Effect of Winter Wheat Cultivar Mixtures on Leaf Rust Severity and Grain Yield

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ABSTRACT

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Three different experiments involving winter wheat cultivar mixtures and their component purelines were conducted at McGregor, TX, in the 1986–1987 and 1987–1988 growing seasons. The same experiments were also conducted during 1987–1988 at Dallas, Prosper, Stephenville, and Uvalde, TX. In three-way mixtures with the leaf rust susceptible cultivar TAM 107 and the moderately resistant wheats, Collin and TX71C8130R, disease severity and area under the disease progress curve (AUDPC) were reduced in all locations and years compared with the mean of the component cultivars, with the exception of one mixture at Stephenville in 1987–1988. Additionally, grain yields and thousand kernel weights were higher in the mixtures as compared with the component cultivars in most cases. Another three-way mixture experiment used the moderately resistant cultivar Thunderbird with the susceptible cultivars Mustang and Vona. In this experiment, disease severity and AUDPC were reduced in all mixture–component comparisons. The third experiment used two-way mixtures of the moderately resistant cultivar Siouxland and the susceptible cultivar Hawk. Reductions in disease and increases in yield were found in several of these mixtures as compared with the component cultivars. Overall, there was a mean reduction in AUDPC of 32% in the mixtures compared with the mean AUDPC of the component cultivars. The AUDPC in the mixtures was always less than that of the most susceptible cultivar grown in a pure stand. Mixtures were equal to or better than the mean grain yield of their component cultivars in 68% of the comparisons. The reduction in leaf rust in mixtures was more accurately expressed in higher thousand kernal weight than in overall grain yield.

Additional keyword: *Puccinia recondita*.

Leaf rust currently is the most widespread disease of wheat in the world (23). The causal fungus, *Puccinia recondita* Roberge. ex Desmaz., is highly variable in terms of its virulence. In 1987, Long et al (15) identified 44 virulence combinations in the United States. Marshall (18) identified 40 virulence combinations in Texas from 1985 to 1987. *P. recondita* has adapted quickly to newly introduced resistance genes in wheat, particularly in the overwintering areas of the fungus, such as the southern plains in the United States (7,17,24). Because of the rapidity with which cultivars succumb to newly selected leaf rust races, strategies that might extend the useful life of wheat cultivars and reduce the risk of leaf rust epidemics have been sought (19,25). One of these strategies is the use of cultivar mixtures. A cultivar mixture has been defined as a heterogeneous crop of a single species (25). Rosen (22), Jensen (11), and Borlaug (3) pioneered early work on the use of intrafield genetic diversity for disease control. From these initial works, multilines (mixtures of near-isogenic breeding lines) subsequently were developed for the control of wheat stem rust (4) and oat crown rust (5). Multilines can be viewed as a breeding approach, and cultivar mixtures as a deployment approach to achieve the common goal of intimate association of unlike genotypes in a field. However, because cultivar mixtures use germ plasm already available, genetic diversity (19) within a field can be accomplished more expeditiously.

Chin and Wolfe (6) have indicated that cultivar mixtures diminish epidemic buildup by reducing the spatial density of susceptible plants, by having resistant plants serve as barriers to propagule transmission, and by induced resistance. Studies of several small-grain rust pathosystems have shown that susceptible plants suffer less damage in mixtures with resistant plants than when grown in pure stands (9,10,13). Typically, disease increase in mixtures is significantly lower than the mean of the component pure stands (25).

The yield of small-grain cultivar mixtures tends to be equal to or slightly greater than that of the mean of the components grown alone (25,26). However, in several cases (26,27) mixtures have significantly out-yielded the component mean and have equaled or exceeded the highest-yielding cultivar.

The objectives of this research were to determine the effectiveness of winter wheat cultivar mixtures in reducing leaf rust severity and to compare the yield of mixtures and component purelines over several environments in Texas. A preliminary report of this research has been published (16).

