Effects of Two-Component Wheat Cultivar Mixtures on Stripe Rust Severity

Shamsul I. Akanda and Christopher C. Mundt

Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis 97331-2902.

Paper 10,790 of the journal series of the Oregon Agricultural Experiment Station.
This study was supported in part by USDA NRI grant 91-37303-6700 and a Rotary Foundation Freedom From Hunger Fellowship.
Accepted for publication 20 December 1995.

ABSTRACT

Akanda, S. I., and Mundt, C. C. 1996. Effects of two-component wheat cultivar mixtures on stripe rust severity. Phytopathology 86:347-353.

Three two-component wheat (*Triticum aestivum*) cultivar mixtures, along with their pure stands, were grown at five ratios in three experiments. Each cultivar was susceptible to either one or two of three *Puccinia striiformis* races inoculated into the plots. Chaff color differences served as markers to distinguish the cultivars in mixture, so that disease could be calculated on a per-cultivar basis. Stripe rust severity on individual cultivars increased linearly with the frequency of that cultivar in mixture, with 16 of 18 possible regressions having significantly ($P \leq 0.05$) positive linear slopes. One cultivar had significantly different levels of rust when mixed with different companion cultivars, suggesting that plant-plant interactions affected susceptibility of that cultivar to rust. In contrast to an earlier study, changes in frequencies of mixture components from planting to harvest had little influence on stripe rust severity. Mixtures with equivalent proportions of cultivars generally provided the highest level of disease control.

Additional keyword: epidemiology.

One strategy to prolong the useful life of resistance genes and increase yield stability is to grow multilines or cultivar mixtures (8,28,31,33). The mechanisms by which multilines or cultivar mixtures reduce disease severity have been discussed (17,28,33) and include the following: physical blockage of propagule transmission among plants of different genotypes, dilution of compatible inoculum via increasing the distance between plants of the same genotype, inducement of resistance, increased tillering for the more resistant cultivar(s) in a mixture, and competitive inhibition among virulent races.

Though multiline cultivars have had commercial success (8,9,27,28,33), the multiline approach for controlling diseases can be laborious and expensive (13). Thus, more recent attention has focused on the use of cultivar mixtures, which requires no further breeding for agronomic uniformity. The advantages of cultivar mixtures over multilines (28,33) include the following: lack of need for breeding mixture components; ability to utilize new, agronomically superior cultivars in mixtures; ability to attain genetic diversity for resistance to multiple diseases; potential limitation of the evolution of pathogen races with multiple virulence; and increased possibilities for positive yield synergism (positive interactions among cultivars resulting in increased yield).

Reductions in disease severity in cultivar mixtures compared with the disease severity mean of the same cultivars grown in pure stands have been demonstrated for polycyclic, foliar pathogens of small grains (8,28,33). In many experimental studies with cultivar mixtures, a single pathogen race was used, with one host genotype being resistant and the other being susceptible to that race (1,5,10,11). In practice, many or all cultivars in a mixture are likely to be susceptible to one or more races, and interactions among races may influence the epidemiological effects of mixtures (14,28). In studies in which more than one race has been used, the ratio of host cultivars was constant (16,17,25,34), which may not always be the case in the commercial application of cultivar mixtures. Thus, we conducted experiments to study the influence of two-component club wheat (*Triticum aestivum* L.) cultivar mixtures on severity of stripe rust (caused by *Puccinia striiformis* Westend.) under the more complex conditions of multiple pathogen races and varying ratios of host cultivars. We utilized mixtures of cultivars with morphological markers so that we could determine if the impact of mixtures on disease severity varies among cultivars.

MATERIALS AND METHODS

Field plot locations. Experimental plots were located at the Columbia Basin Agricultural Research Center field stations at Moro and Pendleton, Oregon. Both sites represent important wheat growing areas of the state and are approximately 200 km apart. Average annual rainfall at Moro and Pendleton is 280 and 490 mm, respectively. Soil type at both sites is a Walla Walla silt loam, though soil depth is significantly greater at Pendleton than at Moro. The experiments were conducted during the 1991 to 1992, 1992 to 1993, and 1993 to 1994 winter wheat seasons.

Cultivars. Four winter club wheat cultivars differing in stripe rust resistance, height, and chaff color were used (Table 1). All cultivars are or have been grown commercially near the study

TABLE 1. Plant height and chaff color of four winter club wheat cultivars and their reactions to different stripe rust races used in field experiments

			Reaction[a] to *Puccinia striiformis* race		
Cultivar	Height	Chaff color	CDL 27	CDL 29	CDL 41
Faro	Medium	Brown	R	S	R
Jacmar	Short	Brown	R	S	S
Tres	Medium	White	R	R	S
Tyee	Medium	White	S	R	R

[a] S = susceptible and R = resistant.

Corresponding author: C. C. Mundt; E-mail address: mundtc@bcc.orst.edu

Publication no. P-1996-0205-03R

areas, and are well adapted locally. Commercial seed of the cultivar Faro in Oregon consists of a mixture of two agronomically indistinguishable lines with slightly different resistance spectra to *P. striiformis*. We purified the line giving resistance to *P. striiformis* race CDL 29 (OR 7142) for use in our studies, but referred to this line as 'Faro' in this paper.

