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Mixing ability analysis of wheat cultivar mixtures under diseased and nondiseased conditions *

E. A. Knott and C. C. Mundt

Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902, USA

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Summary. Mixing ability analyses, adapted from combining ability analyses used in plant breeding, were performed on yield and stripe rust (*Puccinia striiformis*) severity data for two-way mixtures among either four or five club wheat (*Triticum aesitivum*) cultivars grown in five environments. Initially, two statistics were calculated for each trait: general mixing ability (GMA), the average performance of a cultivar over all of the mixtures, and specific mixing ability (SMA), the deviation of a mixture from the estimated performance of the pair based on its average performance in mixtures. General mixing ability was further divided into two components: genotype performing ability (GPA), the innate ability of a cultivar to yield and resist disease in pure stand, and true general mixing ability (TGMA), the average ability of a cultivar to influence yield and disease when mixed with other cultivars. Significant mean squares for genotypes, GMA, SMA, and TGMA were found for all of the traits in most environments. Examination of TGMA and SMA revealed cultivars and cultivar combinations that were statistically better "mixers" than the others. Some of the significant effects were probably due to the use of cultivars that differed in height and stripe rust resistance, but for other combinations there was no apparent explanation for enhanced mixing ability.

Key words: Cultivar mixture – Diallel – General mixing ability – *Puccinia striiformis* – Specific mixing ability

Introduction

Problems arising from the practice of monoculture crop production (e.g., susceptibility to biotic stresses, dependance on chemical pest controls, and reduced life expectancy for crop cultivars) have highlighted the need for alternative crop production methods. One alternative is the use of cultivar mixtures. Mixtures have been shown to reduce disease levels (Mundt and Browning 1985; Wolfe 1985), stabilize yields (Sprague and Tatum 1942; Wolfe 1985), and reduce selection for complex races of pathogens (Chin and Wolfe 1984; Leonard 1969; Wolfe 1985). Instances of mixtures yielding more than the average of the pure stand yields of the lines involved have been recorded for several crop species (Trenbath 1974; Wolfe 1985). It has been found (C. C. Mundt, L. S. Brophy, and M. R. Finckh, in preparation) that mixtures of certain club wheat (*Triticum aesitivum* L.) cultivars decrease stripe and leaf rust (*Puccinia striiformis* Westend., *Puccinia recondita* Rob.) severity by up to 90% relative to the average of the cultivars when grown separately in pure stands, and have shown yield increases of up to 30%.

Not all mixtures are equivalent in yielding ability or disease protection (Trenbath 1974; Wolfe 1985), and mixtures may perform equal to, better, or worse than the mean of the components grown in pure stands (Baker and Briggs 1984; Gizlice et al. 1989; Khalifa and Qualset 1974; Trenbath 1974). Thus, a method for estimating the performance of cultivars in a mixture would be of benefit to growers and breeders interested in selecting cultivars that perform well when mixed.

One method of estimating the mixing ability of a cultivar in a mixture is to use combining ability analysis. Combining ability is an estimate of how well a line does in hybrid combinations, and it is frequently used by plant breeders as a tool for choosing the best parental combinations. To calculate combining ability, each line is crossed with every other line in a diallel arrangement. Combining ability for a mixture is based on data derived

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by mixing cultivars in a 1:1 ratio in all possible two-way combinations.

Combining ability was divided by Sprague and Tatum (1942) into two measurements: general combining ability (GCA) and specific combining ability (SCA). They defined GCA as "... the average performance of a line in hybrid combination...", and SCA "is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved."

Jensen and Federer (1965) used model I, method I of a combining ability analysis developed by Griffing (1956) on wheat cultivar mixtures. They found a significant general combining effect, which they termed general competing effect, but no specific competing (combining) effect. General competing ability was calculated as the average performance of a cultivar in a mixture. Specific competing ability was considered an indication of how well certain combinations performed compared to that expected from their average abilities over all mixtures. Gizlice et al. (1989) adapted method IV, model I of Griffing (1956) to estimate general blending ability (GBA) and an interaction term analogous to SCA of soybean (*Glycine max*) cultivars.

Gizlice et al. (1989) further divided GBA into true general competitive ability (TGCA) and general yielding ability (GYA). General yielding ability was considered an estimate of the yielding ability of a cultivar in pure stand, and TGCA a measure of the competitive ability of a cultivar in a mixture. True general competitive ability is especially helpful in that it allows one to determine the blending ability of a cultivar without being confounded by the cultivar's innate pure-stand abilities. These terms are analogous to some developed by Federer et al. (1982) for use in mixtures and to others suggested by Gardner and Eberhardt (1966) for use in crosses.