MATERIALS AND METHODS

Field plots. Seed of winter wheat cultivars possessing susceptibility or moderate resistance to leaf rust were mixed and sown at the Texas Agricultural Experiment Station research farms at McGregor in 1986 and 1987, and at Dallas, Prosper, Stephenville, and Uvalde in 1987. Seed size and weight did not differ significantly between cultivars, so they were mixed on an equal weight basis. Seeding rate was 84 kg/ha (kernel weight of 30 mg), and plot size was 1.2 m wide by 3.9 m long. At McGregor and Uvalde, row spacing was 30.5 cm and at Dallas, Prosper, and Stephenville it was 17.3 cm. Plots were bordered on all sides by oats (*Avena sativa* L. 'H-833') in addition to a 1.2-m alley of bare soil at the ends of plots. Each experiment was sown as a randomized complete block design with four replicates.

The criteria for cultivar selection within an experiment were leaf rust reaction, and similarity of heading date, maturity, and height. Thus, the moderately resistant (MR) wheats (immune to most races of *P. recondita*) Collin, Siouxland, Thunderbird, and TX71C8130R, and the susceptible (S) wheats Hawk, Mustang, TAM 107, and Vona were used. In experiment 1, TAM 107 (S_1), Collin (MR_1), and TX71C8130R (MR_2) were mixed in proportions of $3.3S_1$:$3.3MR_1$:$3.3MR_2$ and $6.6S_1$:$3.3MR_1 + MR_2$ (equal proportions of Collin and TX71C8130R made up one-third of this mixture). Experiment 2 used Mustang (S_2), Vona (S_3), and

Thunderbird (MR_3) mixed in proportions of $3.3S_2 + S_3{:}6.6MR_3$ and $3.3S_2{:}3.3S_3{:}3.3MR_3$. In experiment 3, Hawk (S_4) and Siouxland (MR_4) were mixed in ratios of $9S_4{:}1MR_4$, $7.5S_4{:}2.5MR_4$, $6.6S_4{:}3.3MR_4$, $5S_4{:}5MR_4$, $3.3S_4{:}6.6MR_4$, $2.5S_4{:}7.5MR_4$, $1S_4{:}9MR_4$. The cultivars in each experiment also were grown as pure stands. Plots were combine-harvested and the grain was weighed to obtain yield (q/ha), thousand kernel weight (g), and test weight (g/L).

Statistical analysis. Leaf rust severity was assessed three to five times during the spring of each year at 10- to 20-day intervals (time intervals varied with location). The modified Cobb scale (21) was used with the aid of standard area drawings (Plant Pathology Laboratory, Herpenden. Herts., UK; Lab key no. 1-3-1) on each of 10 randomly selected flag leaves per plot. Rust severity data were tested for equality of variances by the Burr-Foster Q-test and for normality by the Shapiro and Wilk W-test (2). Because the severity data had unequal variances and non-normal distributions, they were transformed into logits ($\ln[Y/(1-Y)]$), in which Y was rust severity as a proportion of leaf area. Disease progress curves of the percentage of severity over time were generated, and the area under this curve (AUDPC) was calculated for the growing period of flag leaf emergence (Feekes growth stage [GS] 9) (12) to soft dough (Feekes GS 11). AUDPC values had equal variances and normal distributions. Analysis of variance (ANOVA) was used to analyze AUDPC and repeated-measures ANOVA (14) was used for transformed severity values.

Grain yield, thousand kernel weight, and test weight data were found to have equal variances and normal distributions, and were analyzed by ANOVA. In those analyses in which the F test indicated a significant difference among the mixtures, means were separated by the least significant difference (LSD) at a 5% probability level.

RESULTS

Analysis of variance for grain yield, thousand kernel weight, and AUDPC, and repeated-measures ANOVA for leaf rust severity over time indicated significant ($P \leq 0.05$) interactions between all the locations and years attributable to environmental effects on yield and disease parameters. Therefore, statistical comparisons were valid only within a location and year.