Experimental design and treatments. Experiments at both sites and over all 3 years entailed a randomized, split-block design with four replications. Main plots were the presence or absence of stripe rust, and the subplots were pure stands and mixtures of different wheat cultivars. Each subplot was 6.1 m long and four rows wide, with 0.36 m between rows, and was mowed to 4.9 m in length in the spring. Subplots were further separated along their longest dimension by a subplot of the common soft winter wheat cultivar Stephens, which is immune to the *P. striiformis* races used in this study. Seeding rates of 253 and 158 seeds/m^2 were used at Moro and Pendleton, respectively. Fertilization and weed and insect control practices were those typical of commercial wheat production at the two locations. All experimental plots at Pendleton in both seasons were sprayed with benomyl at 1.25 kg a.i./ha once in early April to control foot rot (caused by *Pseudocercosporella herpotrichoides*).

Populations grown in 1991 to 1992 at each location included pure stands of the four cultivars and three two-way mixtures (Faro-Tyee, Faro-Tres, and Jacmar-Tyee), each planted at ratios of 10:90, 25:75, 50:50, 75:25, and 90:10. Additional mixture treatments were included in these experiments, but they formed part of a separate study not reported here.

Treatments for the 1992 to 1993 season were similar to those of 1991 to 1992, except that seed for each mixture was collected from plots grown in the previous season. Similarly, the treatments for 1993 to 1994 were established from seed collected from the 1992 to 1993 experiment. Seeds from all four replications of the previous season were mixed before being packaged for replanting in the next season.

Inoculation. Inoculation was done by transplanting susceptible wheat seedlings infected with races CDL 27, CDL 29, and CDL 41 of *P. striiformis* (race designations are those of the USDA Cereal Diseases Laboratory, Washington State University, Pullman). Each cultivar was susceptible to one of these races, except for Jacmar, which was susceptible to both races CDL 29 and CDL 41 (Table 1).

Peat pots (6 cm) containing 2- to 3-week-old, greenhouse-grown seedlings of the cultivar Nugaines were inoculated with 0.001 mg of fresh urediospores (equiproportional mixture of all three races) per pot. The seedlings were kept in a dew chamber for about 12 h, and then transported to a protected outdoor location to acclimatize to field conditions.

Two to 3 weeks after inoculation, just prior to pustule eruption, seedlings from two pots were transplanted into each of the subplots designated for inoculation. Seedlings were transplanted on 18 and 19 March 1992 at Pendleton and Moro, respectively. For the 1992 to 1993 field season, transplantings were done on 9 and 10 November at Pendleton and Moro, respectively, and again on 11 and 12 March. In the 1993 to 1994 season, a single inoculation was done on 1 and 4 March 1994 at Pendleton and Moro, respectively.

TABLE 2. Stripe rust severity in pure stands of wheat cultivars in experiments conducted at Moro and Pendleton, Oregon, in 1993 and 1994[a]

	Environment		
Cultivar	Moro/93	Pendleton/93	Pendleton/94
Faro	48.8 b	25.9 a	27.8 b
Jacmar	48.2 b	43.2 a	94.6 a
Tres	55.6 ab	32.1 a	38.3 b
Tyee	63.7 a	24.8 a	37.0 b
Mean	54.1	31.5	49.4

[a] Values followed by the same letter within a column were not significantly different at $P = 0.05$ according to Fisher's least significant difference procedure.

Disease recording. Disease severity was assessed by visually estimating the percent leaf area covered with stripe rust lesions on the leaf below the flag leaf (F-1 leaf). An exception was at Pendleton during the 1992 to 1993 field season, when disease was recorded on the F-2 leaf because of low disease severities at the time of assessment. At Moro, disease was always recorded during the last week of May; at Pendleton, disease was assessed during the first week of June. Plants were in the early dough stage at the time of assessment. Disease was assessed on approximately 120 head-bearing tillers in the two middle rows, halfway between the center and the end of each subplot. Each tiller was given a tag that matched numerically with the corresponding disease score. At maturity, tillers on which disease assessments were made were hand-harvested with sickles, bagged, transported to the laboratory, and identified to a cultivar based on chaff color. In calculating overall disease severities for the mixtures, disease severities were averaged over all tillers in each subplot. Tillers with lost tags (5 to 7% of total) could not be included when calculating disease severity for individual cultivars within mixtures.

Data analyses. Data were analyzed by analysis of variance (ANOVA) using the general linear model procedure of the Statistical Analysis System (29). ANOVA over environments indicated significant ($P \leq 0.001$) interactions between treatments and experiments. Therefore, statistical analyses were done only within experiments. Plots of variance × mean indicated no need for data transformation.

The effect of mixtures on rust severity in mixtures was calculated relative to the means of their pure stands, based on disease severity in the pure stands averaged over four replications and weighted by the frequency of the seed of each cultivar in the mixtures planted in that season (seed counts of each cultivar from hand-harvested samples of the previous season were used as estimates of planting frequencies). This calculation gave the total disease effect due to mixing (16,17).