The purpose of this paper is to use combining ability analysis to evaluate the mixing ability of club wheat cultivars for disease severity in plots inoculated with stripe rust and for yield in the presence and absence of stripe rust.

Materials and methods

Field data

Data analyzed in this paper were derived from field studies that will be reported in more detail elsewhere (C. C. Mundt, L. S. Brophy, and M. R. Finckh, in preparation). A summary of field methodology is described below.

In 1987 seeds of five club wheat cultivars, Faro, Jackmar, Moro, Tres, and Tyee, were grown as all possible two-, three-, four-, and five-way mixtures (with equal proportions of seeds of each cultivar), and also in pure stands. The cultivars differed in height and in resistance to two races of stripe rust (*Puccinia striiformis* Westend.) (Table 1). The experiments were carried out at three locations in Oregon that differ in average annual rainfall; Corvallis (1,064 mm/year), Moro (321 mm/year), and Pendleton (554 mm/year). There were two experiments at each location; one with fungicide applied (disease-free) and one inoculated with two races of stripe rust. Each experiment was a randomized complete block design with four replications per treatment. Each plot was 4.3 × 1.5 m. Plots were adjacent in the narrow dimension and there was 1.8 m of fallow ground between plots in the long dimension.

Table 1. Height and resistance reactions to two races of stripe rust for the five club wheat cultivars used in the field experiments

Cultivar	Height	Reaction to *P. striiformis*[a]	
		Race 5	Race 27
Faro (F)	semi-dwarf	mixed[b]	r
Jackmar (J)	dwarf	s	r
Moro (M)	tall	s	r
Tres (R)	semi-dwarf	r	r
Tyee (Y)	semi-dwarf	r	s

[a] r = resistant, s = susceptible
[b] Approximately one-half of the plants were resistant to race 5 and one-half were susceptible

All plots were combine-harvested and yields were recorded in kilograms. Estimates of percent diseased leaf area (DLA) were made on the inoculated plots at anthesis by visual assessment of the amount of leaf surface covered with stripe rust lesions. For the purpose of this paper, DLA was transformed to percent green leaf area (GLA) by subtracting DLA from 100. This transformation was done so that coefficients of the models would always be positive for favorable traits, i.e., high yield and low disease severity.

Statistical analysis

Analyses of variance as described by Griffing (1956) Method IV, Model I were made on the yields of the two-way mixtures for the fungicide-treated experiments and on yield and green leaf area for the inoculated experiments. Analyses were also made on mixture response [statistically analogous to blend response of Gizlice et al. (1989)], which is the deviation of the average of the pure line components from the mixture, for each of the traits measured in each environment.

The Griffing model (1956) provides a method for estimating general and specific combining ability, which will be referred to as general mixing ability (GMA) and specific mixing ability (SMA) when applied to the performance of cultivar mixtures. General mixing ability is the average performance of a cultivar in a mixture, and is calculated by

$$GMA_i = 1/p(p-2)\,[p X_{i.} - 2X_{..}],$$

where p is the number of cultivars used in the experiment, $X_{i.}$ is the sum of yields or green leaf areas over all of the mixtures in which a cultivar was present, and $X_{..}$ is the sum over all of the mixtures. Specific mixing ability is an indication of how well certain combinations of cultivars perform compared to that expected from their average abilities over all mixtures. Specific mixing ability is calculatd by

$$SMA_{ij} = X_{ij} - 1/(p-2)\,[X_{i.} + X_{.j}] + 2/(p-2)\,(p-1)\,X_{..}\,,$$

where X_{ij} is the value of the mixture, $X_{j.}$ is the sum of yield or green leaf area for all mixtures that the other cultivar is present in, and the other terms are as defined above.

For the 1987 data the approach of Federer et al. (1982) and Gizlice et al. (1989) was followed to divide general mixing ability

Table 2. Statistical significance of mean squares for genotype, general mixing ability (GMA), and specific mixing ability (SMA) for four wheat cultivars grown as all possible two-way mixtures in 1988

Treatment	Significance of F-test		
	Genotype	GMA	SMA
Fungicide-treated mixture yields			
Moro	0.1263	0.0483	0.7910
Pendleton	0.1333	0.0843	0.3880
Fungicide-treated mixture response[a]			
Moro	0.4435	0.2430	0.7930
Pendleton	0.6312	0.6820	0.3890
Inoculated mixture yield			
Moro	0.0001	<0.0001	0.4350
Pendleton	0.0001	<0.0001	0.2060
Inoculated mixture response[a]			
Moro	0.2575	0.1920	0.4000
Pendleton	0.0001	<0.0001	0.2060
Green leaf area[b]			
Moro	0.0001	<0.0001	0.0296
Pendleton	0.0001	<0.0001	0.0027
Green leaf area[b] mixture response[a]			
Moro	0.0002	0.0002	0.0295
Pendleton	0.0001	<0.0001	0.0027