Disease severity. Leaf rust severities in the spring of 1987 at McGregor were moderately high. The susceptible cultivars in each experiment and their respective leaf rust severities at 43 days from 30 March (GS 11) were: TAM 107, 52%; Mustang, 65%; Vona, 50%; and Hawk, 65% (Fig. 1). No plants in either the mixtures or the pure stands were rust-free. AUDPCs in the three-way mixtures that contained two-thirds susceptible plants were reduced to about half that of the most susceptible cultivar in experiments 1 and 2 (Table 1). In experiment 2, in which the

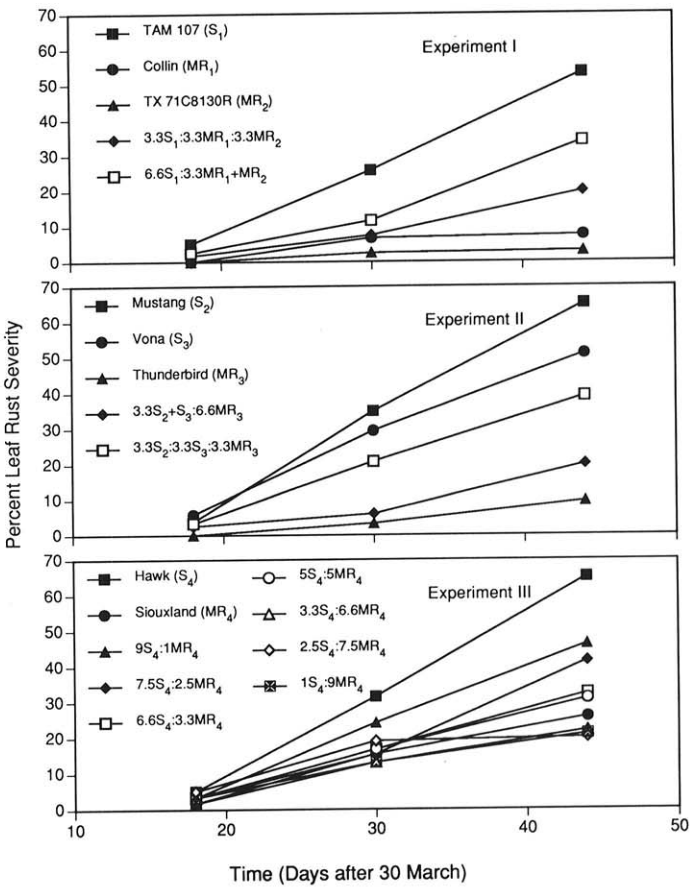

Fig. 1. Progress of leaf rust in winter wheat cultivar mixtures and component purelines at McGregor, 1986–1987.

TABLE 1. Area under the disease progress curve (AUDPC) of leaf rust on winter wheat cultivar mixtures expressed as a percentage of the AUDPC of the mean of the component cultivars (M) and of the most susceptible cultivar in each experiment (S)

