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Christopher C. Mundt

Two experiments involving interactions between wheat (Triticum aesitivium L.) cultivars and rust pathogens were investigated. One experiment evaluated the aggressiveness (measured by infection efficiency and latent period) of populations of Puccinia recondita Rob. when inoculated on the cultivar they were isolated from, their "own" cultivar, and when inoculated onto other cultivars. Statistically significant interactions between host and pathogen were found for latent period, but they were not the result of the pathogen being more aggressive on its "own" cultivar. Considerable variability in infection efficiency and latent period was found among pathogen populations inoculated on the same host, and among cultivars inoculated with the same pathogen population. The presence of such pathogen variability in the field could affect the efficiency with which we detect cultivars with different levels of resistance.

In the second experiment quantitative genetic models were used to analyze field data of club wheat cultivars grown in all possible two-way combinations and in pure stands, to evaluate which cultivars performed best in mixtures. Combining ability analyses were performed on the grain yields for each mixture under disease-free conditions, and for grain yield and percent green leaf area when inoculated with Puccinia striiformis Westend.. The ability to perform in a mixture differed significantly among cultivars. There were also significant differences amongst the mixture performances. These differences were probably due in part to differences in height and disease resistance of the cultivars involved. However, not all of the differences can be explained by discrepancies in height or disease resistance.

Genetic Diversity and Interactions in Populations of Plants and Pathogens

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Elizabeth A. Knott

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Redacted for privacy

Head of Department of Botany and Plant Pathology

Redacted for privacy

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Finally, I send my love and gratitude to my sister, my parents, and Tom Seidel for their long distance encouragement and love.

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GENETIC DIVERSITY AND INTERACTIONS IN POPULATIONS OF PLANTS AND PATHOGENS

Introduction

A common agricultural practice is to grow extensive areas of genetically uniform crop plants. This practice often results in selection for pathogen biotypes that are highly virulent on that host (4,11,20,32), and may also subject crops to risk from abiotic stresses (32,45). For example, corn (Zea mays) cultivars with Texas cytoplasm, susceptible to race 0 of southern corn leaf blight (Cochliobolus heterostrophus), were widely planted in 1970. As a result of the widespread occurrence of the same susceptible cytoplasm, the leaf blight pathogen spread over vast areas of the U.S., resulting in about 15% yield loss for the entire crop (pp.5-16 in 35).

An alternative to monoculture planting is to use mixtures of plants species, or of plant cultivars, so as to slow the development of epidemics. However, there are several questions regarding the use of mixtures that need to be addressed to better understand their potential for improving the performance of crop populations.

It has been theorized that a "superrace" of a plant pathogen may develop as races of a pathogen mutate to virulence for all of the resistance genes present in the host population (7). Part of the evidence against this

hypothesis is that pathogens are more aggressive on the host cultivars which they were cycled on, their "own" cultivars, than on other cultivars (9,10,27). Thus, the presence of several different cultivars in a field could reduce the fitness of a superrace (9,27,32,37). However, confirmation of host specific aggressiveness has not occurred in all plant/ pathogen systems. In the first part of my thesis, I tested the hypothesis that populations of wheat leaf rust (Puccinia recondita Rob.) were more aggressive on the wheat (Triticum aesitivum L.) cultivars they were isolated from than on other cultivars.

There is substantial evidence that some cultivar mixtures can reduce disease, stabilize yields, and increase yields relative to the average of the pure stands of the components (2,15,17,18,29,40). However, there has been little investigation into the means for selecting cultivars which are most likely to provide such benefits when mixed. One method for selecting mixture components is to use combining ability analysis. Combining ability analysis, as it is used by plant breeders, is a measurement of how well the progeny of a cross between two genotypes performs with regards to a specific trait (39). When combining ability analysis is used to quantify the performance of cultivar mixtures, it is called mixing ability, and estimates how well a cultivar performs when mixed with others. As the second part of my thesis, I analyzed the mixing ability of

club wheat cultivars in several environments and in both the presence and absence of stripe rust (Puccinia striiformis Westend.).