Planted seed frequencies and harvested tiller frequencies can differ because of differing tillering and competitive abilities of the cultivars. Therefore, disease effects also were calculated by weighting the component cultivars by their respective harvested tiller frequencies. Disease severities of mixtures relative to the weighted disease severity means of their pure stands measured the effect of mixing on epidemic development, and has been designated as the "epidemiological effect" (16,17). The difference between the total disease reduction and the epidemiological effect is the "selection effect" (16,17), i.e., the effect of changes in frequencies of cultivars on disease severity calculated at the population level (16,17).

Disease severities of each cultivar when grown in mixture were regressed on the harvested tiller frequencies of the respective cultivars to determine the effect of cultivar proportion on disease severity. In doing so, mean disease severity over all tillers in each subplot was regressed on the harvested tiller frequency averaged over all four replications of a treatment. Coefficients of determination (15 [page 42]), significance of slopes, and scatter plots of residuals were used to evaluate the regression relationships.

Linear contrasts were used to determine significances of differences between mixtures, averaged over all mixture proportions, and the means of their component pure stands. For each of the three experiments, contrasts were done for individual mixtures, the mean of all mixtures, the mean of all mixtures initially planted in 50:50 proportions, and the mean of all mixtures initially planted in frequencies other than 50:50. For contrasts averaged over mixtures, disease severities for the pure stands were adjusted by taking into account the number of times the cultivar was represented in the mixtures.

RESULTS

Disease severity averaged over cultivars and ranking of disease severity among the pure stands differed in the three experiments, though differences among cultivars were not always significant (Table 2).

Disease severity of individual cultivars in the mixtures was dependent on their frequency in the stand (Figs. 1 to 3). Linear regressions of stripe rust severity on cultivar proportion were significant for 16 of 18 mixture × environment combinations, and residual patterns appeared random. The frequency-dependence of disease, as indicated by the slopes of the regressions, varied among experiments and companion cultivars in the mixtures.

Disease severity of the 50:50 mixtures was 40% less than the component pure stands averaged across experiments, as compared with 17% for mixtures averaged over all proportions and experiments (Table 3). Disease severities for the 50:50 mixtures were reduced significantly ($P \leq 0.05$) compared with their corresponding pure stand disease severity means in all three experiments. Moreover, disease severities of 50:50 mixtures were significantly ($P \leq 0.05$) lower than the mean severity of the other mixtures at Pendleton in both years, but not in Moro.

Disease severity of mixtures relative to pure stands varied considerably among the three experiments (Table 3). There also was considerable variation in disease severity relative to pure stands among the mixtures. The Faro-Tyee mixtures always provided less disease relative to its pure stands than did the other mixtures,

