

AN ABSTRACT OF THE THESIS OF

Maria Renate Finckh for the degree of Doctor of Philosophy  
in Botany and Plant Pathology presented on October 25, 1991

Title: Interactive Effects of Stripe Rust and Plant  
Competition in Heterogeneous Wheat Populations

Abstract approved: \_\_\_\_\_ Redacted for Privacy \_\_\_\_\_  
Christopher C. Mundt

Disease has been implied as an important selective force acting in plant populations. This study was conducted to determine the effects of stripe rust (Puccinia striiformis) on the population dynamics of wheat (Triticum aestivum) cultivar mixtures.

Five wheat cultivars were grown in pure stands and all possible mixtures at three and two locations in 1987 and 1988, respectively. In 1989, four replacement series and their component pure stands were grown in two locations. All treatments were exposed to or protected from two stripe rust races. Disease severity and yield were determined on a per-cultivar basis for mixtures and also for pure stands.

In all but one mixture, disease severity relative to the pure stands was reduced between 6 and 97%. Disease severity changes could be separated into two effects: First, selection for the more resistant or susceptible genotype reduced or increased disease in mixtures as compared to their pure stands by up to 47 and 11%, respectively. Second, epidemiological effects of host diversity reduced disease severity on individual cultivars

below that of their pure stands. Disease severity on a genotype was often frequency-dependent. However, interactions among plant genotypes sometimes appeared to alter susceptibility and obscured the relationship. Non-diseased and diseased mixtures yielded 0 to 8% and 8 to 15% more than pure stands, respectively. Overall, mixture yields were more influenced by plant-plant interactions than by disease.

Population dynamics over time were studied by applying variable disease pressure to populations of four wheat cultivars for one-to-three generations in two locations. Fitnesses of genotypes were calculated by regressing the logit of a genotype's frequency on generation. Fitnesses were affected by disease and location and appeared constant over time. However, genotype frequency-changes were negatively correlated with planting frequencies, suggesting that fitnesses were frequency-dependent. Analysis of data from longer-term studies in the literature indicated that three generations may not have been sufficient to detect frequency-dependence. Stable equilibria may more likely exist for mixtures of genotypes that are closely related and adapted to the environment in which they are grown than for randomly selected genotypes.

Interactive Effects of Stripe Rust and  
Plant Competition in Heterogeneous  
Wheat Populations

by

Maria Renate Finckh

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Doctor of Philosophy

Completed October 25, 1991

Commencement June 1992

APPROVED:

Redacted for Privacy

Associate Professor of Botany and Plant Pathology in Charge  
of Major

Redacted for Privacy

Head of the Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented October 25, 1991

Typed and formatted for M. R. Finckh by M. R. Finckh



## ACKNOWLEDGEMENTS

I would like to express my gratitude to all the people who throughout the last five years with their love and patience have enabled me to complete this work.

Chris Mundt has guided me along a sometimes rocky and once even a fiery road. He has taught me so much about myself and it is for his support that I always found back to my original motivation for my work. Without his encouragement I would not have been able to finish.

Laura Brophy has been the soul and organizer in our lab throughout the years. She taught me how to organize field work and helped me to suppress and get over major emotional, computer, and other crises. Even during her absence she made sure I knew how to tend the combine harvester.

Many people have spent uncountable hours in the field, on the road and in the lab taking notes, sickling down wheat, running after the combine harvester in the heat and cold of eastern Oregon, threshing, counting, weighing, planting, and proof-reading data: Chris Mundt, Laura Brophy, Libby Bailey, Bettina Falk, Aihong Pan, four high school students from Moro, Oregon and one of their uncles, Elizabeth Knott, Mark Boudreau, Steve Booth, Deborah Clark, Helle Madsen, Erling Johnson, Yuqi Zhao, Larae Wallace, John Spangler, Robin Cochran, and my parents.

None of the field experiments would have been possible

without the support from the field staff at the experiment stations in Moro, Pendleton, and Corvallis, the generosity of Dr. Warren Kronstad, Dept. of Soils and Crop Science, Oregon State University, and his research staff, and the cooperation of Dr. Richard Smiley, Superintendent of the Columbia Basin Agricultural Experiment Stations. People at the Oregon State University seed lab have saved me many hours by making me aware of the phenol staining procedure.

Some of the most exciting parts of my work were made possible by a Hartley Corporation Fellowship granted by Sigma Delta Epsilon, Graduate Women in Science association. I would like to express my gratitude to this organization.

Quite a few roommates and friends have put up with me and still want to be my friends. My special thanks go to Carolee Bull who always fed and petted Katze during my so many trips and put up with his fleas and my moods and to Susanne Finckh who cared for me when months of computer work took their revenge on me. Jacqueline Frizenschaf and Jeff Connor have helped me through some of the hardest times in the past five years and they let me borrow their son Yann for our special Müsli breakfasts so I would not forget that there are other things in life but wheat and stripe rust.

My final thanks go to my parents to whom I would like to dedicate this thesis. Through them I learned to appreciate and love nature and books, which have been the two most important ingredients in my life.

## Table of Contents

	<u>Page</u>
I. Literature Review.....	1
Introduction.....	1
Effects of Host genetic diversity on disease....	4
A. Population Interactions.....	4
B. Considerations Regarding Disease Control...	8
Effects of Genetic diversity on Crop Yield.....	13
Plant Interactions in Mixtures.....	18
The Role of Pathogens in Diverse Systems.....	20
Effects of Disease on Plant-Plant Interactions.	28
Questions yet to be Addressed.....	32
Literature Cited.....	39
II. Effects of Plant Competition on Stripe Rust in Wheat Cultivar Mixtures.....	49
Abstract.....	50
Introduction.....	52
Materials and Methods.....	55
Results.....	62
Discussion.....	66
Literature Cited.....	78
III. Effects of Stripe Rust and Plant Competition on Yield of Wheat Cultivar Mixtures.....	81
Abstract.....	82
Introduction.....	83
Materials and Methods.....	86
Results.....	90
Discussion.....	98
Literature Cited.....	119
IV. Plant Competition and Disease in Genetically Diverse Wheat Populations.....	122
Abstract.....	123
Introduction.....	124
Materials and Methods.....	127
Results.....	134
Discussion.....	142
Literature Cited.....	161
V. Effects of Stripe Rust on the Evolution of Genetically Diverse Wheat Populations.....	166
Abstract.....	167
Introduction.....	169
Materials and Methods.....	172
Results.....	180
Discussion.....	185
Literature Cited.....	210
VI. Bibliography.....	215

## List of Figures

<u>Figure</u>	<u>Page</u>
I.1 Models for the outcome of hypothetical mixtures of species or genotypes in replacement series.....	36
I.2 Model for the yield of different species or genotypes differentially susceptible to a pathogen in the presence of the pathogen. The susceptible genotype S is superior in competitive ability to the resistant genotype R in the absence of disease. S and R have slightly different niches....	37
I.3 Model for the yield of different species or genotypes differentially susceptible to a pathogen in the presence of the pathogen. The susceptible genotype S is inferior in competitive ability to the resistant genotype R in the absence of disease. S and R have slightly different niches....	38
III.1 Correlation of the yield relative to their pure stands of the wheat cultivars Faro, Jacmar, Moro, tres, and Tyee when grown in two-way mixtures in three locations in 1987 and in two locations in 1988 in the presence and absence of disease.....	117
IV.1 Seed yield (g/minipplot) of wheat genotypes Jacmar and Moro in replacement series experiments with Tres in two sites, Moro and Pendelton.....	157
IV.2 Seed yield (g/minipplot) of wheat genotypes Jacmar and Moro in replacement series experiments with Tyee in two sites, Moro and Pendelton.....	159
V.1 Dynamics of populations composed of four wheat genotypes over three generations in two locations..	203
V.2 Rates of change in frequency of four wheat genotypes grown in mixed populations at two locations for three generations.....	205
V.3 Frequency changes of four wheat genotypes grown in mixed populations in two locations versus their planted frequencies.....	207
V.4 Types of curves resulting from plotting logits of the frequencies (p), $(\ln[p/(1-p)])$ versus the number of generations for data from the literature.	209

