reduction between mixtures of a resistant and a susceptible cultivar and mixtures of two differentially susceptible cultivars could be partially ascribed to differential survival and/or tiller production of mixture components.

In small grain production, growers often do not purchase new seed every season. Therefore, growers who want to use cultivar mixtures to stabilize yield and/or control disease need to know how long they can expect the seed harvested from mixtures to contain the mixture components at proportions that still provide the advantages of mixing. Mixtures in which the components perform very unequally will change in composition over time, possibly requiring remixing more often than mixtures of more similar components.

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