Chapter One:
ECOLOGY AND EPIDEMIOLOGY

Differences among *Puccinia recondita* Populations Isolated from Different Cultivars as Measured by Latent Period and Infection Efficiency

E. A. Knott and C.C. Mundt

Graduate student and assistant professor respectively, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902.

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Abstract

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Five bulk populations of Puccinia recondita Rob. were isolated from five susceptible wheat (Triticum aesitivum L.) cultivars showing different levels of disease in the field. Each population was inoculated onto wheat plants of the cultivar from which they were originally isolated from (their "own" cultivar), and onto the other four cultivars. Latent period and infection efficiency were measured in growth chambers for each of the population x cultivar combinations. No evidence of increased aggressiveness on the "own" cultivars was found for either infection efficiency or latent period. No significant cultivar x spore population interactions were detected in the infection efficiency analysis. However, significant interactions were detected with latent period. Spore population and cultivar effects were significant for both latent period and infection efficiency. Ranking of the spore populations varied for infection efficiency and latent period.

Additional key words:aggressiveness,infection efficiency, latent period, Puccinia recondita, Triticum aesitivum.

Introduction

Variability among pathogen populations for quantitative traits such as latent period and infection efficiency is of great importance to the management of plant disease through host resistance. If such variability occurs within pathogen populations, increased aggressiveness could conceivably be selected for over time (1,4,8,12).

Several authors have investigated whether selection for increased aggressiveness occurred after several cycles of pathogen reproduction on the same host (1,6,8,10, 12,13,). Most authors investigating the Phytophthora infestans/ potato (Solanium tuberosum) system (4,9,10,12) found evidence of pathogen isolates performing more aggressively on their own cultivars (the cultivars they were isolated from), but found no evidence of an increase in aggressiveness after cycling. Clifford and Clothier (6) found similar results with barley (Hordeum vulgare) and stem rust (Puccinia hordeii). James and Fry (8), however, found no evidence for increased aggressiveness on the own cultivar, nor any evidence indicating selection after cycling with the potato late blight system. Their results coincide with those of Alexander et al. (1) using the bean (Phaseolus vulgaris), bean rust (Uromyces appendiculatus) system. Alexander et al. suggested that the increase in

aggressiveness they observed was cultivar-specific, but not due to which cultivar the pathogen had been cycled on. On the other hand, Leonard (13) found that after sub-cycling a Puccinia graminis f.sp. avenae population on two different oat (Avenae sativa) cultivars, each sub-population produced more pustules on its own cultivar than on the other cultivar. Sporulation rate did not change significantly from the own to the other cultivar, however.

Chin and Wolfe (5) observed that isolates of powdery mildew (Erysiphe graminis f.sp. hordei) taken from barley cultivars grown in pure stand were more aggressive on their own cultivars than on other equally susceptible cultivars. However, isolates collected from the same cultivars grown in mixtures showed no difference in aggressiveness on their own vs other.

If isolates are selected for increased aggressiveness on specific hosts, the durability of horizontally resistant [sensu Vanderplank (20)] cultivars may be jeopardized (6,12,16). Also, the presence of significant pathogen x cultivar interactions affects our ability to detect true horizontal resistance, since some isolates of the pathogen will not be as aggressive on a cultivar as others. On the other hand, host-specific selection for pathogen aggressiveness may reduce the impact of complex pathogen races in cultivar mixtures (6,15).

In this study, we examined the aggressiveness of

populations of wheat leaf rust (Puccinia recondita) on the cultivar from which they were isolated and on four other cultivars. We quantified infection efficiency and two measures of latent period to determine the variability among our bulk populations and whether the populations were more aggressive on their own cultivars.

MATERIALS AND METHODS

Plants. Seeds for the cultivars used in this experiment, Monopole (MO), Manning (M), Batum (B), Wanser (W), and Hatton (H), were obtained from the Oregon State University Wheat Breeding Project, Corvallis. All of these cultivars are Hard Red Winter Wheats, and have been rated as susceptible to leaf rust of wheat.