## List of Tables

<u>Table</u>	<u>Page</u>
II.1 Wheat cultivars used in field experiments and their chaff colors, heights, and reactions to two stripe rust races.....	70
II.2 Wheat populations studied in cultivar mixture experiments in the field in 1986/87 and 1987/88....	71
II.3 Severity of stripe rust of wheat in pure stands and mixtures and percent reduction in disease severity due to mixing at three locations in 1987 and two locations in 1988.....	72
II.4 Severity of stripe rust in two-way mixtures of wheat cultivars on a per-cultivar basis, on whole plots, or as percent reduction relative to pure stands, and subdivision of percent reduction into selection and epidemiological effects in 1987 and 1988.....	74
II.5 Number of tillers per plot for wheat cultivars grown in pure stands in the presence and absence of stripe rust in field experiments at three locations in 1987 and at two locations in 1988.....	76
II.6 Tiller frequencies <sup>a</sup> of wheat cultivars grown in mixtures in presence and absence of stripe rust in three locations in 1987 and in two locations in 1988.....	77
III.1 Wheat cultivars used in field experiments and their chaff colors, heights, and reactions to two stripe rust races.....	104
III.2 Disease severity, yield, and yield components of five wheat cultivars grown as pure lines in the presence and absence of stripe rust in three locations in 1987 and two locations in 1988.....	105
III.3 Yield of wheat cultivar mixtures relative to the mean of the mixture components in pure stands in the presence and absence of stripe rust in three locations in 1987 and in two locations in 1988....	107
III.4 Yield and yield components for wheat cultivar mixtures and their pure stands in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust.....	109

## List of Tables (continued)

<u>Table</u>	<u>Page</u>
III.5 Relative yield <sup>a</sup> of the wheat cultivars Faro, Jacmar, Moro, Tres, and Tyee when grown in mixtures <sup>b</sup> in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust.....	112
III.6 Yield components of five wheat cultivars grown in two-way mixtures in the presence of stripe rust in three locations in 1987 and two locations in 1988..	113
III.7 Yield components of five wheat cultivars grown in two-way mixtures in the absence of stripe rust in three locations in 1987 and two locations in 1988..	115
IV.1 Wheat genotypes used in field experiments and their chaff colors, heights, and reactions to two stripe rust races.....	146
IV.2 Pure stands and mixtures of wheat genotypes studied in the presence and absence of stripe rust at two locations.....	147
IV.3 Severity of stripe rust of wheat in pure stands and in two-way mixtures, percent reduction relative to pure stands, and subdivision of percent reduction into selection and epidemiological effects in two locations.....	148
IV.4 Coefficients of determination ( $r^2$ ) and significance of slopes (P) for regressions of frequency of genotypes in mixtures on stripe rust severity for wheat genotypes grown in replacement series in two locations.....	151
IV.5 Seed yield, number of heads, number of seed per head, and mean weight per seed for wheat genotypes grown as pure lines in the presence and absence of stripe rust in two locations.....	152
IV.6 Seed yield of miniplots of wheat genotype mixtures and their components relative to their fungicide-treated pure stands at two locations.....	153
IV.7 Coefficients of determination ( $r^2$ ) and significance of slopes (P-values) for regressions of stripe rust severity on seed yield of wheat genotypes in replacement series.....	155

## List of Tables (continued)

<u>Table</u>	<u>Page</u>
IV.8 Seed yield of single wheat genotypes relative to their fungicide-treated pure stands in replacement series in the presence and absence of stripe rust in two locations.....	156
V.1 Wheat varieties used to create mixed populations, their chaff colors, heights, reactions to two stripe rust races, and reactions to a phenol stain.	194
V.2 Mixed populations of the wheat varieties Faro, Jacmar, Tres, and Tyee grown in Pendleton and Moro in three winter wheat seasons.....	195
V.3 Disease severity of whole plots and on single tillers in pure stands and in mixed populations of four wheat genotypes in two locations and three years.....	196
V.4 Disease severity on four wheat varieties in pure stands and when grown in mixtures based on single tiller assessments in two locations in 1989.....	197
V.5 Yield per miniplot and 1000 seed weight of four wheat varieties in pure stands in two locations and three years.....	198
V.6 Genotype seed frequencies in populations composed of four wheat varieties that were continuously exposed to stripe rust, continuously protected from stripe rust, or exposed and protected in alternating seasons for one-to-three generations in two locations.....	199
V.7 Statistics for regressions of frequency change on the planted frequency and the predicted equilibrium frequencies of four wheat varieties in mixed populations that were either exposed to or protected from stripe rust for one-to-three generations at two locations.....	201
V.8 Analysis of data from published papers on population dynamics in small grain mixtures using Leonard's (1969, 1977) model to determine individual relative fitnesses.....	202

# INTERACTIVE EFFECTS OF STRIPE RUST AND PLANT COMPETITION IN HETEROGENEOUS WHEAT POPULATIONS

## I. Literature Review

### Introduction

Early breeding for resistance to plant pathogens relied heavily on the use of simply inherited, race-specific resistance (Johnson, 1961). The hope that such resistance would end devastating epidemics was soon disappointed, however. Often, new pathogen races were selected that were virulent on previously resistant varieties soon after these varieties became popular and occupied large areas (Adams et al., 1971; Johnson, 1961; Vanderplank, 1963). This vicious circle of incorporation of new resistance and subsequent defeat by newly emerging pathogen races has been referred to by plant scientists as the "boom and bust cycle" (e. g., Wolfe, 1973).

Genetic uniformity in crops has been identified as the cause of many devastating epidemics in the past. Irish potato (Solanum tuberosum) production in the first half of the 19<sup>th</sup> century relied mainly on the variety "Lumper" which was highly susceptible to late blight (caused by Phytophthora infestans). An outbreak of late blight in 1846/47 practically destroyed the potato crop which led to the starvation of two million people and the mass emigration of another two million from Ireland (Adams et al., 1971; Harlan, 1972). Victoria blight of oats (Avena



sativa) which is caused by the fungus Cochliobolus victorii) increased to epidemic proportions in the late 1930s because 97% of the oat growing region in Iowa was planted to popular blight susceptible oat lines that were derived from the cultivar Victoria (Adams et al., 1971; Browning et al., 1969).

Other examples include the wheat (Triticum aestivum) stem rust (Puccinia graminis f. sp. tritici) epidemics in the 1930s and 1950s. Those epidemics were caused by race 56 and race 15B, respectively, which were highly virulent on the wheat varieties that were predominantly grown at those times (Adams et al., 1971; Johnson, 1961; Vanderplank, 1963); southern corn (Zea mays) leaf blight in 1970/71 (caused by Cochliobolus carbonum), which resulted in extensive damage on the almost exclusively grown, cytoplasmatically uniform hybrid corn varieties of the time (Adams et al., 1971; Harlan, 1972; Ullstrup, 1972); and Black Sigatoka (caused by Mycosphaerella musicola) and Panama disease (caused by Fusarium oxysporum) on banana (Musa spp.) (Harlan, 1972).

In the 1940's Stevens (1942) and Stakman (1947) called attention to the tremendous potential for variation in pathogen populations. Flor (1953) later revealed the close interrelation between the resistance gene composition of flax (Linum usitatissimum) and the virulence gene composition of flax rust (Melampsora lini). Over the

twenty years that a race survey had been carried out, he found that the prevalence of different races of the rust was largely determined by the resistances carried by the main flax varieties that were grown . The gene-for-gene hypothesis (Flor 1956) provided an explanation for the boom and bust cycles. Flor hypothesized that during the coevolution of the rust and the host complementary genic systems in host and parasite had evolved, and that for each gene controlling resistance / susceptibility in the host there is a corresponding gene controlling avirulence / virulence in the pathogen. The resistance genes in the host were found to be dominant multiple alleles of several loci whereas the virulence genes in the rust were recessive and not allelic.

The findings described above made it clear that alternative approaches to the wide and uniform use of race specific resistances to control disease were necessary. Flor (1956) proposed the use of resistance gene combinations in the hosts to decrease the probability of a new pathogen race occurring. The use of polygenically inherited resistances that appear to be race-nonspecific is thought by many scientists to be more stable than race-specific resistance (Vanderplank, 1968). However, race non-specific resistance is not always available and it is often very difficult to identify and incorporate into a crop (Johnson, 1984; Leonard and Mundt, 1984; Vanderplank,

1968). Linkage to undesirable agronomic traits in many cases may make it difficult or impossible to use them.