[a] Mixture response data were from diallel analyses of data derived by subtracting the average of the pure-stand yields or green leaf areas of the components of a mixture from the mixture value

[b] Green leaf area (GLA) is the percentage of leaf area covered by rust subtracted from 100

Table 3. Statistical significance of mean squares for genotype, general mixing ability (GMA), and specific mixing ability (SMA) for five wheat cultivars grown in all possible two-way mixtures in 1987

Treatment	Significance of F-test		
	Genotype	GMA	SMA
Fungicide-treated mixture yields			
Corvallis	0.0029	0.0040	0.0250
Moro	0.0001	<0.0001	0.1620
Pendleton	0.0001	<0.0001	0.2100
Fungicide-treated mixture response[a]			
Corvallis	0.0972	0.8010	0.0250
Moro	0.2101	0.3580	0.1620
Pendleton	0.3452	0.5780	0.2100
Inoculated mixture yield			
Corvallis	0.0023	0.0002	0.6010
Moro	0.0019	0.0040	0.0140
Pendleton	0.0001	<0.0001	0.0160
Inoculated mixture response[a]			
Corvallis	0.1137	0.0310	0.6010
Moro	0.0332	0.3410	0.0140
Pendleton	0.0001	<0.0001	0.0160
Green leaf area[b]			
Corvallis	0.0001	<0.0001	<0.0001
Moro	0.0001	<0.0001	0.1420
Pendleton	0.0001	<0.0001	0.2960
Green leaf area[b] mixture response[a]			
Corvallis	0.0001	0.0190	<0.0001
Moro	0.0012	0.0003	0.1420
Pendleton	0.0096	0.0022	0.2960

[a] Mixture response data were from diallel analyses of data derived by subtracting the average yield or green leaf area of the pure lines of the components of a mixture from the mixture value

[b] Green leaf area (GLA) is the percentage of leaf area covered by rust subtracted from 100

into two components: true general mixing ability (TGMA) and genotype performing ability (GPA). A similar analysis could not be done for the 1988 data because there was a diallel of only four cultivars in that year, which is not enough for biologically interpretable estimates. True general mixing ability is statistically analogous to the true general competitive ability of Gizlice et al. (1989), and represents the average ability of a cultivar to influence yield and disease when mixed with other cultivars. True general mixing ability is estimated by the same analysis as general mixing ability except that it is performed on mixture responses. Genotype performing ability is statistically analogous to general yielding ability as described by Gizlice et al. (1989). Genotype performing ability describes the performance of mixture components in pure stand, in terms of ability to yield and to resist disease. Genotype performing ability is calculated as the deviation of TGMA from GMA.

Estimates of mixture yields and green leaf area for a mixture can be calculated as follows:

$$Y_{ij} = u + \mathrm{GPA}_i + \mathrm{GPA}_j + \mathrm{TGMA}_i + \mathrm{TGMA}_j + \mathrm{SMA}_{ij} + e_{ij}$$

where u is the population mean, e_{ij} is an error term, and GPA, TGMA, and SMA are as defined above.

Results

Genotype mean squares in 1988 for the fungicide-treated plots were not statistically significant ($P \leq 0.05$) for any environment (Table 2). In contrast, the genotype mean square was almost always statistically significant for yield in the inoculated plots and for green leaf area.

Both GMA and SMA differences are tested with the same error term, so levels of significance are proportional to the size of the mean square terms. For yield in the inoculated plots in 1988, general mixing ability was a more important effect than specific mixing ability. For green leaf area, however, both the general and specific terms were highly ($P \leq 0.01$) significant (Table 2).

The genotype mean squares for the mixture yields and percent green leaf area of the 1987 data were significant for all treatments and locations (Table 3). For the mixture responses, several genotype mean squares were not significant, most noticeably in the fungicide-treated mixture responses. There was no clear trend in terms of the importance of general mixing ability versus specific mixing abil-

Table 4. General mixing ability (GMA), true general mixing ability (TGMA), and genotype performing ability (GPA) estimates of yield from fungicide-treated and inoculated plots and green leaf area from the inoculated plots for five cultivars grown as all possible two-way mixtures in 1987[a]