Cultivars used in this experiment were grown from seed in the greenhouse at 24/ 18 C with a 16-hour day/ 8-hour night. Seeds were planted in 6.4-cm plastic pots, one plant per pot, in sterilized medium composed of pumice, peat, sand, and soil in a ratio of 2:1:1:1. All plants were watered daily and fertilized every two weeks with Miracle Gro. The fungicide fenarimol (Rubigan, Elanco Products Co.) was vaporized in the greenhouse on a weekly basis to eliminate powdery mildew (Erysiphe graminis).

Pathogen Populations. Uredospores from 30 - 50 infected wheat leaves were collected from each of five different cultivars. Each cultivar was grown in one 5 x 14-ft. plot in each of two adjacent fields. Populations of uredospores were collected by vacuum into test tubes. Populations from different cultivars were kept separate, but populations from a given cultivar collected from different fields were bulked. The collecting apparatus was cleaned after use on each cultivar with acetone, followed

by a distilled water rinse.

After collection, the populations were placed in a drying chamber with calcium phosphate for 36 hours, weighed, and stored in liquid nitrogen. Upon removal from liquid nitrogen, spores were thawed in a 48C water bath for eight minutes (3).

The populations collected are referred to in this paper by the first letter of the cultivar from which they were isolated. These are w, h, b, mo, and m and correspond to the five cultivars referred to above as W, H, B, MO, and M.

Inoculations. Five-week-old plants of W, H, B, MO, and M were used for each inoculation. The cultivars had been grown in randomized complete blocks in the greenhouse under the conditions described earlier. All cultivars were approximately at the same stage of growth at the time of inoculation.

Each spore population was inoculated onto each cultivar by placing 0.002 g per pot of viable spores in 6 ml of distilled water with two drops of Tween 80 per 50 ml added as a surfactant. Before inoculation, the percentage of viable spores per population was determined from a germination test on water agar plates. The top two fully extended leaves from the main shoot of each plant were inoculated. The spores were sprayed onto the leaves with an aspirator from a distance of about 0.3 m. The aspirator

was rinsed with 3.0 ml of distilled water, which was also sprayed onto the plants. The leaves were turned during spraying so that both sides of the leaves were coated.

Once sprayed, the plants were moved to a dark, 18-20C mist chamber for 12 to 16 hours then moved to a growth chamber at a constant 21C and a 12 hour day/night schedule.

There were three replications of each spore population x cultivar combination per block, and four blocks. There was only one replication of the spore population w in block three, and none in block four due to a shortage of inoculum. Each block of plants was inoculated separately and subsequently placed in separate growth chambers because all of the plants would not fit into the mist chamber or a single growth chamber. The use of a randomized complete block design in the statistical analysis allowed effects of inoculation time and growth chamber to be accounted for.

The leaves were examined for signs of sporulation beginning six days after inoculation. These examinations were conducted twice daily, approximately seven hours apart. Pustules were considered as sporulating an orange color was visible, and the leaf epidermis had been broken. Lesions were counted in a 4-cm marked length on the leaf approximately 2 cm from the shoot. Both sides of the leaf were counted, because lesions would often break through one side but not the other. Leaves were examined until the pustule count was the same for three time-periods in a row.

This was usually around the 13th or 14th day after inoculation.

Infection efficiency was calculated by dividing the maximum number of lesions counted by the area of the leaf. The lengths of the marked areas were measured on each individual leaf after 100% sporulation occurred to account for any leaf growth that occurred after the initial marks were made. An average width was used for the marked areas of both the upper and lower leaves of each cultivar, because some plants had been discarded before their widths were measured. The average was calculated from 10-to-20 plants of each cultivar.

Two latent periods were calculated. First latent period was the time in hours from inoculation to first sporulation. Mid latent period was calculated as the time in hours when half of the maximum number of lesions were sporulating. A linear interpolation was used to estimate this time.