## **Effects of host genetic diversity on disease**

### **A Population Interactions**

All of the resistance approaches described above are designed to be used in genetically uniform host populations. Before the rediscovery of the Mendelian laws of inheritance visual uniformity of crop plants was obtained by phenotypic selection within local populations of plants. This resulted in landraces that were adapted to the particular region in the which they had been selected (Harlan, 1972, 1975; Marshall, 1977). Where landraces are still grown today they appear highly diverse for disease resistance (van Leur, 1989). Selection and propagation of single plants of self-pollinated crops, the development of hybrids, and the wide scale distribution of a small number of new varieties greatly increased the genetic uniformity of many crops (Anonymous, 1972; Barrett, 1981; Frey et al., 1973; Harlan, 1972; Marshall, 1977; Mooney, 1979).

This change from heterogeneous crops to genetically uniform ones that are grown over much larger areas than the old landraces had a marked effect upon the environment for pathogens. Johnson (1961) described the "man-guided evolution in plant rusts", and stated that changes in

pathogenicity of rusts "can be causally related to the man-made modifications of their hosts". Johnson et al. (1967) found that the cereal rusts had changed their racial composition from a large number of "standard races" in earlier epidemics towards one or a group of related races that have overcome the predominantly used resistance genes.

The direct, strong, and mutual influence of host and pathogen genetic composition has long been recognized in agroecosystems (Flor, 1953; Frey et al., 1973; Harlan, 1976; Johnson, 1961; Johnson et al. 1967; Kilen and Keeling, 1990; Leonard, 1977; Leonard and Czocho, 1980; McDonald et al., 1989; Person, 1966; Stakman, 1947; Stevens, 1942; Wolfe, 1973; Wolfe and Barrett, 1977, 1980; Young and Hartwig, 1988). However, agroecosystems are strongly influenced by humans and the influence of pathogens on the genetic composition of the host population usually is altered or eliminated by replanting the crop from an independent seed source every year, thus preventing coevolution between hosts and pathogens.

In contrast to agroecosystems, there is usually a high degree of interspecific and intraspecific variability in natural ecosystems. Also, the biotic and abiotic environment is more diverse, the spatial distribution of plants is usually more irregular, and the process of coevolution is functioning (Alexander, 1988; Anikster and Wahl, 1979; Browning, 1974; Harlan, 1976; Mundt and

Browning, 1985a). Because of those differences, it appears to be more difficult to study genetic interactions between pathogens and their hosts in natural ecosystems. For example, Manisterski (1987) surveyed the race composition of oat stem rust (Puccinia graminis f.sp. avenae) on wild oats (Avena sterilis) in their natural habitats in Israel for six years. Shifts in race composition of the rust population were pronounced but, in contrast to the studies in agroecosystems, could not be related to shifts in the resistance gene composition of the host.

At least three factors have contributed to the difference between agricultural systems and the natural ecosystem studied by Manisterski (1987). First, shifts in host genetic composition that occur in agriculture due to human influence are much more drastic than occur in natural ecosystems during equivalent periods of time. Thus, changes in the host population would be expected to be small over the six years of Manisterski's (1987) survey. Second, host genetic diversity reduces disease severity (see part II B) and disease levels in natural ecosystems have been reported to be typically low (Antonovics and Levin, 1980; Borlaug, 1981; Burdon, 1978, 1982; Burdon and Shattock, 1980; Dinoor and Eshed, 1984) and epidemics to be rare or of short duration (Alexander, 1988). If in most seasons the disease pressure on the host population is small, the fitnesses of plant and pathogen may be

determined by independent factors. Therefore, genetic interactions between pathogen and host populations may be less pronounced and an effect of the pathogen genetic composition on the host population may not be detectable. Third, if environmental conditions are unfavorable for the pathogen, its population size may become small enough to allow random genetic drift to occur. Small population sizes may cause genetic drift only in some generations, but this drift is permanent and cumulative (Falconer, 1981).

By using a different methodology than Manisterski (1987), Wahl (1970) could show that there was an effect of oat crown rust (caused by Puccinia coronata) on the genetic composition of wild oats in Israel. He mapped the resistance gene composition of populations of wild oats to oat crown rust and the virulence gene composition of the respective crown rust populations in a number of different environments in Israel. In regions where environmental conditions are generally conducive to disease the number of resistance genes in the oat populations was greater than in regions where the disease plays only a minor role. Similar results were obtained by Burdon et al. (1983) and Oates et al. (1983) who surveyed Australian populations of wild oats and crown rust.

Disease problems in agriculture tend to worsen under human interference (Antonovics and Levin, 1980; Borlaug, 1981; Browning, 1974; Burdon, 1978; Wahl et al., 1985).

Epidemics in nature are often caused by the introduction of a pathogen into an area where the host had been evolving separately from the pathogen e.g. the Dutch elm (Ulmus americana) disease (caused by Ophiostoma ulmi) or chestnut (Castanea dentata) blight (caused by Endothia parasitica) (Stakman, 1947).

The observation of high diversity and the usual lack of epidemics in undisturbed systems led many workers to hypothesize that diversity is a "natural" means of disease control (Browning, 1974; Burdon, 1978; Burdon and Shattock, 1980; Dinoor and Eshed, 1984; Harlan, 1976). Alexander (1988), however, criticized this view since plant-pathogen interactions in natural systems have not been studied with critical experiments to determine if there might be factors besides diversity that contribute to disease control in natural systems. Leonard (1977) developed mathematical models of selection pressures on plant pathogens and their hosts. He concluded that, if there was a cost of virulence to the pathogen and a cost of resistance to the host, i. e., stabilizing selection (sensu Vanderplank, 1968) is acting, then "the establishment of mixed populations in balanced equilibrium with several genes for resistance and virulence is one way in which host species can minimize disease damage".

## **B Considerations Regarding Disease Control**

The recognition of the importance of population dynamics and the consideration of natural ecosystems has led to a new approach to plant disease management - the deployment of resistance genes in space and time. This strategy can be employed on a regional and local scale.

For regional deployment, host genotypes diverse for their resistances are planted in different fields or geographic areas. This is most useful against pathogens that are transported from areas where they overwinter or oversummer to areas where they usually cannot persist. In this case, an epidemic in the latter area is fully dependent on outside inoculum being introduced, e.g., by wind (Browning et al., 1969; Knott, 1972; Vanderplank, 1968). If the resistances in the host populations differ among the regions, then a pathogen race dispersed along its usual seasonal pathway will be stopped when encountering only resistant hosts in an area. However, if inoculum virulent on the hosts grown in a region can persist in that region the strategy will fail (Vanderplank, 1963). Vanderplank proposed a gene deployment strategy for potato late blight (Vanderplank 1963) and for wheat stem rust in North America (Vanderplank, 1968). Gene deployment strategies have been suggested for the breaking of the "Puccinia path" of oat crown rust (caused by Puccinia coronata) in the central United States (Browning et al. 1969) and wheat stem rust (Knott, 1972) and to control



barley (Hordeum vulgare) powdery mildew (caused by Erysiphe graminis) in the UK (Wolfe and Barrett, 1977).

Intrafield diversification as a means of disease control was first promoted by Jensen (1952) and Borlaug (1959) who proposed multiline varieties for the control of small grain rusts. Jensen's (1952) proposed multiline was a selection of pure lines of oats that were similar for important agronomic traits so they could be grown together but which possessed genetic diversity for reaction to abiotic and biotic stresses, including disease. In contrast, Borlaug (1959) promoted the development of near-isogenic lines (NIL) diverse for reaction to rust diseases of wheat but homogeneous for their remaining genetic background.

Several mechanisms have been suggested to contribute to disease reduction in diverse host populations: (1) a reduction of host tissue susceptible to each pathogen race; (2) an increased distance between host plants possessing the same resistances; (3) pathogen spread is inhibited by resistant plants that function as barriers; (4) pathogens non-virulent on a host genotype may sometimes induce resistance reactions that work against virulent races; and (5) interactions among pathogen races (e.g., competition for available host tissue) may reduce disease severity. These mechanisms have been studied and discussed by a number of authors (Barrett, 1978; Browning and Frey, 1969;

Burdon, 1978; Chin and Wolfe, 1984; Leonard, 1969 a,b,c; Mundt and Browning, 1985a,b; Prakash and Heather, 1988; Van der Plank, 1968; Wolfe, 1973, 1978, 1985).