	Cultivars					FPLSD[b] values
	Faro (F)	Jackmar (J)	Moro (M)	Tres (R)	Tyee (Y)	
Fungicide-treated yields (kg/plot)						
Corvallis						
GMA	0.048	−0.045	−0.198	−0.019	0.215	0.170
TGMA	−0.029	−0.053	0.002	0.023	0.057	N.S.
GPA	0.077	0.008	−0.200	−0.042	0.158	N.S.
Moro						
GMA	0.162	0.025	−0.301	0.054	0.060	0.123
TGMA	0.005	−0.073	0.039	−0.029	0.057	N.S.
GPA	0.157	0.097	−0.340	0.082	0.004	N.S.
Pendleton						
GMA	0.241	0.113	−0.637	0.146	0.136	0.154
TGMA	0.065	−0.055	−0.051	0.035	0.006	N.S.
GPA	0.176	0.167	−0.586	0.111	0.130	N.S.
Inoculated yields (kg/plot)						
Corvallis						
GMA	−0.034	−0.181	−0.141	0.322	0.033	0.175
TGMA	−0.100	−0.109	−0.050	0.093	0.166	0.175
GPA	0.066	−0.072	−0.091	0.229	−0.133	0.175
Moro						
GMA	0.031	−0.065	−0.128	0.173	−0.010	0.128
TGMA	−0.071	−0.016	−0.022	0.073	0.036	N.S.
GPA	0.102	−0.049	−0.106	0.100	−0.046	N.S.
Pendleton						
GMA	0.324	−0.314	−0.518	0.497	0.011	0.086
TGMA	−0.008	−0.149	−0.178	0.221	0.114	0.086
GPA	0.332	−0.165	−0.340	0.276	−0.103	0.086
Green leaf area (%)[c]						
Corvallis						
GMA	8.18	−5.44	4.41	15.12	−22.28	4.81
TGMA	0.48	0.73	−5.98	3.76	1.02	4.81
GPA	7.71	−6.17	10.39	11.37	−23.29	4.81
Moro						
GMA	1.22	−14.37	−2.28	16.13	−0.70	5.51
TGMA	−4.91	5.76	−8.03	3.26	3.93	5.51
GPA	6.13	−20.13	5.75	12.87	−4.63	5.51
Pendleton						
GMA	5.55	−15.20	−3.78	18.88	−5.45	4.07
TGMA	−2.57	−4.07	−1.41	3.63	4.43	4.07
GPA	8.13	−11.13	−2.37	15.25	−9.87	4.07

[a] Values in the table represent deviations from the mean over all mixtures for the trait in question
[b] Values of Fischer's protected least significant difference for the 5% probability level. N.S. = effect not significant at $P = 0.05$ in the analysis of variance
[c] Percent green leaf area (GLA) is the percentage of leaf area covered by stripe rust lesions subtracted from 100

ity for the different variables. However, the general mixing ability mean squares were significant more often than the specific.

Although not all of the general mixing ability mean squares were significant, calculations for TGMA and GPA were made to compare treatment trends among all of the environments. Cultivars differed considerably for GMA, TGMA, and GPA (Table 4).

The cultivar Tyee (Y) had the highest TGMA for yield and GLA over all treatments and locations, with positive

Table 5. Yield, genotype performing ability (GPA), true general mixing ability (TGMA), specific mixing ability (SMA), total mixture effect (TME), and total performance (TP) estimates for five cultivars grown in all possible two-way combinations and pure stands under fungicide-treated conditions in three locations

Mixture[a]	Yield (kg/plot)	GPA[b]	TGMA[b]	SMA[c]	TME[d]	TP[e]
Corvallis 1987						
F F	3.21	–	–	–	–	–
J J	3.07	–	–	–	–	–
M M	2.65	–	–	–	–	–
R R	2.97	–	–	–	–	–
Y Y	3.37	–	–	–	–	–
F J	3.19	0.085	−0.082	0.097	(0.015)	0.100
F M	2.91	−0.123	−0.027	−0.037	−(0.064)	−0.187
F R	3.05	0.035	−0.006	−0.073	−(0.079)	−0.044
F Y	3.37	0.235	0.028	0.012	(0.040)	0.275
J M	2.60	−0.192	−0.051	−0.250	−(0.301)	−0.493
J R	3.03	−0.034	−0.030	−0.005	−(0.035)	−0.069
J Y	3.42	0.166	0.004	0.158	(0.162)	0.327
M R	3.14	−0.242	0.025	0.267	(0.292)	0.050
M Y	3.13	−0.042	0.059	0.020	(0.080)	0.037
R Y	3.10	0.116	0.080	−0.190	−(0.110)	0.006
Moro 1987						
F F	2.39	–	–	–	–	–
J J	2.27	–	–	–	–	–
M M	1.40	–	–	–	–	–
R R	2.25	–	–	–	–	–
Y Y	2.09	–	–	–	–	–
F J	2.39	0.254	−0.067	0.097	(0.029)	0.284
F M	2.00	−0.183	0.045	0.033	(0.078)	−0.105
F R	2.16	0.239	−0.023	−0.165	−(0.188)	0.051
F Y	2.36	0.161	0.062	0.039	(0.101)	0.262
J M	1.74	−0.243	−0.033	−0.085	−(0.119)	−0.361
J R	2.21	0.180	−0.101	0.022	−(0.079)	0.101
J Y	2.16	0.101	−0.016	−0.034	−(0.050)	0.051
M R	1.96	−0.258	0.011	0.098	(0.109)	−0.149
M Y	1.82	−0.336	0.096	−0.046	(0.050)	−0.286
R Y	2.26	0.086	0.028	0.045	(0.073)	0.159