Statistical Analysis. The experiment was subjected to analysis of variance and treated as a factorial randomized complete block design with growth chambers (GC) as blocks, and cultivars (CVAR), spore populations (SPOP) and leaves (LF) as treatments. Interaction terms were calculated for the spore population x cultivar (SPOP x CVAR) interaction, spore population x leaf (SPOP x LF) interaction, spore population x growth chamber (SPOP x GC), and cultivar x

growth chamber (CVAR x GC). Analyses for the latent period measurements were run again on a growth chamber by growth chamber basis because of large SPOP x GC interaction terms. No growth chamber by growth chamber analysis was run on the infection efficiency data because the SPOP x GC interaction term was six times smaller than the SPOP main effect and so could be ignored. A linear contrast (own vs others) was run between spore populations on the cultivar from which they were isolated, their "own", and all other cultivars, "others".

Tukey's honestly significant difference (HSD) values were calculated for those terms that were significantly different ($P \leq 0.05$) in the analysis of variance. HSD-values for the infection efficiency spore population mean differences were reported only at the 0.01 probability level to ensure that no false differences were detected. Only the values of the combined means were tested for significant differences because the SPOP x LF interaction was not statistically significant ($p=0.01$) for infection efficiency, first latent period, or mid latent period. All analyses were done on a Samsung personal computer using the SAS statistics package (SAS Statistics Institute, Inc.) (18).

Results

A significant difference between leaves was found for each trait examined (Table 1.1). On the average, the spore populations exhibited 25% higher infection efficiency, 3 % shorter first latent periods, and 4% shorter mid latent period on the upper leaves than the lower leaves. This could be because the upper leaves were more susceptible, or more likely it was because the lower leaves were often more chlorotic or necrotic. The SPOP x LF interaction term however, was not significant for any of the traits examined. Thus, HSD-values were calculated only for the bulked means.

The cultivar effect was significant at $P \leq 0.05$ for all three traits measured, indicating that the cultivars differed in their level of resistance to leaf rust. The spore population effect, which indicates the influence of the source cultivar on the aggressiveness of the pathogen, was significant at $P \leq 0.01$ for infection efficiency. The spore population effect was also significant at $P < 0.05$ for first latent period in two growth chambers and in one growth chamber for mid latent period. The influence of source cultivar on infection efficiency of the pathogen was considerable, with infection efficiency increasing four-fold from the least to the most favorable source (Table 1.1). There was no evidence of the pathogen being more

aggressive on the cultivar from which it was isolated (Table 1.1-1.3), and the own vs. other contrast was not significant for any trait.

The importance of spore population x cultivar interactions depended on the trait measured. For infection efficiency, there were only minor changes in the ranking of the cultivars depending on the spore population used (Table 1.1). Consequently, the spore population x cultivar interaction was not statistically significant. With both measurements of latent period, the interactions were much larger. For example, with first latent period, the cultivar MO is ranked as least resistant with spore population h, but most resistant with populations mo and w (Table 1.2). The ranking of the cultivars varied among growth chambers as well as with different spore populations (Table 1.2-1.3).

Discussion

The own vs. other contrast in this experiment was not significant for any of the traits measured. There were also no individual cases where pathogen populations were statistically more aggressive on their own cultivar than on any other cultivar (Table 1.1-1.3). Previous studies have revealed several instances where pathogen populations were more aggressive on the cultivar from which they were originally isolated (4,5,6,9,13), but there are a few studies which had results similar to ours (8,16,19).

Significant pathogen x cultivar interactions have been seen in several studies (2,6,11,12,16,17,19), including interactions between races of leaf rust and winter wheat cultivars (14). Increased aggressiveness for pathogens on their own cultivars can cause a statistically significant interaction term. In other cases, significant interaction terms can arise with no evidence of increased aggressiveness on the own cultivars, as was the case in our study.