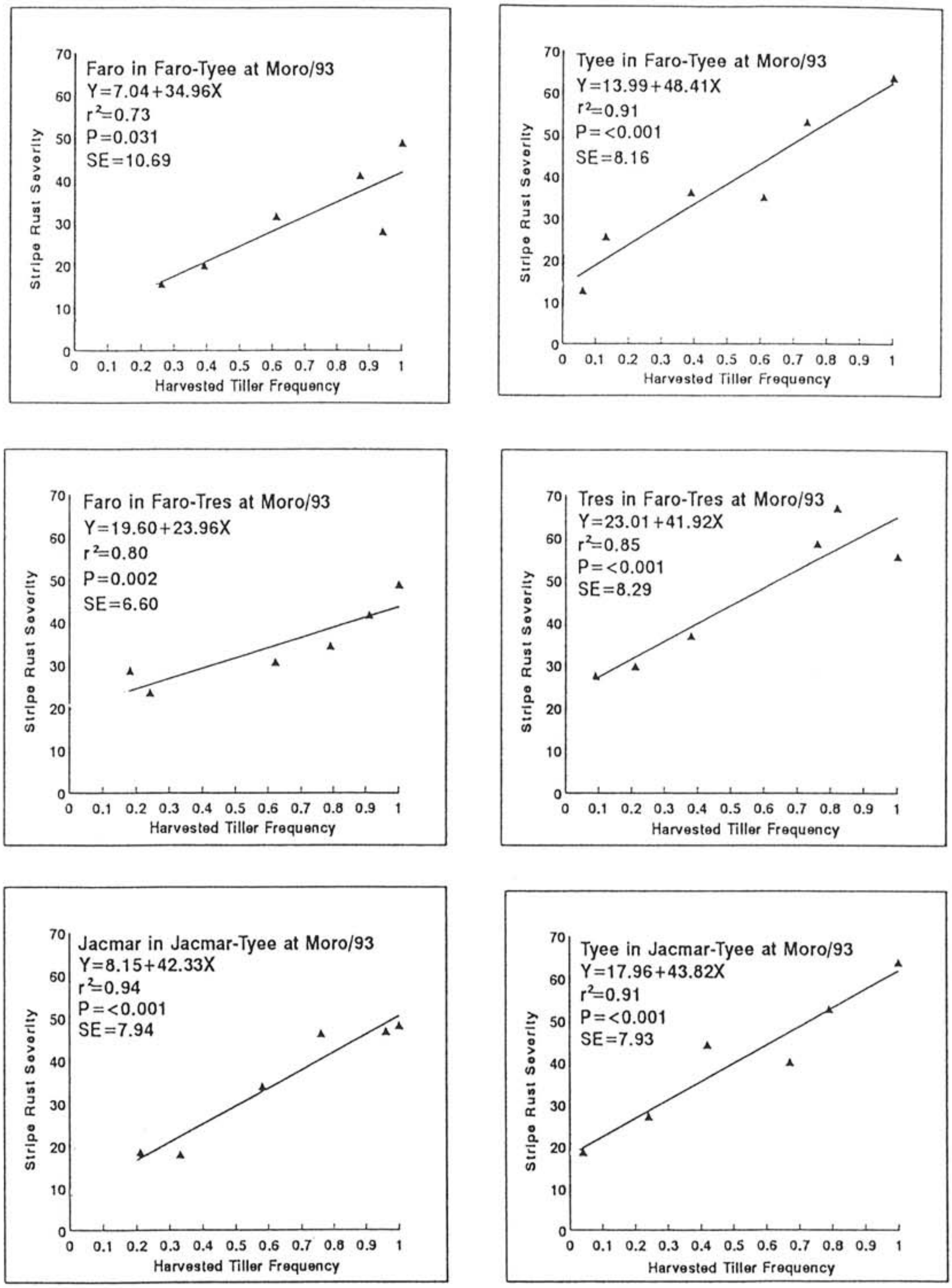

Fig. 1. Regression of stripe rust severity on harvested tiller frequency for wheat cultivars grown in mixtures and pure stands at Moro in 1993.

irrespective of the experiment. Jacmar-Tyee usually ranked second with respect to disease reductions. At Pendleton in both seasons, Tyee had significantly ($P = 0.05$) lower disease, averaged over all mixture proportions, when grown with Faro than when grown with Jacmar . A similar trend occurred at Moro, but this difference was not significant. Stripe rust severities on the component cultivars within the mixtures also differed substantially, though not always significantly (Table 3). Overall disease reductions attributable to mixing were due mostly to epidemiological effects, and the contributions of selection effects were negligible (Table 3).

DISCUSSION

The optimum proportion of mixture components for disease control and yield has often been discussed. Proportions of resistance as high as 75% (31) and 87 to 94% (3) have been suggested for a multiline to control stem rust (*P. graminis tritici*) in wheat. For stem rust of oats (*Avena sativa*), Jensen and Kent (19) suggested 60% resistance, whereas Luthra and Rao (23) observed that a multiline of wheat would not suffer appreciable loss from leaf rust (caused by *P. recondita*), even if it contained as many as 50% susceptible plants. Leonard (22) suggested that, when 35 to 40% of plants are susceptible to all races of the pathogen, simple races will be maintained and the race structure will stabilize. Browning and Frey (8) suggested that a multiline with 35 to 40% susceptible plants might be sufficient to control oat stem rust. Browning (6) indicated that, in indigenous ecosystems, only 30% resistance to a given crown rust (*P. coronata* var. *avenae*) race, combined with a background of general resistance, is sufficient to protect a population. This 30% figure was confirmed with studies