More recently, attention has turned to the use of cultivar mixtures to attain disease control. There are several advantages to the use of cultivar mixtures over multilines. 1) A cultivar mixture is quicker and cheaper to synthesize than a multiline (Wolfe, 1973; Wolfe and Barrett, 1977; Frey, 1982). 2) The different mixture components are likely to possess, in addition to the race-specific resistance genes different race non-specific resistances which may provide additional disease control (Wolfe 1973, 1978; Wolfe and Barrett, 1977). 3) Selection exerted by the different host genetic backgrounds may hinder the development of a superrace (a race virulent on all host components in the mixture). For example, Chin and Wolfe (1984) found that disruptive selection exerted by different barley (Hordeum vulgare) cultivars containing the same race-specific resistance could further split races of barley powdery mildew (caused by Erysiphe graminis f.sp. hordei) into subraces that are differentially adapted to the genetic background of the barley lines. 4) Heterogeneity in genetic background could provide resistance to non-target diseases (Wolfe 1978, Wolfe and Barrett 1980) and an increase in capacity of the crop to buffer against other environmental variables (Allard,

1960, 1969; Grafius, 1966; Jensen, 1952; Wolfe, 1978; Wolfe and Barrett, 1980).

Merely diversifying a crop for resistance does not transform it into a host population capable of "taking care of itself" (sensu Stevens 1942). The close interrelation between the host and the pathogen population dynamics have to be taken into account. In order to obtain durable disease control, a balanced host-pathogen relationship is needed (Harlan, 1976). Such a balanced polymorphism in a mixed host population requires that the host genotypes are represented in precise frequencies (Leonard and Czochoz, 1980).

Since the coevolution of hosts and pathogens is very much restricted in agricultural systems (Alexander, 1988; Harlan, 1976; Mundt and Browning, 1985a) stability has to be achieved by creating functional diversity (Mundt and Browning 1985a). Some researchers feel that "effective diversity needs to be ... molded by selection pressure of the parasite under specific environmental conditions" (Wahl et al., 1985) and that "the optimum evolutionary strategy may be development, within local populations, of complementary patterns of genetic variation for resistance in the host and virulence in the pathogen" (McDonald et al., 1989). Alternatively, when consciously selecting resistance genes for deployment humans can freely change the resistance gene composition, e.g., by alternating use

of resistance genes in different years, or by using different mixtures in different areas to exert disruptive selection on the pathogen population (Browning and Frey, 1969; Mundt and Browning, 1985; Van der Plank, 1968; Wolfe, 1973; Wolfe and Barrett, 1977) and might thus prevent the build-up of "superraces" capable of attacking all of the host genotypes grown. It has also been proposed to use resistance gene combinations for which the matching virulence gene combination is linked to a negative effect on the survival of the pathogen (Wolfe, 1973). For barley powdery mildew and wheat leaf rust it has been shown that such virulence gene combinations exist (Browder and Eversmeyer, 1977; Wolfe and Barrett, 1977).

### **Effects of genetic diversity on crop yield**

Host heterogeneity affects not only disease but also yield. The effects of diversity on yield are not straight forward, however.

Competitive ability of a cultivar in a mixture and its yielding ability in pure stand are not necessarily correlated. For example, Suneson and Wiebe (1942) and Suneson (1949) found that competition among barley cultivars in mixtures lead to the practical extinction of some of the components. One of the components that decreased greatly in frequency had a significantly better

yield and leaf disease resistance record than any of the others when grown in pure stands. The outcome of competitive interactions among different genotypes is not always unexpected, however. If phenotypic differences (e.g. height) are pronounced, one will expect the shorter plants to suffer more from competition for light in mixtures than the taller plants, as for example in a mixture of morphologically very distinct varieties or genotypes of rice (Jennings and De Jesus, 1968; Jennings and Herrera, 1968).

Some plant breeders have argued that a successful crop ideotype, as a prerequisite for maximum yield, has to be a weak competitor (Donald, 1968; Hamblin, 1975) and will thus suffer from a better competitor in a mixture. Therefore Hamblin and Donald (1974) stated that the yield of a cereal genotype in a mixture should be negatively correlated to its yield in monoculture. The cereal genotypes that Hamblin and Donald (1974) referred to in their work were lines that had been selected in early generations from crosses and had therefore not been exposed to intergenotypic competition throughout the breeding and selection process.

Another approach to breeding has been developed in Davis, California with the barley composite crosses. For a composite cross a set of diverse varieties or lines is completely intercrossed, i.e., each line is crossed with

each of the other lines. The  $F_1$  combinations are then blended and grown as a bulked hybrid population for subsequent generations without conscious selection (Harlan, 1929; Suneson, 1956).

When selecting lines from the  $F_{24}$  of such a composite cross, Suneson (1956) found that nine out of ten lines tested were far superior in yield and test weight to Atlas 46, a widely grown commercial variety of the time, indicating that the superior genotypes in the bulked populations were also superior in pure stands.

Yield increases in genotype mixtures have frequently been reported (e.g. Allard, 1960; Allard and Adams, 1969; Borlaug, 1959; Jensen, 1952; Montgomery, 1912; Nitzsche and Hesselbach, 1983; Norrington-Davies et al., 1972; Wolfe, 1978; Wolfe et al., 1981). Such positive yield interactions could probably be at least partially explained by niche differentiation. Allelopathy and synergisms of unknown origin might also play a role in the performance of a mixture. Mixing genotypes at random does not always result in higher yield, however. For example, in an experiment with two-way mixtures of four different wheat varieties the yield in the mixtures was almost always lower than expected (Klages, 1936).

Such contrasting results of mixture experiments indicate that interactions among genotypes are complex. This was confirmed by Allard and Adams (1969) who found

that genotypes of a composite cross of barley that had not been exposed to conscious selection by humans over eighteen generations showed significantly higher positive yield synergisms when grown in mixtures than did a mixture of cultivars that had not coevolved. A parallel analysis of the effect of neighboring genotypes on each other led the authors to the conclusion that, in the composite cross, two types of selection had been acting: i) selection for good competitors, i.e. a genotype yields higher when bordered by another genotype than by itself, and ii) selection for good neighbors, i.e. a genotype induces a mean increase in yield when bordering the other genotype. It is the combination of good neighborhood effects and competitive ability that they refer to as "ecological combining ability". In an earlier experiment, Allard (1960) had obtained similar results indicating that the  $F_8$  of a two-way cross of lima beans that had not been subjected to any conscious selection had a higher relative yield than a mixture of 30  $F_4$  families, each derived by bulk propagation without conscious selection from single, randomly selected  $F_2$  plants of the same two-way cross.

As with disease control, functional diversity is necessary to obtain good ecological combining ability for yield. To achieve this, it seems most effective to expose populations to natural selection (Allard and Adams, 1969; Clay and Allard, 1969; Suneson, 1956). Another approach

has been taken by Knott and Mundt (1990) who borrowed combining ability analysis procedures from plant breeders and applied them to wheat cultivar mixtures with respect to yielding ability and disease control. Mixing ability analysis does not require the separation of the mixture components to evaluate their performance. Also, mixing ability estimates derived from two-way mixtures might be useful in predicting the performance of mixtures with more than two components. However, the analysis cannot predict the end composition of a mixture at harvest making it unsuitable for studying population dynamics over time (Knott and Mundt, 1990).

Mixtures of genotypes have mostly been studied either for their effect on disease (Barrett, 1978; Borlaug, 1959; Browning and Frey, 1969; Jensen, 1952; Leonard, 1969a; Leonard and Czocho, 1980; Mundt and Browning, 1985a,b; Mundt and Leonard, 1985; 1986a,b; Wolfe, 1978; Wolfe and Barrett, 1980; Wolfe et al., 1981; among others) or for their effect on yield (Allard, 1960; Allard and Adams, 1969; Clay and Allard, 1969; Frey and Maldonado, 1967; Nitzsche and Hesselbach, 1983; Norrington-Davies et al., 1972; Suneson, 1956). Of course, when studying one phenomenon the other was usually recognized by the researchers. For example, Wolfe (1978), in a trial with barley cultivar mixtures and powdery mildew, found a positive correlation between increase in yield of mixtures



and mildew severity at different sites. However, there is little or no data available that separates the contribution of disease control from other factors that influence the yield of mixtures.

### Plant interactions in mixtures

The yield of mixtures is usually evaluated by analyzing their overall performance (Allard, 1960; Borlaug, 1959; Jensen, 1952; Nitzsche and Hesselbach, 1983; Wolfe, 1978; e.g.). If a mixture yields higher than expected based on the average of the pure-stand yields of its components, the genotypes or species are said to have good ecological combining ability. In the studies cited thus far, mechanisms responsible for differential mixture performance have not been discussed.