The effect of the source cultivars on population aggressiveness was evidenced by the significant differences between the spore populations. There are two possible explanations for this result. One is that the source cultivars had different selective effects on the pathogen in the field. This would alter the composition of the populations collected from the field. Holub (7) found such

selectivity in an experiment on Aphanomyces euteiches. He observed that if pea (Pisum sativum) was used as the baiting host, isolates of A.euteiches retrieved were more aggressive on pea. However, when other species were used as the baiting host no differences in aggressiveness were observed. Holub (7) suggested that pea plants may have been more resistant than the other species and so selected only those isolates that were aggressive on pea.

Another explanation for the significant spore population effects in our study is that the populations we collected arose from immigration into the fields of genetically different isolates that maintained a degree of physical isolation within the fields. Thus, genetically different pathogen populations would be increasing in different plots.

We can not distinguish which, if any, of the above explanations are responsible for our results. However, either mechanism would be of great importance to the conduct of resistance screening trials and other field experiments. Our results indicate that pathogen populations originating from natural inoculum are much less uniform than is often assumed. Thus, host genotypes grown in the field may be tested with pathogen genotypes that differ considerably in their degree of aggressiveness.

Table 1.1. Infection efficiency values (lesions per cm^2 of leaf) for the combined (upper and lower) leaf data from inoculation of five *Puccinia recondita* populations collected from five different wheat cultivars in the field on the same five cultivars in growth chambers

	Spore Population (Source Cultivar)				
Cultivar	b	h	m	mo	w
B	7.83	12.33	21.98	35.16	20.97
H	7.88	3.71	19.36	24.24	16.55
M	8.54	8.74	16.95	33.80	32.90
MO	17.19	19.16	23.01	44.93	27.89
W	0.98	4.94	9.65	24.47	23.84
Spore Population Mean[a]	8.49	9.77	18.19	32.52	24.43

[a]Tukey's honestly significant difference (HSD) value for the spore population mean at the 0.01 probability level = 6.923

Table 1.2. First latent period values (time from inoculation to first spore production) for combined leaf data from four growth chambers (GC) resulting from inoculation of five Puccinia recondita populations collected from five different wheat cultivars in the field onto the same five cultivars

		Spore Populations				
Cvar	GC	b	h	m	mo	w
B	1	171.5	167.9	162.3	171.5	178.3
	2[a]	188.3	181.8	192.0	192.0	193.5
	3	169.6	156.6	152.7	156.7	151.0
	4	156.3	179.3	169.2	168.4	-
H	1	168.0	187.6	159.5	160.0	189.5
	2	200.8	171.5	184.9	158.3	180.0
	3	146.6	161.9	149.2	147.5	151.0
	4	171.5	153.1	166.3	169.2	-
M	1	175.0	187.7	159.5	165.2	164.7
	2	187.7	177.2	192.0	161.3	181.8
	3	167.6	173.1	169.1	159.5	173.1
	4	188.6	195.5	170.3	162.3	-
MO	1	175.5	165.1	160.7	192.7	178.3
	2	182.3	168.0	180.0	187.0	190.3
	3	146.3	162.4	162.9	146.3	159.5
	4	198.7	168.0	182.3	175.5	-
W	1	168.0	184.3	168.7	164.7	168.4
	2	197.5	181.2	203.3	173.2	175.5
	3	184.4	172.7	175.0	170.1	156.0
	4	183.5	191.3	172.7	168.0	-
Spore Population Mean[b]						
	1	171.6	178.5	162.1	170.8	175.9
	2	191.3	175.9	190.4	174.3	184.2
	3	162.9	165.3	161.8	156.0	158.1
	4	179.7	177.4	172.2	168.7	-

[a] Tukey's honestly significant difference (HSD) value for the spore population * cultivar interaction term for GC 2 at the 0.05 and 0.01 probability levels = 5.2, and 5.9 respectively. The SPOP * CVAR interaction terms for GC 1, GC 3, and GC 4 were not significant at the 0.05 level in the analysis of variance.