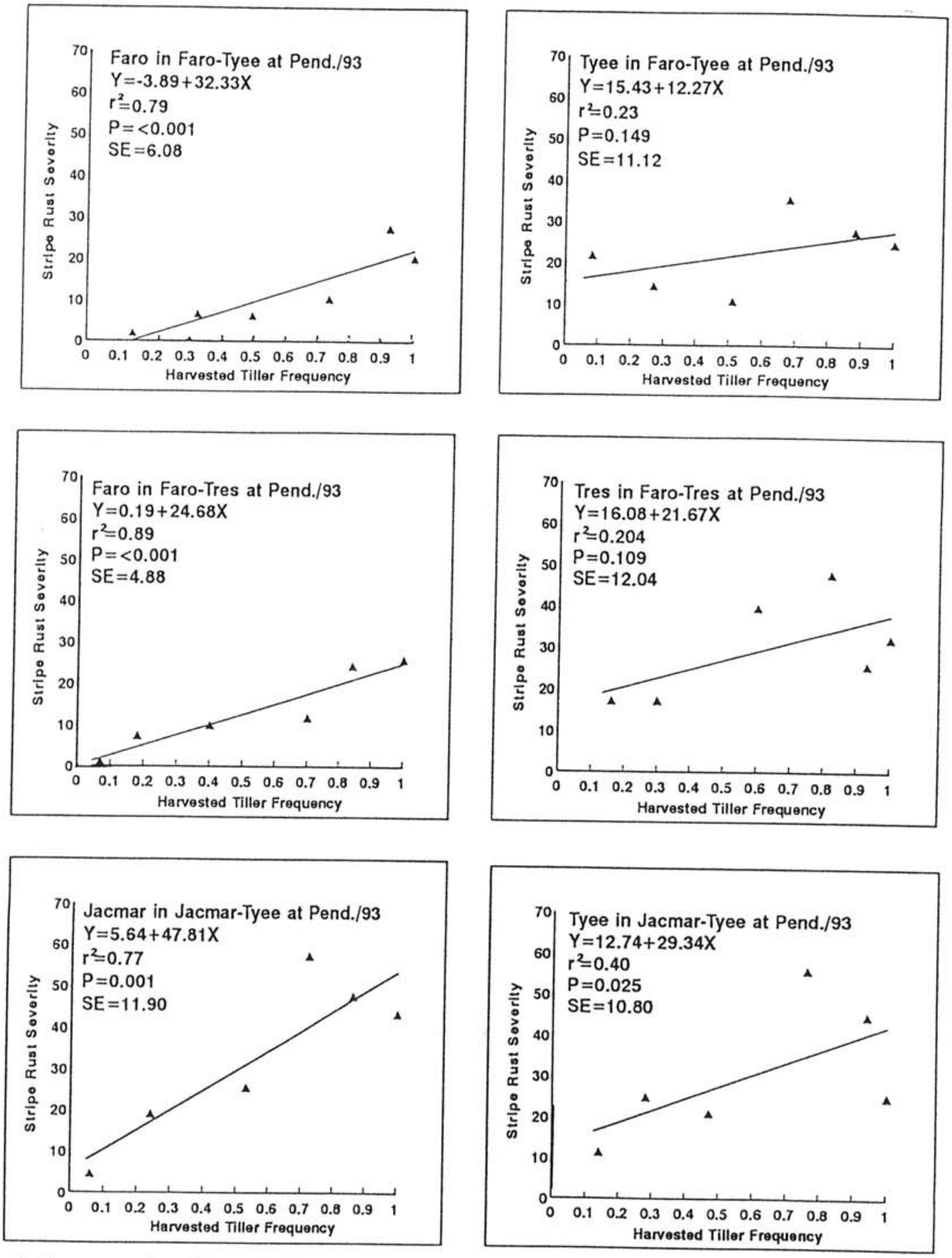

Fig. 2. Regression of stripe rust severity on harvested tiller frequency for wheat cultivars grown in mixtures and pure stands at Pendleton in 1993.

of oat crown rust in agricultural systems (7). In our experiments, in which each component cultivar was susceptible to a different race, the mixtures with equal proportions seemed to be optimum in reducing disease. Disease severities of mixtures relative to pure stands in our experiments were in general agreement with studies of other foliar pathogens of cereals (4,16,17,27,34). Equiproportional cultivar mixtures have been shown to provide reductions of more than 50% in the severity of barley (*Hordeum vulgare*) powdery mildew (caused by *Erysiphe graminis*) in the United Kingdom (34) and of wheat stripe rust (induced by *P. striiformis*) in Oregon (4,16,17,27).

Disease severity on individual cultivars in the mixtures decreased linearly with cultivar frequency. In contrast, other studies have indicated a logarithmic relationship between rate of disease increase and proportion of a susceptible genotype in mixture (10,22). Similarly, it has been theorized that a diminishing return to disease control would be obtained by adding resistance genes to a host mixture (24), a relationship that also would yield a logarithmic relationship between disease and proportion of susceptible plants. On the other hand, a linear relationship between infection rate and proportion of susceptible plants was reported by Burdon and Whitbread (12).

The three mixtures studied differed in their ability to control stripe rust. It previously has been shown that all mixtures are not equivalent in yielding ability and/or disease reduction (16,17,21, 32,33), and mixtures may perform equal to, better, or worse than the means of their component pure stands (2,16,17,20,21,32). Thus, both percentage composition and specific component com-