Experiment no./ mixture[a]	AUDPC per location and year (%)[b] McG 1987 M	McG 1987 S	McG 1988 M	McG 1988 S	Dal 1988 M	Dal 1988 S	Pro 1988 M	Pro 1988 S	Ste 1988 M	Ste 1988 S	Uva 1988 M	Uva 1988 S
1												
$3.3S_1{:}3.3MR_1{:}3.3MR_2$	71	*30*[c]	51	*21*	42	*14*	39	*19*	79	*40*	91	60
$6.6S_1{:}3.3MR_1{+}MR_2$	75	*53*	78	*55*	*41*	*27*	67	*52*	101	76	89	75
Mean observed AUDPC	398		277		58		488		212		416	
2												
$3{:}3S_2{:}3.3S_3{:}3.3MR_3$	*44*	*17*	*36*	*12*	*39*	*11*	71	*31*	63	*23*	48	*41*
$3.3S_2{+}S_3{:}6.6MR_3$	*77*	*49*	*57*	*31*	88	*49*	*60*	*40*	*43*	28	81	57
Mean observed AUDPC	666		432		104		720		232		574	
3												
$9S_4{:}1MR_4$	81	77	103	96	82	*74*	96	90	84	*78*	*71*	*66*
$7.5S_4{:}2.5MR_4$	81	*72*	82	*69*	*69*	*53*	88	75	*67*	*54*	*64*	*52*
$6.6S_4{:}3.3MR_4$	88	*56*	81	*63*	74	*50*	91	73	*37*	*28*	*67*	*50*
$5S_4{:}5MR_4$	*68*	*53*	*67*	*45*	*57*	*29*	80	*55*	*42*	*26*	73	*46*
$3.3S_4{:}6.6MR_4$	*60*	*42*	*63*	*35*	89	*31*	91	*50*	*48*	*23*	*53*	*26*
$2.5S_4{:}7.5MR_4$	74	*49*	*55*	*28*	*28*	*7*	65	*35*	*49*	*21*	58	*25*
$1S_4{:}9MR_4$	84	*50*	62	*25*	62	*7*	93	*41*	91	*28*	67	*21*
Mean observed AUDPC	704		408		96		586		159		540	

[a] S = susceptible wheat cultivars, and MR = moderately resistant cultivars. S_1 = TAM 107; S_2 = Mustang; S_3 = Vona; S_4 = Hawk; MR_1 = Collin; MR_2 = TX71C8130R; MR_3 = Thunderbird; and MR_4 = Siouxland.

[b] Locations in Texas are McG = McGregor, Dal = Dallas, Pro = Prosper, Ste = Stephenville, and Uva = Uvalde.

[c] Percentages italicized indicate a significant difference ($P = 0.05$) between the AUDPC of either the mean of the components or the most susceptible cultivar in the experiment.

moderately resistant plants in mixtures were all the same cultivar (Thunderbird), AUDPCs were significantly less than the mean of the component cultivars. When the moderately resistant plants in the three-way mixtures were composed of two cultivars (experiment 1), the mean AUDPC tended to be less than the mean of the components, but was not significantly different (Table 1).

In the two-way mixtures of Siouxland and Hawk (experiment 3), leaf rust severity at GS 11 was reduced compared with the pure stand of Hawk (Fig. 1). The AUDPCs of the two-way mixtures were all significantly lower than that of the susceptible cultivar, Hawk, in pure stand, with the exception of the $9S_4$ (Hawk):$1MR_4$ (Siouxland) mixture (Table 1). The two-way mixtures that contained one-half and two-thirds moderately resistant plants had significantly lower AUDPCs than the means of the component cultivars (Table 1).

In the 1987–1988 growing season, the same three experiments were conducted at five Texas locations, including McGregor. Leaf rust severities varied by location with the lowest occurring at Dallas, and the highest at McGregor (Figs. 2 and 3). At Dallas, the three moderately resistant wheats, Collin, TX71C8130R, and Thunderbird each had leaf rust severities below 1% at 54 days after 30 March (GS 11). The AUDPCs of the three-way mixtures at Dallas and McGregor were all significantly lower than the most susceptible cultivar in each experiment (Table 1). Compared with the mean of the component cultivars, the three-way mixtures reduced AUDPCs at Dallas and McGregor.

At McGregor in 1987–1988, leaf rust severity at 57 days after 30 March (GS 11) in the two-way mixtures was reduced as the proportion of Siouxland increased (Fig. 2). However, at Dallas, final severities in the two-way mixtures were variable (Fig. 3). Significant reductions in AUDPC below those of Hawk were found in all of the two-way mixtures at Dallas and McGregor, with the exception of the $9S_4$ (Hawk):$1MR_4$ (Siouxland) mixture at McGregor (Table 1).