When increasing plant density in a pure stand, there is a certain threshold density at which the yield per plant starts to decrease. At this point the plant starts to respond to the presence of its neighbors. Different species or genotypes have different threshold densities at which they start to interfere with each other (Antonovics and Levin, 1980; Firbank and Watkinson, 1985a,b; Harper, 1977).

Two different kinds of competition are acting in mixtures: intragenotypic and intergenotypic (Jolliffe et

al. 1984). Firbank and Watkinson (1985a) analyzed a mixture of Agrostemma githago and Triticum aestivum and found that, because of the different competitive abilities and different density response thresholds of the two species, Triticum plants responded to the average Agrostemma plant as if the latter were equivalent to 1.63 Triticum plants, while Agrostemma responded to the average Triticum plant as if it were 0.41 Agrostemma plants. Such unequal interference among species or genotypes has been referred to as asymmetric competition (Firbank and Watkinson, 1987; Thomas and Weiner, 1989).

The differentiation between intergenotypic and intragenotypic competition is important. If the average intragenotypic competition is greater than the average intergenotypic competition, the mixture will yield higher than the pure stand average. In Firbank and Watkinson's (1985a) experiment, one species suffered more from competition than the other. In an experiment with Secale cereale genotype mixtures, one genotype yielded higher than expected and the other lower (Norrington-Davies and Hutto, 1972). The competitive effects within mixtures were not compensatory, however, as the yield increase of the former genotype was higher than the decrease of the latter, resulting in a higher than expected overall yield. Hill et al. (1987) found considerable differences between intergenotypic and intragenotypic competition among

genotypes of perennial ryegrass (Lolium perenne).

If a mixture yields higher than expected this has to be due to the utilization of more resources or to the more efficient use of resources by the mixture than by the average of the pure stands. More resources can be exploited if there is some kind of niche differentiation among genotypes that results in the use of resources by one genotype that are not available to or not needed by the other.

Besides niche differentiation and differential competitive abilities, the components in mixtures might interact through allelopathy or other unknown mechanisms of positive or negative mutual effects (Allard, 1960; Allard and Adams, 1969). Fig. I.1 illustrates a number of possible outcomes of the yield composition of hypothetical two-way mixtures.

### The role of pathogens in diverse systems

Ecologists usually explain the coexistence of different species or genotypes by niche differentiation. The competitive exclusion principle was defined by Gause (1934, cited by Burdon and Shattock, 1980), who stated that "two similar species scarcely ever occupy similar niches". Experiments indicated that in the controlled environment of a greenhouse the inferior competitor should eventually be

exterminated (Chilvers and Brittain, 1972; Harper, 1977). In nature, however, there are species and genotypes coexisting that are different in competitive ability and seem to compete for essentially the same resources.

In an attempt to explain the coexistence of plant genotypes, Chilvers and Brittain (1972) published a simple model of how plant competition might be mediated in a frequency-dependent manner by host-specific pathogens. In this model, host A and B are attacked by pathogen a and b, respectively. Disease severity is positively correlated with host density. This leads to a balanced, cyclic increase and decrease of the host frequencies. As the more abundant host A is more severely attacked by its pathogen, it gets weakened and host B is favored and increases in frequency. Pathogen a will decrease as host A decreases in frequency which, in turn, will improve the competitive ability of A. Simultaneously, pathogen b is increasing as the frequency of B increases and the competitive ability of B is weakened. Eventually, A will become superior to B again, and start to increase in frequency, etc. If the competitive abilities of the hosts are similar, a four-component equilibrium will establish as described. If the competitive abilities are too divergent, however, the pathogen of the weaker competitor becomes negligible and a three-component equilibrium will establish.

Trenbath (1977) developed models of systems in which

one mixture component is susceptible and one is resistant. In these models, only one pathogen is influencing the competitive ability of the susceptible host. He tested the predictions of his models with data from the literature and found a good fit. He also developed a theoretical model that included two differentially susceptible hosts and their respective pathogens. The predictions were similar to those of Chilvers and Brittain's model, but Trenbath was not able to test the four-component model with experimental data.

Chilvers and Brittain (1972) and Trenbath (1977) did not distinguish between competitive ability and reproductive output (fitness) of an organism. Observations of the direct effects of disease on plant-plant interactions do not necessarily reveal all interactions in the system, however. For example, it seems that individuals of grasses, sedges, and rushes, that are parasitized by species of the Balansiae (Ascomycotina) are more vigorous than uninfected ones, however, the relation of infection to fecundity seems to be negative (Clay, 1984). Burdon (1982) classified the possible effects of disease on plants in mixtures into the effects on (a) reproduction, (b) competitive ability, and (c) on both.

Gates et al. (1986) analyzed mathematically the conditions under which an equilibrium can occur in plant mixtures in the presence of disease. In the model the

level of a host-specific disease is dependent on the host's frequency in the mixture. The frequency-dependence of disease levels causes the relative competitive abilities of plants to be also frequency-dependent.

In general, the model predicted what had been suggested by earlier ones (Chilvers and Brittain, 1972; Trenbath, 1977). However, the results of simulations suggested that an upward concave yield curve of the susceptible component in the presence of disease is not a sufficient condition by itself for long term stability of the system. The model predicts that a stable equilibrium in which two plant species or genotypes and their respective specific pathogen(s) coexist can only occur if a susceptible genotype at some disease level is still a superior competitor than the other genotype. This is possible if the plant-plant-pathogen interactions are dependent on the frequency of pathogen and host.

Frequency-dependent selection "leads to a stable equilibrium frequency and so to a balanced polymorphism" (Falconer, 1981). The type of frequency-dependent selection described by Falconer applies to systems in which the rarity of a genotype by itself enhances its survival ability. This can be seen for example in the self-incompatibility system in plants. The rarer genotype has a higher chance to reproduce.

In the case of self-incompatibility in plants the

competitive abilities of genotypes are likely not to be frequency-dependent, nevertheless fitness as a function of reproductive output is frequency-dependent. Therefore it is possible to predict equilibrium frequencies of the genotypes. If the fitnesses and the relative competitive abilities of plants are frequency-dependent, as suggested in the host-pathogen interaction model of Gates et al. (1986), the case becomes far more complex and "any discussion of the relations among the population parameters that characterize an infectious disease must ultimately take account of the evolutionary pressures on both, hosts and parasites. Population dynamics is always confounded with population genetics" (May and Anderson, 1979). Antonovics and Alexander (1987) therefore distinguish between an evolutionary prediction of host-pathogen interactions that describes the effects on gene or genotype frequencies and an ecological prediction that deals with effects on population growth.

The importance of diseases in maintaining or creating diversity in natural communities has been the focus of some discussion (Alexander, 1988; Antonovics and Alexander, 1988; Anderson and May, 1986; Burdon, 1982; Burdon and Chilvers, 1982; Burdon and Shattock, 1980; Harlan, 1976; May, 1985; May and Anderson, 1979, 1983b). Augspurger (1984) and Augspurger and Kelly (1984) showed that the species composition of some tropical forests is influenced

by pathogens. The genotype composition of Plantago lanceolata in its natural environment is influenced by the pathogen Fusarium moniliforme (Alexander, 1984; Alexander et al., 1984a). When measuring small-scale environmental heterogeneity using clonal transplants of Anthoxanthum odoratum and Danthonia spicata, Antonovics et al. (1987) found that a Danthonia clone that was infected systemically by a fungus was much more strongly affected by plant density than a healthy clone. This different response could be attributed to disease.

The strongest indication for the importance of pathogens in the ecology of plant communities is given in cases where pathogens are used for the control of weeds. Alexander and Burdon (1984) found that disease induced by Albugo candida or Peronospora parasitica had a significant effect on the survival and reproductive output of affected individuals of Capsella bursa-pastoris. Attempts to control introduced weeds by introducing their respective pathogens have been at least partially successful, e.g., in Australia with Chondrilla juncea and in the UK with groundsel (Senecio vulgaris), when their respective rust pathogens were introduced (Hasan and Ayres, 1990; Burdon et al., 1984; Paul and Ayres, 1986).

There are only a few studies concerning the influence of pathogens on the genotypic composition of agricultural crops, partly because selection by humans usually



interferes with natural selection in agricultural systems. Murphy et al. (1982) studied the fate of a mixture of equal percentages of five near isogenic lines of oats (Avena sativa) when infected by crown rust (Puccinia coronata) and when they were kept disease free over four successive generations. The oat lines presumably differed only in their resistance gene composition to six crown rust races. At the end of four years the rust free mixture contained the five components in frequencies ranging from 10 % to 38 % of the population. In the rusted mixture the frequencies ranged from 15 % to 28 %.