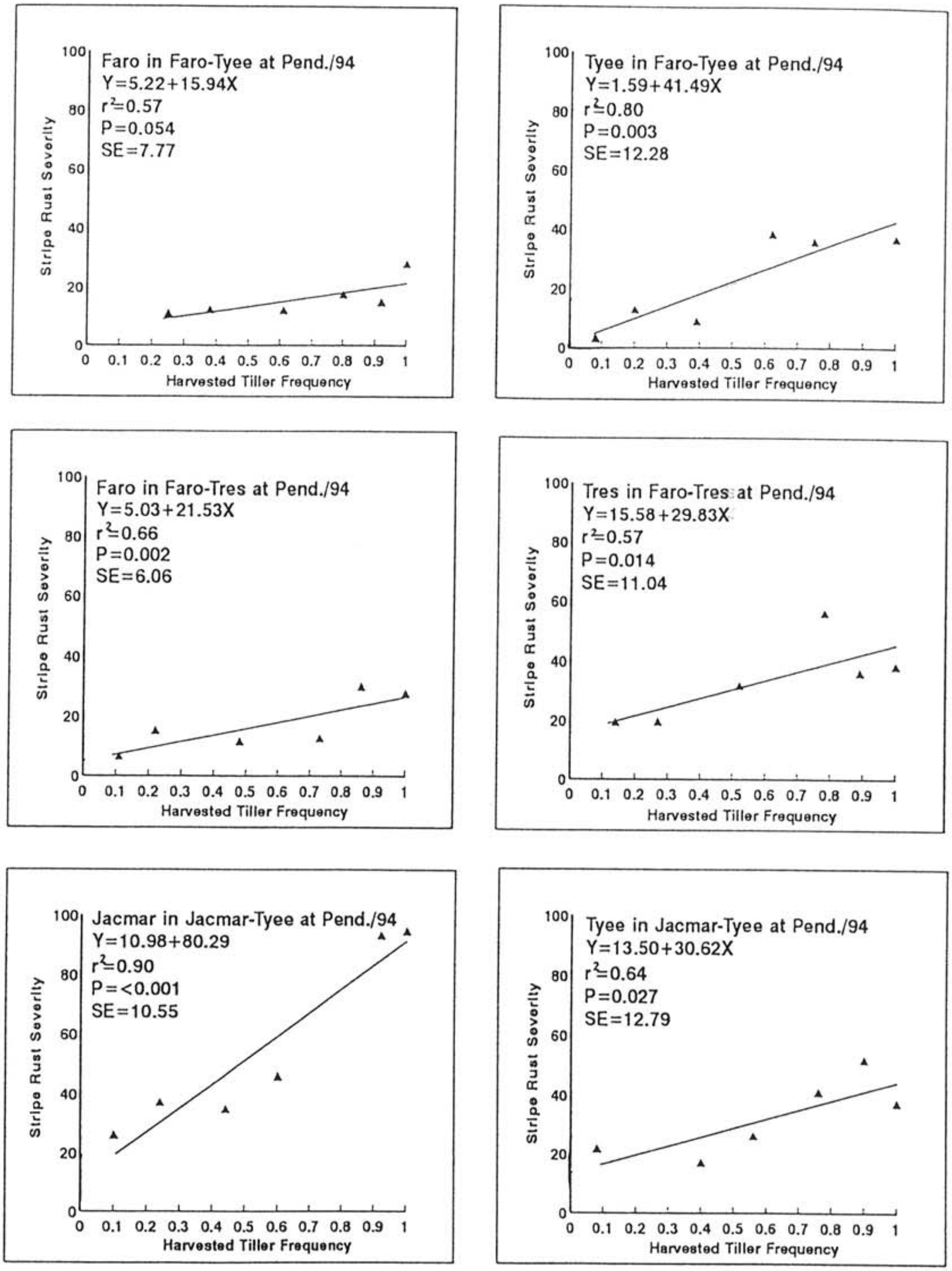

Fig. 3. Regression of stripe rust severity on harvested tiller frequency for wheat cultivars grown in mixtures and pure stands at Pendleton in 1994.

binations are important considerations in constructing useful mixtures.

The individual cultivars also differed in reducing disease severity, as previously reported by Finckh and Mundt (16,17). Mixing always reduced rust on Faro and Jacmar, but did not always significantly reduce rust on Tres and Tyee. Thus, cultivars either differed inherently in their frequency-dependent response to disease, or interactions between cultivars in mixture altered their degree of susceptibility to stripe rust.

Epidemiological effects played the most significant role in impacting disease in the mixtures, with very negligible selection effects. In contrast, Finckh and Mundt (16,17) found a highly significant role of cultivar shifts on stripe rust severity in experiments incorporating many of the same cultivars reported in this study. In their studies, mixtures often contained components that were resistant to all rust races used to inoculate the plots, and most of the selection effects reduced disease severity. However, they did report an occasional negative selection effect, suggesting that selection was for increased tiller number of the more susceptible component of a mixture.

Our results likely underestimated the stripe rust control provided by cultivar mixtures in commercial production (27) for at least two reasons. First, experiments with cultivar mixtures are very sensitive to interplot interference (27,33). Though we separated subplots by an equal area of a completely resistant cultivar, this precaution may have been insufficient to prevent significant exchange of spores among the subplots. Second, in order to guarantee that epidemics began simultaneously in all subplots, we were forced to use an unnaturally large amount of initial inoculum. Shaner and Powelson (30) reported that one infected leaf per acre (0.47 ha) in mid-February would provide sufficient inoculum for an epidemic, given favorable weather. A high level of initial infection will decrease the number of pathogen generations and increase the rate of approach to the host's carrying capacity for disease; both of these factors reduce the efficacy of mixtures for disease control (26).

Because of differences in competitive abilities of the component cultivars in mixtures, one cultivar may eventually dominate the mixture, thus reducing mixture effectiveness. In other studies with mixtures, considerable drift in mixture composition was reported (1,20). Finckh and Mundt (18), however, found evidence for equilibria among adapted wheat cultivars with similar yield. MacKenzie (24) suggested that component cultivars should be remixed every season. Similarly, Wolfe (33) suggested that, for maximum effectiveness, mixtures should be reconstituted every 2 to 3 years. In our studies, compositional shifts were rather small (Figs. 1 to 3), suggesting that mixtures could safely be replanted for 3 to 4 years without remixing. In fact, this is a common commercial practice in Oregon (27).