Table 5. Continued

Mixture[a]	Yield (kg/plot)	GPA[a]	TGMA[b]	SMA[c]	TME[d]	TP[e]
Pendleton 87						
F F	3.21	–	–	–	–	–
J J	3.19	–	–	–	–	–
M M	1.68	–	–	–	–	–
R R	3.08	–	–	–	–	–
Y Y	3.11	–	–	–	–	–
F J	3.21	0.343	0.010	0.016	(0.026)	0.369
F M	2.44	−0.410	0.013	0.003	(0.016)	−0.394
F R	3.13	0.287	0.100	−0.093	(0.007)	0.294
F Y	3.29	0.306	0.071	0.074	(0.144)	0.450
J M	2.19	−0.419	−0.106	−0.119	−(0.225)	−0.644
J R	3.10	0.278	−0.019	0.007	−(0.013)	0.265
J Y	3.18	0.297	−0.049	0.096	(0.047)	0.345
M R	2.53	−0.475	−0.016	0.186	(0.170)	−0.305
M Y	2.27	−0.456	−0.045	−0.070	−(0.115)	−0.571
R Y	3.02	0.241	0.041	−0.100	−(0.059)	0.182

[a] Two-way mixtures and pure stands of the cultivars Faro (F), Jackmar (J), Moro (M), Tres (R), and Tyee (Y). Pure stands are indicated by a double letter

[b] GPA and TGMA entries are the sums of the GPA and TGMA values, respectively, of both components in the mixture

[c] Fischer's protected least significant difference for SMA at 5% probability level for Corvallis = 0.17. SMA effects were not significant at $P = 0.05$ in the analysis of variance for Moro or Pendleton

[d] Total mixture effect (TME) is a measure of the total effects due to mixing a pair of cultivars, and is calculated as the sum of TGMA and SMA for that mixture

[e] Total performance (TP) is the sum of GPA, TGMA, and SMA for a mixture, and estimates the deviation from the mean performance of all mixtures

estimates in all cases. Overall, the cultivar Jackmar (J) had the lowest TGMA, with negative estimates in seven of nine cases. GMA values were not always correlated with TGMA because of the strong influence of the cultivar's pure-stand abilities. General mixing ability values were not always correlated with GPA or actual pure-stand values (Tables 4–7), due to the influence of TGMA. Location also influenced the performance of several of the cultivars. For example, Jackmar showed high GMA and TGMA estimates for green leaf area in Corvallis and Moro but not in Pendleton (Table 4).

The 1987 mixtures also differed significantly for SMA (Tables 5–7). Specific mixing ability estimates for each treatment and location were also ranked (Table 8). The rank of each mixture across traits (yields and green leaf area) within locations indicates the effect of disease on yield. For example, the FY mixture had positive SMA values for both fungicide-treated and inoculated yields, but the green leaf area estimate was negative, i.e., the mixture yielded better than predicted, but had worse than predicted disease resistance.

The ranking of a mixture within traits across locations (Table 8) gives an indication of the effect of location on mixture performance. The SMA rankings for fungicide-treated yields do not vary much across locations, except for the combinations JY and RY. However, the yields under disease conditions and the green leaf area show variation in rank among locations, as might be expected if the environment interacted with disease progress.

The sum of TGMA, GPA, and SMA estimates for each mixture describes the actual yield and green leaf area of 1987 with an average accuracy of 98%. The extreme estimates were 24% more yield than observed for combination MY in Moro in the fungicide-treated plots,

Table 6. Yield, genotype performing ability (GPA), true general mixing ability (TGMA), specific mixing ability (SMA), total mixture effect (TME), and total performance (TP) estimates for five cultivars grown in all possible two-way combinations and pure stands in three locations when inoculated with stripe rust