Even if there is no comparison of diseased and non-diseased mixtures, the influence of pathogens on host genetic composition can be studied when a host population is observed over a long time. Muona et al. (1982) analyzed changes in resistance to scald disease caused by Rhynchosporium secalis in a barley composite cross that had not been exposed to conscious selection over 45 generations. They tested the selfed progeny of plants out of four of the 45 generations for the occurrence of resistances to four Rhynchosporium races. The frequencies of these genes were not distributed at random, and a positive correlation among three of the resistances was found. The authors hypothesized that there are favored combinations of different genetic loci in inbreeding populations that are subject to epistatic selection. In a

subsequent study, Webster et al. (1986) analyzed 19 generations of the same barley composite cross. The non-randomness of the resistance gene distribution was confirmed. Patterns of change in allelic frequencies indicated that, in seasons when the pathogen was prevalent, selection favored alleles for resistance in the barley population but that resistance genes were detrimental to reproductive capacity in disease-free years. McDermott et al. (unpublished) analyzed mixtures of resistant and susceptible barley lines that were exposed to or protected from scald for two years. The selection coefficients for the resistant plants were negative in the control populations but positive in the inoculated populations and thus, consistent with Webster et al.'s (1986) study.

It is not only race-specific, simply inherited resistance genes that are subject to selection through pathogen pressure. Kilen and Keeling (1990) compared the effect of Phytophthora megasperma race 1 (which causes root rot) on two different soybean (Glycine max) bulk populations over five generations. They crossed the cultivar Tracy which carries the dominant Rps1-b and Rps3 alleles which confer resistance to race 1 and 3 of P. megasperma with either the breeding line D55-1492 or the cultivar Forrest. Neither of the two latter lines carries the resistance genes of Tracy. D55-1492 is highly susceptible to root rot. Forrest, however, exhibits

tolerance to the pathogen, i.e., with the same level of disease a susceptible, tolerant cultivar suffers less yield loss than a susceptible, non-tolerant cultivar. In the progeny of Tracy x D55-1492, the frequency of the Rps1-b allele increased significantly. The Rps3 allele, however stayed constant over the five generations. No change in the frequencies for either of the resistance genes could be detected in the Tracy x Forrest cross, suggesting that the tolerance of Forrest was competitive with the Rps1-b allele so that the selective advantage for both traits was equal.

#### Effects of disease on plant-plant interactions

Alexander et al. (1984b) pointed out that, in order to understand why mixtures do or do not yield better than their respective pure stands, yield data on a per-genotype basis are needed. They developed graphs of the theoretical outcome of per- genotype yields in the absence of disease that are similar to Fig. I.1 and in the presence of disease as shown in Figs. I.2 and I.3. Fig. I.2 is a graphical presentation of Trenbath's (1977) models. The situation depicted in Fig. I.3 is not likely to be found in a natural ecosystem because the susceptible genotype would become extinct, unless the system had recently been disturbed and both genotypes migrated to the site simultaneously or the susceptible genotype had an advantage in early successional

stages.

An analysis of yield on a per-genotype basis allows for distinction between the effect of disease on plant reproduction and the effect of disease on the competitive ability of a plant in relation to its neighbors. To distinguish between these two effects, it is necessary to grow healthy and diseased plants in monoculture and in mixtures. This allows one to determine the effect of disease on yield and to determine if the healthy and the diseased plants are differentially affected by healthy and by diseased neighbors.

In a series of experiments with healthy and rusted groundsel (Senecio vulgaris), Paul and Ayres (1986) found that yield reductions through disease caused by Puccinia lagenophorae were greater in mixtures of inoculated and non-inoculated plants than in pure stands of diseased plants. The inoculated plants also responded more to mixing than the healthy plants, i.e., the rusted plants inhibited the yield of the healthy plants to a lesser degree than the healthy plants inhibited rusted plants. This was illustrated when comparing the ratios of reproductive output (measured as number of heads produced). In the mixture, the ratio of healthy:inoculated plants was greater than 2; there were only 1.4 times the number of heads in the healthy pure stands than in the inoculated pure stands, however. When grown in mixed stands with

either lettuce (Lactuca sativa) or petty spurge (Euphorbia peplus), rusted groundsel plants were less affected by the presence of the other species than healthy groundsel.

However, both lettuce and petty spurge suffered significantly less from rusted than from healthy groundsel when grown in mixtures, indicating that the effect of disease on plant-plant interactions may be asymmetric (Paul, 1989; Paul and Ayres, 1987)

Burdon et al. (1984) investigated the influence of rust (Puccinia chondrillina) on the interactions between a susceptible and a resistant genotype of Chondrilla juncea grown in mixtures of different ratios. In the non-diseased situation the susceptible genotype was the better competitor and yielded more than expected when grown in association with the resistant genotype. Rust reversed the competitive abilities of the two genotypes, resulting in a superiority of the resistant genotype in the diseased situation. The replacement series diagram of the diseased mixture follows essentially the pattern outlined in Fig. I.2, except that the susceptible genotype is affected by disease so heavily that its competitive ability remained inferior to the resistant genotype at all mixture ratios. No data were reported in this experiment on the disease severity in the different mixtures, but the plants were inoculated several times uniformly in the greenhouse. This is likely to have eliminated frequency-dependent changes in

disease severity and could explain the consistently strong effect of disease throughout the experiment.

Few studies on the effects of disease on plant interactions have been conducted with agricultural crops. Alexander et al. (1986) mixed two wheat cultivars at different proportions in the field. One cultivar was susceptible and the other resistant to race 15-TNM of wheat stem rust. All mixtures and pure stands were grown as both inoculated and fungicide-protected treatments. Disease severities were determined on the susceptible cultivar in the different mixtures. Severities differed depending on the percentage of the resistant cultivar within the mixtures. The susceptible cultivar was superior in competitive ability in all mixtures and treatments. In contrast to the experiment of Burdon et al. (1984), no reversal of the relative competitive abilities was observed between the two cultivars in the presence of disease.

Alexander et al. (1986) hypothesized that, because stem rust affects plants only late in the season, there is no capacity for healthy plants to compensate for reduced competition by producing additional tillers. The yield reduction of the susceptible cultivar was expressed in reduced head weight but not in the number of kernels produced nor in the number of heads. In the long run, a reduction in seed weight is likely to affect the overall fitness of a genotype when left to natural selection, but

this cannot be detected within one season. Such effects of seed size have been shown in wheat when infected with powdery mildew (Jarosz et al., 1989) and when seed size was experimentally reduced by cutting off part of the endosperm (Giles, 1990). The results of Alexander et al. emphasize again that being a good yielder in pure stand does not allow for prediction of the performance of a variety in a mixture (see also Suneson, 1949). This performance is dependent on the relative competitive ability of a cultivar in a mixture. The experiment also illustrates the difficulty in evaluating the effect of disease on plants because fitness and relative competitive ability are measures that may not be used interchangeably.

#### **Questions yet to be addressed**

Most of the work on plant-pathogen interactions in mixtures has been theoretical and descriptive. In order to understand the mechanisms by which host plants and their parasites interact and coevolve, it is necessary to first study the effects of plant-plant interactions on the genetic composition of the host population; second, how plant-plant interactions and thus the host composition are influenced by disease; and third, how the genetic composition of the host population affects disease and plant-plant interactions.

The barley-composite cross / Rhynchosporium secalis system is the only model system in which these questions have been addressed. Self-pollinated small grain crops allow for determination of the genetic composition of the host population relatively easily since they are composed of pure lines with very little outcrossing. Multilines and cultivar mixtures of self-pollinated small grains offer, therefore, ideal systems for the study of host-pathogen interactions in the short, intermediate, and long term.

Multilines or cultivar mixtures are usually composed of more than two components. These components are chosen because of good yielding abilities in pure stands and because they contain different resistances to the target disease they are composed to control. In agricultural production, these mixtures are confronted with a mixture of pathogen races, each of which might affect one or more of the mixture components. In contrast, most studies of disease effects on plant interactions have used a single race of one pathogen and only two host genotypes (e.g. Alexander et al., 1986). In addition, host genotypes used in such studies are often not those that would be used in production agriculture. For example, the cultivars used by Alexander et al. (1986) are very different in their inherent yielding abilities, which makes them unsuitable for use in a commercial mixture. Therefore, there is a need to study the influence of disease on plant



interactions in more complex mixtures that could be used for practical benefit.