With mixtures of differentially susceptible cultivars, disease was directly proportional to cultivar frequencies for both components. Thus, decreasing disease on one component by decreasing its frequency will increase disease severity on the other component of the mixture, and equiproportional mixtures appeared to be superior with respect to disease reduction. Thus, in this system, greater disease control could potentially be obtained by increasing the number of cultivars to reduce the proportion of plants susceptible to a given race than by searching for optimum proportions of components in a mixture. Disease reductions in our studies were due mostly to epidemiological effects. It was also evi-

TABLE 3. Stripe rust severity in mixtures of wheat cultivars, averaged over five mixture proportions, on a population and per-cultivar basis, and percent reduction of stripe rust relative to their component pure stands in three field experiments conducted in Moro and Pendleton, Oregon, in 1993 and 1994

Mixture components		Stripe rust severity (%)[a]			Disease reduction (%)				
Cultivar 1	Cultivar 2	Cultivar 1	Cultivar 2	Overall[b]	Cultivar 1	Cultivar 2	Overall[c]	EE[d]	SE[e]
Moro/93									
Faro	Tyee	27.2***[f]	32.4***	34.4***	44.2	49.1	37.6	36.6	0.96
Faro	Tres	_31.7***_[g]	_43.8_	43.4*	35.0	21.2	17.0	16.7	0.32
Jacmar	Tyee	32.7**	36.5***	41.4***	32.2	42.7	24.2	23.4	0.77
Mixture (all)[h]				39.7***			26.2	25.6	0.68
50:50 mixture[h,i]				35.4***			34.2	33.7	0.50
Pendleton/93									
Faro	Tyee	_13.2*_	_21.9_[j]	22.2	49.0	11.8	12.4	12.5	–0.08
Faro	Tres	_10.8**_	_29.4_	26.4	58.3	8.4	9.0	10.7	–1.63
Jacmar	Tyee	30.7*	31.4	40.4	29.0	–26.5	–22.1	–24.2	2.05
Mixture (all)				29.7			–0.1	–0.2	0.07
50:50 mixture				19.5*			35.1	35.9	–0.81
Pendleton/94									
Faro	Tyee	13.3**	19.7	19.8*	52.1	46.8	39.4	38.2	1.20
Faro	Tres	_15.1**_	_32.5_	29.3	45.6	15.0	14.1	13.0	1.15
Jacmar	Tyee	_47.2***_	_31.4_	47.0***	50.1	15.2	23.3	22.9	0.36
Mixture (all)				32.0***			25.6	24.7	0.90
50:50 mixture				21.1***			51.6	49.7	1.98

[a] Percent leaf area covered by stripe rust on the leaf below the flag leaf (F-1 leaf) for Moro 1993 and Pendleton 1994, and the F-2 leaf for Pendleton 1993.

[b] Mean stripe rust severity for all tillers (both cultivars).

[c] Overall disease reduction $= 1 - \frac{\text{mean stripe rust severity in a mixture}}{\text{mean pure stand rust severity weighted by planted frequency in that mixture}} \times 100$.

[d] EE = epidemiological effect (the percent change in disease severity relative to the pure stand disease severity mean weighted by the harvested tiller frequency [17]).

[e] SE = selection effect (the percent change in disease severity because of changes in frequencies of the component genotypes in mixture from planting to harvest [17]).

[f] The symbols *, **, and *** indicate that treatment means for the component cultivars or the overall mixture were significantly different from their respective pure stand(s) at $P \leq 0.1$, $P \leq 0.05$, and $P \leq 0.01$, respectively (linear contrasts).

[g] The component genotype means averaged over all planted frequencies differed significantly at $P \leq 0.05$ (linear contrasts) when shown in italics.

[h] For comparing the disease severity means of all mixtures or 50:50 mixtures with overall means of the pure stands, pure stand means were adjusted to account for the number of times they were included in mixtures (details in text).

[i] Data were pooled from the treatments initially planted at 50:50 proportions in fall 1991.

[j] Disease severity means for the same component cultivar within different mixtures were significantly different at $P \leq 0.05$ (linear contrasts) when shown underlined.

dent that some mixtures performed better than others, and one mixture component was influenced differentially by its companion cultivars. Thus, in addition to knowledge of resistance and virulence characteristics of a pathosystem, empirical testing is also essential.