Mixture[a]	Yield (kg/plot)	GPA[b]	TGMA[b]	SMA[c]	TME[d]	TP[e]
Corvallis 1987						
F F	2.68	–	–	–	–	–
J J	2.41	–	–	–	–	–
M M	2.37	–	–	–	–	–
R R	3.01	–	–	–	–	–
Y Y	2.28	–	–	–	–	–
F J	2.62	−0.006	−0.209	0.120	−(0.089)	−0.095
F M	2.48	−0.025	−0.150	−0.057	−(0.207)	−0.232
F R	2.99	0.295	−0.007	−0.007	−(0.014)	0.281
F Y	2.66	−0.067	0.066	−0.055	(0.011)	−0.056
J M	2.45	−0.163	−0.159	0.057	−(0.102)	−0.265
J R	2.75	0.157	−0.016	−0.105	−(0.121)	0.036
J Y	2.49	−0.205	0.057	−0.072	−(0.015)	−0.220
M R	2.89	0.138	0.043	−0.007	(0.036)	0.174
M Y	2.61	−0.224	0.116	0.007	(0.123)	−0.101
R Y	3.19	0.096	0.259	0.120	(0.379)	0.475
Moro 1987						
F F	1.45	–	–	–	–	–
J J	1.15	–	–	–	–	–
M M	1.04	–	–	–	–	–
R R	1.45	–	–	–	–	–
Y Y	1.16	–	–	–	–	–
F J	1.16	0.053	−0.087	−0.081	−(0.168)	−0.115
F M	1.36	−0.004	−0.092	0.182	(0.090)	0.086
F R	1.28	0.202	0.002	−0.194	−(0.192)	0.010
F Y	1.39	0.056	−0.035	0.093	(0.058)	0.114
J M	1.02	−0.155	−0.038	−0.056	−(0.094)	−0.249
J R	1.48	0.051	0.057	0.096	(0.153)	0.204
J Y	1.24	−0.095	0.020	0.041	(0.061)	−0.034
M R	1.37	−0.006	0.051	0.053	(0.104)	0.098
M Y	0.95	−0.152	0.014	−0.179	−(0.165)	−0.317
R Y	1.48	0.054	0.108	0.045	(0.153)	0.207
Pendleton 1987						
F F	2.49	–	–	–	–	–
J J	1.50	–	–	–	–	–
M M	1.15	–	–	–	–	–
R R	2.38	–	–	–	–	–
Y Y	1.63	–	–	–	–	–
F J	2.11	0.167	−0.157	0.063	−(0.095)	0.072
F M	1.87	−0.008	−0.186	0.023	−(0.163)	−0.171
F R	2.75	0.608	0.213	−0.110	(0.103)	0.711
F Y	2.40	0.229	0.106	0.025	(0.131)	0.360
J M	1.19	−0.505	−0.327	−0.015	−(0.342)	−0.847
J R	2.14	0.111	0.072	−0.079	−(0.007)	0.104
J Y	1.77	−0.268	−0.035	0.031	−(0.004)	−0.272
M R	2.14	−0.064	0.043	0.119	(0.162)	0.098
M Y	1.41	−0.443	−0.064	−0.127	−(0.191)	−0.634
R Y	2.62	0.173	0.335	0.071	(0.406)	0.579

[a] Two-way mixtures and pure stands of the cultivars Faro (F), Jackmar (J), Moro (M), Tres (R), and Tyee (Y). Pure stands are indicated by a double letter

[b] GPA and TGMA entries are the sums of GPA and TGMA values, respectively, for both components in the mixture

[c] Fischer's protected least significant difference values for SMA at the 5% significance level for Moro = 0.128, and for Pendleton = 0.0859. SMA effects were not significant at $P = 0.05$ in the analysis of variance for Corvallis

[d] Total mixture effect (TME) is a measure of the total effects due to mixing a pair of cultivars, and is calculated as the sum of TGMA and SMA for that mixture

[e] Total performance (TP) is the sum of GPA, TGMA, and SMA for a mixture, and estimates the deviation from the mean performance of all mixtures

and 8% less yield for combination FR in the stripe-rust-inoculated plots.

The relative importance of TGMA, GPA, and SMA varied considerably among the mixtures. For example, the mixtures FR and RY at Corvallis both yielded well under disease conditions. With the former mixture, the high yield was due mostly to a high GPA effect for both cultivars (Table 6). With the latter mixture, however, high yield was due to high combined TGMA and SMA effects (Table 6).

Discussion

In this study, as in other studies on combining ability in mixtures (Baker and Briggs 1984; Federer et al. 1982; Gizlice et al. 1989; Jensen and Federer 1965; Schutz and Brim 1971), statistically significant general "mixing" abilities were found. Upon dividing the general effects into components, we discovered that the differences between cultivars were often due to statistically significant differences in true general mixing ability (TGMA). Some of these differences are easily explained. For example, one would expect Tyee and Tres to have positive TGMA values for green leaf area and yield under inoculated conditions, because both cultivars possess a resistance gene different from all other cultivars in the mixtures. This should cause a large reduction in disease severity and be reflected in large yield increases. Other results have no apparent explanation, e.g., the consistently positive TGMA for the yield of Tyee in fungicide-treated plots, while in fungicide-treated pure stands Tyee is consistently low yielding. Studying the competitive abilities of individual cultivars in mixtures may elucidate the mechanisms of such findings.