The rust severity and AUDPC results at Prosper, Stephenville, and Uvalde followed the same general trends as those from McGregor and Dallas. The AUDPC always was less in the mixtures as compared to the most susceptible cultivar in each experiment (Table 1). With the exception of the two-thirds susceptible to one-third resistant mixture in experiment 1 at Stephenville, all mixtures had AUDPC values less than the mean of the components. Thus, over locations and years, every mixture tended to have an AUDPC less than or equal to the most susceptible component cultivar (86% were significantly less). Also, 97% of the mixtures had AUDPC values less than or equal to the mean of the component cultivars, with 41% of those statistically significant (Table 1). Comparing the AUDPC in the mixtures with the component means (Table 1), there was a range from a 3% increase (experiment 3, $9S_4$:$1MR_4$, McGregor 1988) to a 72% decrease (experiment 3, $2.5S_4$:$7.5MR_4$, Dallas 1988), with a mean of 32% decrease in AUDPC.

Yield and thousand kernel weight. Tables 2 and 3 show, respectively, grain yield and thousand kernel weight of the mixtures expressed as a percentage of the mean of the component cultivars and as a percentage of the highest-yielding or highest thousand kernel weight cultivar in each experiment. Over locations and years, about 68% of the mixtures had grain yields greater than or equal to the mean of the components, and 45% had grain yields greater than or equal to the highest-yielding cultivar in each experiment (Table 2). Eighty-three percent of the mixtures had a thousand kernel weight greater than the mean of the components, but only 36% had a thousand kernel weight greater than the highest thousand kernel weight in each experiment (Table 3). No obvious linear correlations were found between the measured disease parameters and yield components.

DISCUSSION

With the exception of the mixture containing TX71C8130R, all the mixtures tested were made of cultivars that are at present

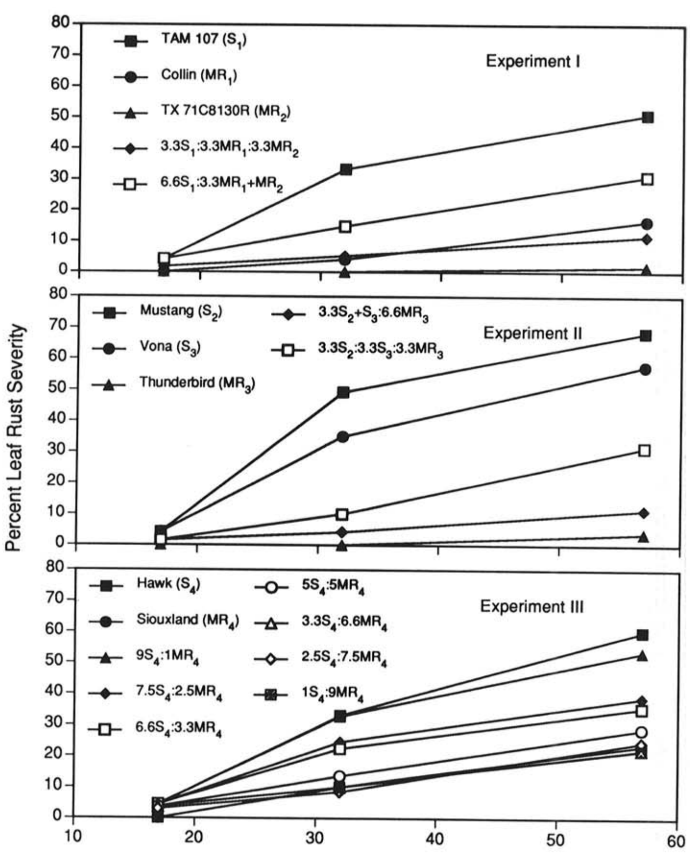

Fig. 2. Progress of leaf rust in winter wheat cultivar mixtures and component purelines at McGregor, 1987–1988.