The relative competitive ability of a plant genotype cannot be predicted a priori. For example, if genotype A is superior to genotype B, and genotype B is superior to genotype C, can it then be concluded that genotype A will be superior to genotype C ? To obtain such information, it will be necessary to test a number of cultivars in all possible combinations and to analyze the yields of the mixture components.

Competitive ability is usually measured in biomass yield of a genotype in a mixture relative to the pure stand. In agricultural production, the total marketable yield is generally of more interest than the number of seed produced. When investigating the compositional stability of a mixture over time the relative fitnesses of the mixture components will be the crucial measure. However, fitness and marketable yield are not necessarily related. For example, the seed number of different bean (Phaseolus vulgaris) genotypes could not be related to their total seed weight (Hamblin, 1975). The cultivar Panameno produced an average of 16.9 seeds per plant with an average total seed weight of 9.2 g per plant. In contrast, the cultivar Seaway produced an average of 44.2 seeds per plant with an average total seed weight of 8.0 g per plant (Hamblin, 1975).

For the practical use of mixtures in agriculture to control disease, it is important to know if a mixture will perform well compared to the pure stands in seasons with and without disease and if and how long the replanting of the mixed seed will be practical for a farmer. Therefore, to understand the interactions that may have practical relevance, mixtures have to be investigated with respect to the level of disease control that can be achieved, for the yield-performance of the mixture components under diseased and non-diseased conditions, and for their compositional stability and stability of performance over time.

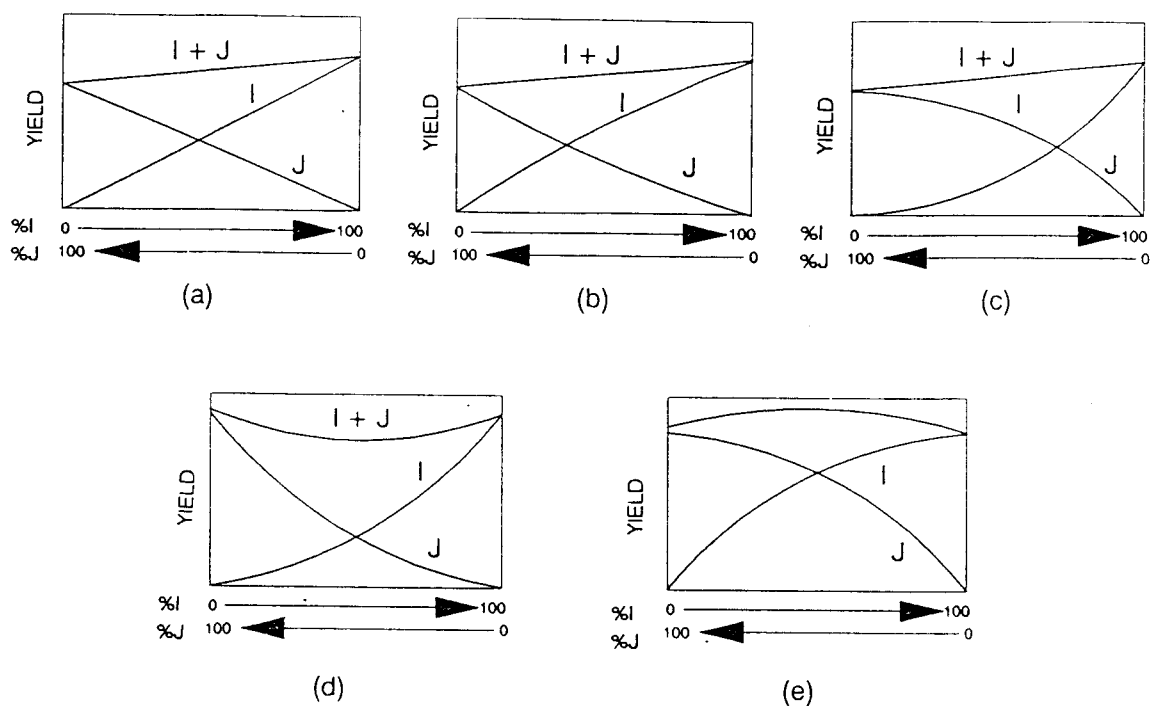


Fig. I.1. Models for the outcome of hypothetical mixtures of species or genotypes in replacement series. a: Intergenotypic competition equals intragenotypic competition. I has higher yielding ability than J, yield is additive. b: I suppresses the yield of J. The yield of I is increased by the same amount as J is decreased, i.e. no niche differentiation but different competitive abilities. c: Reverse competitive abilities as in b, no niche differentiation. d: I and J suppress each other in yielding abilities by allelopathy or other unknown mechanisms. e: I and J both yield higher than in pure stands due to either niche differentiation or unknown beneficial interactions or both (after Harper, 1977)

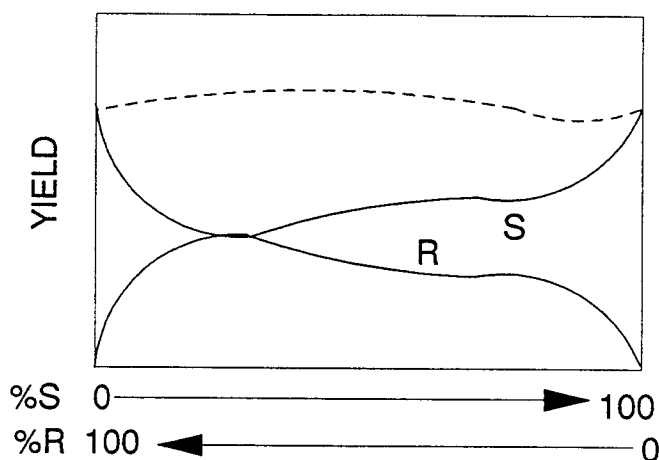


Fig. I.2. Model for the yield of different species or genotypes differentially susceptible to a pathogen in the presence of the pathogen. The susceptible genotype S is superior in competitive ability to the resistant genotype R in the absence of disease. S and R have slightly different niches. High % R: Disease levels are low, S is the superior competitor. Low % R: Disease levels are high, diseased S plants have reduced yield and are poor competitors, healthy R plants respond to reduced competition by increasing yield (after Alexander et al., 1984b)

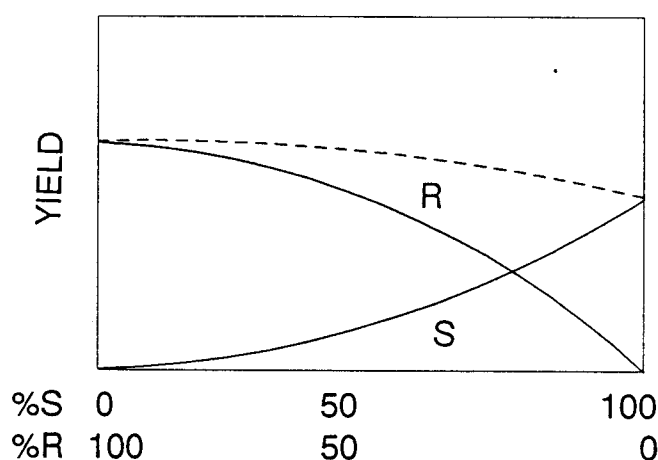


Fig. I.3. Model for the yield of different species or genotypes differentially susceptible to a pathogen in the presence of the pathogen. The susceptible genotype S is inferior in competitive ability to the resistant genotype R in the absence of disease. S and R have slightly different niches. High % R: Disease levels are low, R is the superior competitor. Low % R: Disease levels are high, competitive ability of S is reduced further by effects of disease (after Alexander et al., 1984b)

## Literature Cited

- Adams, M. W., Ellingboe, A. H., and Rossman, E. C. 1971. Biological uniformity and disease epidemics. *Bioscience* 21:1067-1070.
- Alexander, H. M. 1984. Spatial patterns of disease induced by Fusarium moniliforme var. subglutinans in a population of Plantago lanceolata. *Oecologia* 62:141-143.
- Alexander, H. M. 1988. Spatial heterogeneity and disease in natural populations. In: Spatial components of epidemics. M. J. Jeger, ed. Prentice-Hall, Englewood Cliffs, NJ, pp. 144-164.
- Alexander, H. M., Antonovics, J., and Rausher, M. D. 1984a. Relationship of phenotypic and genetic variation in Plantago lanceolata to disease caused by Fusarium moniliforme var. subglutinans. *Oecologia* 65:89-93.
- Alexander, H. M., and Burdon, J. J. 1984a. The effect of disease induced by Albugo candida (white rust) and Peronospora parasitica on the survival and reproduction of Capsella bursa-pastoris. *Oecologia* 64:314-318.
- Alexander, H. M., Burdon, J. J., and Roelfs, A. P. 1984b. Applications of competition models to studies of yield in mixtures: need for yield data on a per-component basis. Handout from poster presented at 1984 Am. Phytopathol. Soc. meeting, Guelph, Ontario.
- Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition in monocultures and mixtures of two wheat cultivars. *Plant Pathol.* 35:457-465.
- Allard, R. W. 1960. Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1:127-133.
- Allard, R. W., and Adams, J. 1969. Population studies in predominantly self-pollinating species XIII. Intergenotypic competition and population structure in barley and wheat. *Am. Naturalist* 103:620-645.
- Anderson, R. M., and May, R. M. 1986. The invasion, persistence and spread of infectious diseases within animal and plant communities. *Phil. Trans. R. Soc. Lond. B.* 314:533-570.