Statistically significant specific mixing abilities were also found in this study. This has not been previously reported for mixtures, to the best of our knowledge. Sig-

Table 7. Percent green leaf area (GLA), genotype performing ability (GPA), true general mixing ability (TGMA), specific mixing ability (SMA), total mixture effect (TME), and total performance (TP) estimates for five cultivars grown in all possible two-way combinations and as pure stands in three locations when inoculated with stripe rust

Mixture[a]	GLA[b] (%)	GPA[c]	TGMA[c]	SMA[d]	TME[e]	TP[f]
Corvallis 1987						
F F	92.3	–	–	–	–	–
J J	64.5	–	–	–	–	–
M M	97.6	–	–	–	–	–
R R	99.6	–	–	–	–	–
Y Y	30.3	–	–	–	–	–
F J	87.5	1.53	1.20	0.24	(1.45)	2.98
F M	97.0	18.10	−5.50	−0.12	−(5.62)	12.48
F R	99.4	19.07	4.23	−8.45	−(4.22)	14.85
F Y	78.7	−15.59	1.49	8.33	(9.82)	−5.77
J M	93.0	4.22	−5.25	9.51	(4.26)	8.48
J R	98.3	5.20	4.48	4.05	(8.53)	13.73
J Y	43.0	−29.47	1.75	−13.80	−(12.05)	−41.52
M R	98.8	21.76	−2.22	−5.23	−(7.45)	14.31
M Y	62.5	−12.90	−4.96	−4.16	−(9.12)	−22.02
R Y	87.0	−11.92	4.77	9.63	(14.41)	2.48
Moro 1987						
F F	83.3	–	–	–	–	–
J J	30.7	–	–	–	–	–
M M	82.5	–	–	–	–	–
R R	96.7	–	–	–	–	–
Y Y	61.7	–	–	–	–	–
F J	68.0	−14.00	0.85	−0.13	(0.73)	−13.27
F M	85.5	11.87	−12.94	5.29	−(7.65)	4.23
F R	95.3	19.00	−1.65	−3.37	−(5.03)	13.97
F Y	80.0	1.50	−0.98	−1.79	−(2.77)	−1.27
J M	57.5	−14.37	−2.27	−7.13	−(9.40)	−23.77
J R	88.3	−7.25	9.02	5.21	(14.22)	6.97
J Y	68.3	−24.75	9.68	2.04	(11.73)	−13.03
M R	95.3	18.63	−4.77	0.13	−(4.65)	13.97
M Y	80.0	1.13	−4.11	1.71	−(2.40)	−1.27
R Y	94.7	8.25	7.18	−1.96	(5.23)	13.47

Table 7. Continued

Mixture[a]	GLA[b] (%)	GPA[c]	TGMA[c]	SMA[d]	TME[e]	TP[f]
Pendleton 1987						
F F	73.0	–	–	–	–	–
J J	34.5	–	–	–	–	–
M M	52.0	–	–	–	–	–
R R	87.3	–	–	–	–	–
Y Y	37.0	–	–	–	–	–
F J	59.3	−3.00	−6.65	3.13	−(3.53)	−6.53
F M	65.3	5.75	−3.98	−2.29	−(6.27)	−0.53
F R	87.0	23.37	1.06	−3.21	−(2.15)	21.23
F Y	68.3	−1.75	1.85	2.37	(4.23)	2.47
J M	45.3	−13.50	−5.48	−1.54	−(7.03)	−20.53
J R	70.5	4.13	−0.44	1.04	(0.60)	4.73
J Y	42.5	−21.00	0.35	−2.63	−(2.27)	−23.27
M R	83.7	12.87	2.23	2.87	(5.10)	17.97
M Y	57.5	−12.25	3.02	0.96	(3.97)	−8.27
R Y	78.5	5.37	8.06	−0.71	(7.35)	12.73

[a] Two-way mixtures and pure stands of the cultivars Faro (F), Jackmar (J), Moro (M), Tres (R), and Tyee (Y). Pure stands are indicated by a double letter

[b] Percent green leaf area (GLA) is the percentage of leaf area covered by rust subtracted from 100

[c] GPA and TGMA entries are the sums of the GPA and TGMA values, respectively, of both components in the mixture

[d] Fischer's protected least significant difference for SMA at the 5% significance level for Corvallis = 4.81. SMA effects were not significant at $P = 0.05$ in the analysis of variance for Moro and Pendleton

[e] Total mixture effect (TME) is a measure of the total effects due to mixing a pair of cultivars, and is calculated as the sum of TGMA and SMA