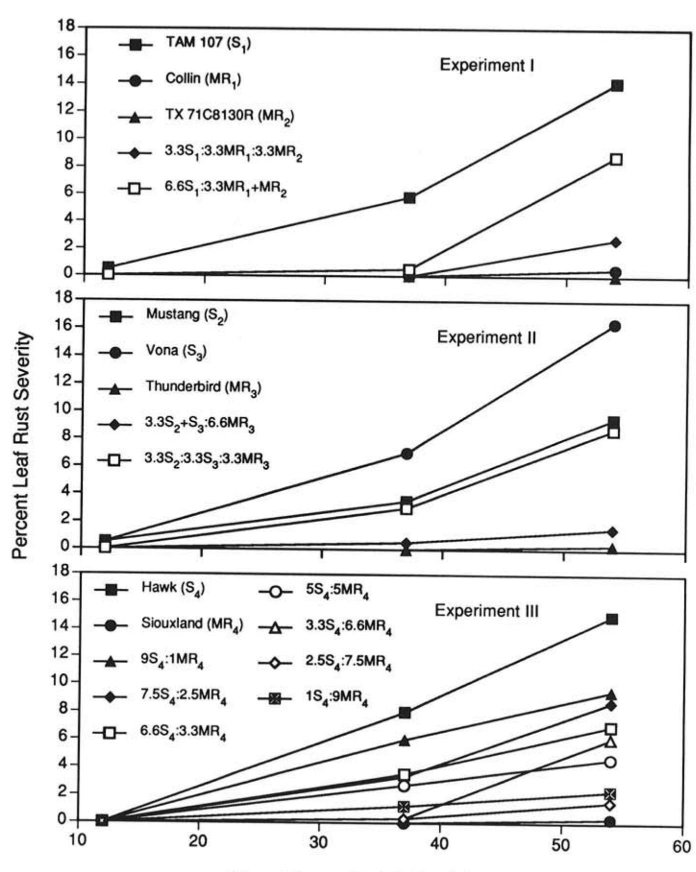

Fig. 3. Progress of leaf rust in winter wheat cultivar mixtures and component purelines at Dallas, 1987–1988.

grown commercially in Texas. (TX71C8130R is a Texas A&M University breeding line not released as a cultivar because of deficiencies in breadmaking quality.) Because the genotypes within each mixture were agronomically similar, the mixtures represent commercially viable options to growing a single cultivar. Over the five locations and the years of testing, a fairly wide range of leaf rust intensities was encountered (Table 1). Regardless of the level of leaf rust, there was nearly always a reduction in AUDPC in the mixtures compared with the mean of the components. The mean AUDPC reduction of 32% compares to a 26% reduction of leaf rust in wheat mixtures in Germany (8). In only two instances (experiment 3, $6.6S_4{:}3.3MR_4$, Stephenville 1988; experiment 3, $9S_4{:}1MR_4$, McGregor 1988) out of 66 comparisons were the AUDPCs somewhat larger than the mean of the components (1 and 3%, respectively). The AUDPC in mixtures was always less than that of the most susceptible component grown in a pure stand. Therefore, the results from this study indicated that leaf rust could be significantly reduced in mixtures containing one-third or more moderately resistant plants. Furthermore, in the two-way mixture of Hawk and Siouxland, as few as one-tenth moderately resistant plants were sufficient to reduce leaf rust AUDPC in the range of 4–34% below that of Hawk (Table 1).

The mean observed AUDPC was always less in experiment 1 as compared with experiment 2 (Table 1). Perhaps this indicates that two genetically different, moderately resistant cultivars con-

TABLE 2. Grain yield of winter wheat cultivar mixtures expressed as a percentage of the mean of the component cultivars (M) and of the highest-yielding cultivar in each experiment (H)