[b] HSD-values for the spore population mean at the 0.05 and 0.01 probability levels for GC 1 = 13.44 and 16.15, and for GC 2 = 8.8, and 10.7. The spore population effects for GC 3, and GC4 were not significant at the 0.05 level in the analysis of variance.

Table 1.3. Mid latent period values (time from inoculation until the median pustule begins to sporulate) for combined leaf data from four growth chambers (GC) resulting from inoculation of five populations of Puccinia recondita collected from five different wheat cultivars in the field onto the same five cultivars

		Spore Populations				
Cvar	GC	b	h	m	mo	w
B	1	192.7	183.1	204.5	205.0	201.5
	2[a]	199.9	208.0	200.5	203.5	199.0
	3	189.5	192.3	174.1	183.5	190.5
	4	184.6	204.3	193.2	205.6	-
H	1	174.3	185.9	207.7	193.8	213.0
	2	197.7	190.5	194.1	187.7	191.2
	3	164.7	160.9	148.5	162.7	153.5
	4	189.5	180.6	185.7	177.6	-
M	1	185.4	196.7	188.2	197.8	202.5
	2	194.6	194.2	189.0	192.0	194.5
	3	174.1	189.1	180.1	179.5	176.6
	4	206.7	227.8	197.8	193.7	-
MO	1	200.7	185.3	200.7	239.0	208.8
	2	190.2	190.7	201.8	208.3	214.3
	3	164.0	171.3	174.2	177.5	193.0
	4	196.3	190.8	210.8	208.5	-
W	1	178.0	191.3	191.0	182.5	186.4
	2	200.1	193.5	216.3	195.5	197.8
	3	196.8	174.3	178.8	183.8	173.5
	4	218.1	209.8	187.8	178.5	-
Spore Population Mean[b]						
	1	186.2	188.5	198.4	203.6	202.4
	2	196.5	195.4	200.3	197.4	199.4
	3	177.8	177.6	171.1	177.4	177.4
	4	199.0	202.6	195.1	192.8	-

[a] Tukey's honestly significant difference (HSD) values for the SPOP * CVAR interaction term for GC 2 at the 0.05 and 0.01 probability levels = 4.9, and 5.7 respectively. The SPOP * CVAR interaction terms for GC 1, GC 3, and GC 4 were not significant at the 0.05 level in the analysis of variance.

[b] THe HSD-values for the spore population means at the 0.05 and 0.01 probability levels for GC 1 = 16.0, and 19.2 respectively. The spore population terms for GC 2, GC 3, and GC 4 were not significantly different at the 0.05 level in the analysis of variance.

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Chapter Two:

Mixing Ability Analysis of Wheat Cultivar Mixtures under Diseased and Non-diseased Conditions*

E. A. Knott[1], and C. C. Mundt[2]

[1] Graduate Student Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902. USA.

[2] Assistant Professor 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 severity data for two-way mixtures among either four or five club wheat 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 their 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 which were statistically better "mixers" than the others. Some of the significant effects were probably due to the use of cultivars which differed in height and stripe rust resistance, but for other combinations there was no apparent explanation for enhanced 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 (12,19), stabilize yields (16,20), and reduce selection for complex races of pathogens (3,10,11,19). Instances of mixtures yielding more than the average of the pure stand yields of the lines involved have been recorded for several crop species (13,17,19). Mundt et al (13) found that mixtures of certain club wheat (Triticum aesitivum E.M. Thell.) 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 (17,19), and mixtures may perform equal to, better, or worse than the mean of the components grown in pure stands (2,6,10,17). 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 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 by mixing cultivars in a 1:1 ratio in all possible two-way combinations.

Combining ability was divided by Sprague and Tatum (16) 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 (9) used model I method I of a combining ability analysis developed by Griffing (7) 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. (6) adapted method IV model I of Griffing (7) to estimate general blending ability (GBA) and an interaction term analogous to SCA of soybean (Glycine max) cultivars.