[f] Total performance (TP) is the sum of GPA, TGMA, and SMA for a mixture, and estimates the deviation from the mean performance of all mixtures

nificant SMA estimates indicate that certain mixtures did better (or worse) than predicted based on their average performance. As with TGMA, some of the SMA results are readily explained. For example, it has been hypothesized that mixing a tall, low-yielding cultivar with a dwarf, high-yielding one should result in low mixture yields and negative SMA effects, due to the shading effects on the dwarf cultivar (Baker and Briggs 1984; Jennings and De Jesus 1968). The dwarf: dwarf combination should have higher yields and positive SMA estimates (Baker and Briggs 1984; Jennings and De Jesus 1968). In our study, the tall: dwarf mixture JM had consistently low SMA values and low yields. However MR, a tall: semidwarf pair, had high SMA values and high yields in the fungicide-treated experiments. The semidwarf: semidwarf mixtures did not always have high SMA values as expected. For example, FR had negative SMA values for yield under fungicide conditions in all environments.

Another possible mechanism that might have generated statistically significant SMA values was the difference in disease resistance among the cultivars. Combinations of cultivars having resistance to both races of stripe rust should overshadow those with resistance to only one. Significant SMA terms due to differences in disease resistance should be found for the percent green leaf area estimates, which are a direct measure of disease resistance. Based on the resistance reactions designated in Table 1, we would expect the combination RY or FY to have higher SMA values for green leaf area than JM, FJ, or FM. This is not the case in all locations. Values for JM and FY were similar in Corvallis, and FM and FJ outperformed FY in Moro and Pendleton, respectively. Differences in the number of resistance genes in a mixture are apparently not the only factors affecting the ability of a mixture to resist disease.

The closeness of plots in our experiments may have resulted in considerable interplot interference and an

Table 8. Ranking of two-way mixtures of cultivars grown in 1987, according to their specific mixing ability (SMA) estimates for yield when treated with fungicide, and estimates of SMA for yield and percent green leaf area when inoculated with stripe rust. The number 1 indicates the highest SMA estimate and 10 the lowest, for each combination of trait and location

Mixture	Fungicide yield			Inoculated yield			Green leaf area		
	C[b]	M[b]	P[b]	C	M	P	C	M	P
F J	3	2	4	1,2	8	3	5	6	1
F M	7	5	6	8	1	6	6	1	8
F R	8	10	8	6,5	10	9	7	9	10
F Y	5	4	3	7	3	5	3	7	3
J M	10	9	10	3	7	7	2	10	7
J R	6	6	5	10	2	8	4	2	4
J Y	2	7	2	9	6	4	10	3	9
M R	1	1	1	6,5	4	1	8	5	2
M Y	4	8	7	4	9	10	7	4	5
R Y	9	3	9	1,2	5	2	1	8	6

[a] Percent green leaf area is the percentage of leaf area covered by stripe rust subtracted from 100
[b] C, M, P, are the experiment locations Corvallis, Moro, and Pendleton/OR, respectively

underestimation of the effectiveness of the mixtures in reducing disease severity (Wolfe 1985). In more recent experiments where a resistant genotype was planted between experimental plots, the mixtures on average reduced rust severity by greater than 60% as compared to the means of the pure stands (C. C. Mundt, M. R. Finckh, and L. S. Brophy, unpublished results).

The significant SMA mean squares for yield in the inoculated plots cannot be attributed only to differences in disease resistance. There were several examples of cultivar combinations yielding well in spite of being very susceptible. Composition with regard to disease resistance and height did play a role in some cases. RY was resistant to both races and of equal height, and had higher SMA values than JM, which was susceptible to race 5 of the pathogen and a dwarf: tall mix. When examining a cultivar for potential use in a mixture, all components of mixing ability should be considered. There are mixtures with similar total performance (TP) that have vastly different GPA, TGMA, and SMA effects. For example, the mixtures FR and RY have similar TP values for green leaf area in Moro (13.975 and 13.475, respectively), but RY has a TGMA of 7.183 and FR has a TGMA of -1.65 (Table 7). A cultivar with a high GPA but a low TGMA would not be as good a mixer as a cultivar with the opposite effects, and this cannot be seen from observing just the total performance or GMA of a cultivar.

Deriving mixing ability estimates to evaluate the performance of a cultivar in a mixture is a simple, straightforward procedure. Other methods that have been suggested for determining the performance of cultivars in a mixture have required separation of the components, which can be time-consuming and costly (Alexander et al. 1986; Norrington-Davies 1967; Williams 1962). Future uses of mixing ability estimates may include using general mixing ability and TGMA estimates derived from two-way mixtures to predict the performance of three- and four-component mixtures. A drawback to the mixing ability procedure, however, is that one cannot tell what the end composition of a mixture is, and thus the dynamics of the component interactions cannot be explained.

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