LITERATURE CITED

1. Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition on yield in monoculture and mixtures of two wheat cultivars. Plant Pathol. 35:457-465.
2. Baker, R. J., and Briggs, K. G. 1984. Comparison of grain yield of uniblends and biblends of 10 barley cultivars. Crop Sci. 24:85-87.
3. Borlaug, N. E. 1958. The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants. Proc. Int. Genet. Symp. 1:12-27.
4. Brophy, L. S., and Mundt, C. C. 1991. Influence of plant spatial patterns on disease dynamics, plant competition and grain yield in genetically diverse wheat populations. Agric. Ecosyst. Environ. 35:1-12.
5. Browning, J. A. 1957. Studies of the effect of field blends of oat varieties on stem rust losses. (Abstr.) Phytopathology 47:4-5.
6. Browning, J. A. 1974. Relevance of knowledge about natural ecosystems to development of pest management systems for agroecosystems. Proc. Am. Phytopathol. Soc. 1:191-199.
7. Browning, J. A. 1980. Genetic protective mechanisms of plant pathogen populations: Their coevolution and use in breeding for resistance. Pages 452-475 in: Tex. Agric. Exp. Stn. Misc. Publ. MP-1451.
8. Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. Annu. Rev. Phytopathol. 14:355-382.
9. Browning, J. A., and Frey, K. J. 1981. The multiline concept in theory and practice. Pages 37-46 in: Strategies for the Control of Cereal Disease. J. F. Jenkyn and R. T. Plumb, eds. Blackwell Scientific Publications Ltd., Oxford.
10. Burdon, J. J., and Chilvers, G. A. 1977. Controlled environment experiments on epidemic rates of mildew in different mixtures of barley and wheat. Oecologia 28:141-146.
11. Burdon, J. J., Groves, R. H., Kaye, P. E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of *Chondrilla juncea* differentially infected with rust. Oecologia 64:199-203.
12. Burdon, J. J., and Whitbread, R. 1979. Rates of increase of barley mildew in mixed stands of barley and wheat. J. Appl. Ecol. 16:253-258.
13. Caldwell, R. M. 1966. Advances and challenges in the control of plant diseases through breeding. Pages 117-126 in: Pest Control by Chemicals, Biological, Genetic, and Physical Means. U.S. Dep. Agric., ARS, 33-110. U.S. Dep. Agric., Washington, DC.
14. DiLeone, J. A., and Mundt, C. C. 1994. Effect of wheat cultivar mixtures on populations of *Puccinia striiformis* races. Plant Pathol. 43:917-930.
15. Draper, N. R., and Smith, H. 1981. Applied Regression Analysis. 2nd ed. John Wiley & Sons, Inc., New York.
16. Finckh, M. R., and Mundt, C. C. 1992. Plant competition and disease in genetically diverse wheat populations. Oecologia 91:82-92.
17. Finckh, M. R., and Mundt, C. C. 1992. Stripe rust, yield, and plant competition in wheat cultivar mixtures. Phytopathology 82:905-913.
18. Finckh, M. R., and Mundt, C. C. 1993. Effects of stripe rust on the evolution of genetically diverse wheat populations. Theor. Appl. Genet. 85:809-821.
19. Jensen, N. F., and Kent, G. G. 1963. New approach to an old problem in oat production. Farm Res. 29:4-5.
20. Khalifa, M. A., and Qualset, C. O. 1974. Intergenotypic competition between tall and dwarf wheats. I. In mechanical mixtures. Crop Sci. 14:795-799.
21. Knott, E. A., and Mundt, C. C. 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and nondiseased conditions. Theor. Appl. Genet. 80:313-320.
22. Leonard, K. J. 1969. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. Phytopathology 59:1845-1850.
23. Luthra, J. K., and Rao, M. V. 1979. Multiline cultivars–How their resistance influences leaf rust epidemics in wheat. Euphytica 39:137-144.
24. MacKenzie, D. R. 1979. The multiline approach to the control of some cereal diseases. Pages 199-216 in: Proc. Rice Blast Workshop. International Rice Research Institute, Los Banos, Philippines.
25. McDonald, B. A., Allard, R. W., and Webster, R. K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. Crop Sci. 28:447-452.
26. Mundt, C. C. 1990. Disease dynamics in agroecosystems. Pages 263-299 in: Agroecology. C. R. Caroll, J. H. Vandermeer, and P. M. Rossett, eds. McGraw-Hill Book Co., New York.
27. Mundt, C. C. 1994. Use of host genetic diversity to control cereal diseases: Implications for rice blast. Pages 293-307 in: Proceedings of the International Symposium on Rice Blast Disease. S. A. Leong, R. S. Zeigler, and P. S. Teng, eds. CABI International, Cambridge.
28. Mundt, C. C., and Browning, J. A. 1985. Genetic diversity and cereal rust management. Pages 527-560 in: The Cereal Rusts, vol. 2. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Inc., Orlando, FL.
29. SAS Institute, Inc. 1988. SAS/STAT Users Guide, 6.03 ed. SAS Institute, Cary, NC.
30. Shaner, G., and Powelson, R. L. 1971. Epidemiology of Stripe Rust of Wheat, 1961-1968. Oreg. Agric. Exp. Stn. Bull. 117.
31. Suneson, C. A. 1960. Genetic diversity–A protection against plant diseases and insects. Agron. J. 52:319-321.
32. Trenbath, B. R. 1974. Biomass productivity of mixtures. Adv. Agron. 26:177-210.
33. Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease control. Annu. Rev. Phytopathol. 23:251-273.
34. Wolfe, M. S., and Barrett, J. A. 1980. Can we lead the pathogen astray? Plant Dis. 64:148-155.