Gizlice et al. (6) 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. (4) for use in mixtures and to others suggested by Gardner and Eberhardt (5) 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 (13). 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 2.1). The experiments were carried out at three locations in Oregon that differ in average annual rainfall; Corvallis (1064 mm/yr), Moro (321 mm/yr), and Pendleton (554 mm/yr). 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.

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 (7) 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.(6)], 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 (7) 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

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

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 in, 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 calculated 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. (4), and Gizlice et al. (6) was followed to divide general mixing ability 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. (6), 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. (6). Genotype performing ability describes the performance of mixture components in pure stand, in terms of ability to yield and

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:

$$\hat{Y}_{ij} = u + GPA_i + GPA_j + TGMA_i + TGMA_j + SMA_{ij} + e_{ij}$$

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 2.2). 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 2.2).

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 2.3). 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 vs. specific mixing ability 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 2.4).

The cultivar Tyee (Y) had the highest TGMA for yield and GLA over all treatments and locations, with positive estimates in all cases. Overall the cultivar Jackmar (J) had the lowest TGMA, with negative estimates in seven out 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 (Table 2.4-2.7) 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 2.4).

The 1987 mixtures also differed significantly for SMA (Table 2.5-2.7). Specific mixing ability estimates for each treatment and location were also ranked (Table 2.8). 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 2.8) 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 describe 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, 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 diseased conditions. With the former mixture, the high yield was due mostly to a high GPA effect for both cultivars (Table 2.6). With the latter mixture, however, high yield was due to high combined TGMA and SMA effects (Table 2.6)

Discussion

In this study, as in other studies on combining ability in mixtures (2,4,6,9,15), 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 when 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. Significant 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 (2,8). The dwarf:dwarf combination should have higher yields and positive SMA estimates (2,8). In our study, the tall:dwarf mixture JM had consistently low SMA-values and low yields. However MR, a tall:semi-dwarf pair, had high SMA-values and high yields in the fungicide-treated experiments. The semi-dwarf:semi-dwarf 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 2.1, 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 is apparently not the only factor affecting the ability of a mixture to resist disease.

The significant SMA mean squares for yield in the inoculated plots can not 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 2.7). 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 can not 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 (1,14,18). 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 can not tell what the end composition of a mixture is, and thus can not explain the dynamics of the component interactions.

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Table 2.1. 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	mr	r
Tyee(Y)	semi-dwarf	r	s

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

Table 2.2. 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	Pr > F Genotype	Pr > F GMA	Pr > F 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 2.3. 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	Pr > F Genotype	Pr > F GMA	Pr > F 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.

Table 2.4. 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]

Table 2.4 (continued)

	Cultivars					FPLSD[b]
	Faro(F)	Jackmar(J)	Moro(M)	Tres(R)	Tyee(Y)	values
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.

Table 2.5. 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 2.5. (continued)

Mixture[a]	Yield (kg/plot)	GPA[b]	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.

Table 2.6. 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

Table 2.6. (continued)

Mixture[a]	Yield (kg/plot)	GPA[b]	TGMA[b]	SMA[c]	TME[d]	TP[e]
			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 cultivas 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.

Table 2.7. 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 2.7 (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.

Table 2.8. 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.

	Fungicide Yield			Inoculated Yield			Green Leaf Areaa		
Mixture	C	M	P	C	M	P	C	M	P
FJ	3	2	4	1,2	*8	3	5	*6	1
FM	*7	5	6	*8	1	6	*6	1	*8
FR	*8	*10	*8	*6,*5	*10	*9	*7	*9	*10
FY	5	4	3	*7	3	5	3	*7	3
JM	*10	*9	*10	3	*7	*7	2	*10	*7
JR	*6	6	5	*10	2	*8	4	2	4
JY	2	*7	2	*9	6	4	*10	3	*9
MR	1	1	1	*6,*5	4	1	*8	5	2
MY	4	*8	*7	4	*9	*10	*7	4	5
RY	*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.
* SMA-values are negative.

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