Experiment no./ mixture[a]	Grain yield per location and year (%)[b]											
	McG 1987		McG 1988		Dal 1988		Pro 1988		Ste 1988		Uva 1988	
	M	H	M	H	M	H	M	H	M	H	M	H
1												
$3.3S_1{:}3.3MR_1{:}3.3MR_2$	103	97	102	94	111	104	110	101	113	110	101	91
$6.6S_1{:}3.3MR_1{+}MR_2$	100	97	97	*83*[c]	118	107	106	95	103	103	*110*	105
Mean observed yield[d]	40		40		41		50		22		39	
2												
$3.3S_2{:}3.3S_3{:}3.3MR_3$	102	98	*110*	102	99	94	99	95	96	93	106	104
$3.3S_2{+}S_3{:}6.6MR_3$	110	100	*112*	95	97	93	110	100	126	116	105	99
Mean observed yield	39		35		41		50		23		42	
3												
$9S_4{:}1MR_4$	110	109	100	*84*	93	87	109	95	104	104	111	111
$7.5S_4{:}2.5MR_4$	99	97	104	90	96	90	*116*	107	109	109	96	96
$6.6S_4{:}3.3MR_4$	106	104	101	*89*	101	95	106	96	108	108	96	96
$5S_4{:}5MR_4$	108	107	110	100	94	90	108	99	113	111	89	89
$3.3S_4{:}6.6MR_4$	109	109	90	90	96	93	*115*	110	112	111	97	97
$2.5S_4{:}7.5MR_4$	108	108	105	100	98	97	*113*	109	114	112	91	91
$1S_4{:}9MR_4$	*111*	*111*	99	97	98	98	92	90	112	110	94	94
Mean observed yield	38		32		42		41		20		50	

[a]S = susceptible wheat cultivars, and MR = moderately resistant cultivars. S_1 = TAM 107; S_2 = Mustang; S_3 = Vona; S_4 = Hawk; MR_1 = Collin; MR_2 = TX71C8130R; MR_3 = Thunderbird; and MR_4 = Siouxland.
[b]Locations in Texas are McG = McGregor, Dal = Dallas, Pro = Prosper, Ste = Stephenville, and Uva = Uvalde.
[c]Percentages italicized indicate a significant difference ($P = 0.05$) between the yield of the mixture and the yield of either the mean of the components or the highest-yielding cultivar in the experiment.
[d]Yield is in quintals per hectare.

TABLE 3. Thousand kernel weight (TKW) of winter wheat cultivar mixtures expressed as a percentage of the TKW of the mean of the component cultivars (M) and of the highest-TKW cultivar in each experiment (H)

Experiment no./ mixture[a]	TKW per location and year (%)[b]											
	McG 1987		McG 1988		Dal 1988		Pro 1988		Ste 1988		Uva 1988	
	M	H	M	H	M	H	M	H	M	H	M	H
1												
$3.3S_1{:}3.3MR_1{:}3.3MR_2$	105	*91*[c]	96	*89*	106	102	105	*92*	99	93	104	*94*
$6.6S_1{:}3.3MR_1{+}MR_2$	101	*90*	96	*87*	106	102	108	*90*	100	98	100	*88*
Mean observed TKW[d]	35		28		27		32		28		32	
2												
$3.3S_2{:}3.3S_3{:}3.3MR_3$	*107*	100	*105*	99	94	90	102	100	96	*87*	100	97
$3.3S_2{+}S_3{:}6.6MR_3$	101	*92*	*109*	*95*	104	92	*110*	103	98	*89*	100	92
Mean observed TKW	32		25		26		28		26		29	
3												
$9S_4{:}1MR_4$	*110*	*109*	*118*	104	98	96	106	103	103	103	105	96
$7.5S_4{:}2.5MR_4$	103	100	99	*89*	105	103	103	100	100	99	106	99
$6.6S_4{:}3.3MR_4$	*107*	104	104	95	101	99	102	99	100	98	98	*92*
$5S_4{:}5MR_4$	105	100	103	96	95	94	106	104	100	98	103	98
$3.3S_4{:}6.6MR_4$	106	98	102	97	103	103	103	102	100	97	103	100
$2.5S_4{:}7.5MR_4$	103	95	103	100	102	102	105	104	101	98	104	101
$1S_4{:}9MR_4$	104	94	100	99	106	106	102	102	101	97	97	97
Mean observed TKW	33		27		27		30		28		30	

[a]S = susceptible wheat cultivars, and MR = moderately resistant cultivars. S_1 = TAM 107; S_2 = Mustang; S_3 = Vona; S_4 = Hawk; MR_1 = Collin; MR_2 = TX71C8130R; MR_3 = Thunderbird; and MR_4 = Siouxland.
[b]Locations in Texas are McG = McGregor, Dal = Dallas, Pro = Prosper, Ste = Stephenville, and Uva = Uvalde.
[c]Percentages italicized indicate a significant difference ($P = 0.05$) between the TKW of the mixture and the TKW of either the mean of the components or the highest-TKW cultivar in the experiment.
[d]TKW is in grams.

stituting the resistant fraction of the mixture were superior to a single moderately resistant component. However, this effect was probably due more to the diversity of leaf rust resistance genes in Collin and TX71C8130R compared with those in Thunderbird. Published (20) and unpublished results from our laboratory indicated that the effective leaf rust resistance gene in Collin was *Lr*24; in TX71C8130R: *Lr*9, *Lr*11, and *Lr*23; in Thunderbird: *Lr*24; in Siouxland: *Lr*24 and *Lr*26; and in Hawk, Mustang, Vona, and TAM 107: no effective *Lr* genes. Thus, it could be expected that a single cultivar possessing several effective *Lr* genes would reduce leaf rust as much as two cultivars together possessing several effective *Lr* genes. This highlights the importance that cultivar choice plays in the effectiveness of mixtures to reduce disease. It is probable that mixing cultivars, all of which possess the same ineffective *Lr* genes, would have little effect in reducing leaf rust in Texas. The present study indicated a diversity of effective *Lr* genes (Collin + TX71C8130R) was more effective in reducing leaf rust in mixtures than a single effective *Lr* gene (Thunderbird). Thus, mixtures for leaf rust control will be more effective when the component cultivars are chosen judiciously and their proportional deployment is strategically planned.

The grain yield data showed cultivar mixtures equaled or exceeded the mean yield of the components in 68% of the comparisons (mixtures ranged from 11% below to 26% above component mean yields with an overall mean of 4% above). No trends in yield were evident in mixtures comparing low- vs. high-yielding environments, or low- vs. high-rust severities. The thousand kernel weight in mixtures was equal to or greater than that of the component means in 83% of the comparisons (mixtures ranged from 6% below to 18% above component means with an overall mean of 3% above). Therefore, the reduction in leaf rust severity in mixtures was reflected in a higher percentage of experiments in preserving thousand kernel weight than in overall grain yield. This result is not totally unexpected because overall grain yield is determined by many factors extraneous to leaf rust severity. These other factors include the inherent yield potential of different cultivars, the effect of mixture composition on other biotic and abiotic stresses (and their associated effects on yield), and the effect of plant competition in the mixtures (1).

It is of interest that grain yield and thousand kernel weight were greater than or equal to the best cultivar in 45 and 36% of the experiments, respectively (Tables 2 and 3). This compares with Wolfe and Barrett's (26) results in barley mixtures to control powdery mildew, in which 26% of the mixtures exceeded the yield of the highest-yielding component cultivar. However, as the authors point out, comparisons of mixtures with the highest-yielding cultivar must be done a posteriori, because it cannot be reliably predicted which cultivar will be the highest-yielding before sowing, in most instances.

The results of this study showed that winter wheat cultivar mixtures can significantly reduce leaf rust under Texas conditions. The results also demonstrated an increase in yield and thousand kernel weight in certain mixtures over the component mean, and occasionally over the best cultivar. Thus, if cultivars are judiciously chosen and mixed before sowing, the leaf rust risks associated with production could be reduced.

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