- Anikster, Y., and Wahl, I. 1979. Coevolution of the rust fungi on Gramineae and Liliaceae and their hosts. *Ann. Rev. Phytopathol.* 17:367-403.
- Anonymous, 1972. Genetic vulnerability of major crops. National Academy of Sciences, Washington, D. C.
- Antonovics, J., and Alexander, H. M. 1987. The concept of fitness in plant-pathogen interactions in natural populations. *In: Plant Disease Epidemiology Vol. II.* K. J. Leonard and W. Fry, eds. McGraw-Hill, New York, pp. 185-214.
- Antonovics, J., Clay, K., and Schmitt, J. 1987. The measurement of small-scale environmental heterogeneity using clonal transplants of Anthoxanthum odoratum and Danthonia spicata. *Oecologia* 71:601-607.
- Antonovics, J., and Levin, D. A. 1980. The ecological and genetical consequences of density-dependent regulation in plants. *Annu. Rev. Ecol. Syst.* 11:411-452.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-1712.
- Augsburger, C. K., and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211-217.
- Barrett, J. A. 1978. A model of epidemic development in variety mixtures. *In: Plant Disease Epidemiology.* P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 129-137.
- Barrett, J. A. 1981. The evolutionary consequences of monoculture. *In: Genetic Consequences of Man Made Change.* J. A. Bishop and L. M. Cook, eds. Academic Press, New York, pp. 209-248.
- Borlaug, N. E. 1959. The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants. *Proc. 1st Int. Wheat Genet. Symp.*, 1958, pp.12-27.
- Borlaug, N. E. 1981. Increasing and stabilizing food production. *In: Plant Breeding II*, K. J. Frey, ed. Iowa State University Press, Ames Iowa, pp. 467-492.
- Browder, L. E., and Eversmeyer, M. G. 1977. Pathogenicity associations in Puccinia recondita f. sp. tritici.

Phytopathology 67:766-771.

- Browning, J. A. 1974. Relevance of knowing about natural ecosystems to development of pest management programs in agroecosystems. Proc. Am. Phytopathol. Soc. 1:191-199.
- Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. Annu. Rev. Phytopathol. 7:355-382.
- Browning, J. A., Simons, M. D., Frey, K. J., and Murphy, H. C. 1969. Regional deployment for conservation of oat crown rust resistance genes. Spec. Rep.-Iowa Agric. Home Econ. Exp. Stn. 64:49-56.
- Burdon, J. J. 1978. Mechanisms of disease control in heterogeneous populations - an ecologists view. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford, pp. 193-200.
- Burdon, J. J. 1982. The effect of fungal pathogens on plant communities. In: The Plant Community as a Working Mechanism. E. I. Newman, ed. Blackwell, Oxford, pp. 66-112.
- Burdon, J. J., and Chilvers, G. A. 1982. Host density as a factor in disease ecology. Annu. Rev. Phytopathol. 20:143-166.
- Burdon, J. J., Groves, R. H., Kaye, P. E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. Oecologia 64:199-203.
- Burdon, J. J., Oates, J. D., and Marshall, D. R. 1983. Interactions between Avena and Puccinia species I. The wild hosts: Avena barbata Pott ex Link, A. Fatua L., A. Ludoviciana Durieu. J. Appl. Ecology 20:571-584.
- Burdon, J. J., and Shattock, R. C. 1980. Disease in plant communities. Appl. Biol. 5:145-219.
- Chilvers, G. A., and Brittain, E. G. 1972. Plant competition mediated by host-specific parasites. A simple model. Aust. J. Biol. Sci. 25:749-756.
- Chin, K. M., and Wolfe, M. S. 1984. Selection on Erysiphe graminis in pure and mixed stands of barley. Plant Pathol. 33:535-546.



- Clay, R. E., and Allard, R. W. 1969. A comparison of the performance of homogeneous and heterogeneous barley populations. *Crop. Sci.* 9:407-412.
- Clay, K. 1984. The effect of the fungus Atkinsonella hypoxylon (Clavicipitaceae) on the reproductive system and demography of the grass Danthonia spicata. *New. Phytol.* 98:165-175.
- Dinoor, A., and Eshed, N. 1984. The role and importance of pathogens in natural plant communities. *Annu. Rev. Phytopathol.* 22:443-466.
- Donald, C. M. 1968. The breeding of crop ideotypes. *Euphytica* 17:385-403.
- Falconer, D. S. 1981. Introduction to quantitative Genetics. Second edition. Longman, Scientific & Technical, Wiley, New York, 340 pp.
- Firbank, L. G., and Watkinson, A. R. 1985a. On the analysis of competition within two-species mixtures of plants. *J. Appl. Ecol.* 22:503-517.
- Firbank, L. G., and Watkinson, A. R. 1985b. A model of interference within plant monocultures. *J. Theor. Biol.* 116:291-311.
- Flor, H. H. 1953. Epidemiology of flax rust in the North Central States. *Phytopathology* 43:624-628.
- Flor, H. H. 1956. The complementary genic systems in flax and flax rust. *Adv. Genet.* 8:29-54.
- Frey, K. J. 1982. Multiline breeding. In: Plant Improvement and somatic cell genetics. I. K. Vasil, W. R. Scowcroft, and K. J. Frey, eds. Academic Press, New York, pp. 43-72.
- Frey, K. J., Browning, J. A., and Simons, M. D. 1973. Management of host resistance genes to control diseases. *Z. Pflanzenkr. Pflanzenschutz* 80:160-180.
- Frey, K. J., Browning, J. A., and Simons, M. D. 1977. Management systems for host genes to control disease loss. *Ann. N. Y. Acad. Sci.* 287:255-274.
- Frey, K. J., and Maldonado, U. 1967. Relative productivity of homogeneous and heterogeneous oat cultivars in optimum and suboptimum environments. *Crop Sci.* 7:532-535.

- Gates, D. J., Westcott, M., Burdon, J. J., and Alexander, H. M. 1986. Competition and stability in plant mixtures in the presence of disease. *Oecologia* 68:559-566.
- Gause, G. F. 1934. The struggle for existence. Hafner publishing Co., New York.
- Giles, B. E. 1990. The effects of variation in seed size on growth and reproduction in the wild barley Hordeum vulgare ssp. spontaneum. *Heredity* 64:239-250.
- Grafius, J. E. 1966. Rate of change of lodging resistance, yield, and test weight in varietal mixtures of oat. *Crop Sci.* 6:369-370.
- Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York.
- Hamblin, J. 1975. Effect of environment, seed size, and competitive ability on yield and survival of Phaseolus vulgaris (L.) genotypes in mixtures. *Euphytica* 24:435-445.
- Hamblin, J., and Donald, C. M. 1974. The relationship between plant form, competitive ability and grain yield in a barley cross. *Euphytica* 23:535-542.
- Hasan, S., and Ayres, P. G. 1990. The control of weeds through fungi: principles and prospects. *New Phytol.* 115:201-222.
- Harlan, H. V., and Martini, M. L. 1929. A composite hybrid mixture. *J. Am. Soc. Agron.* 21:487-490.
- Harlan, J. R. 1972. Genetics of disaster. *J. Environ. Qual.* 1:212-215.
- Harlan, J. R. 1975. Our vanishing genetic resources. *Science* 188:618-621.
- Harlan, J. R. 1976. Disease as a factor in plant evolution. *Annu. Rev. Phytopathol.* 14:31-51.
- Hill, J., Mather, K., and Caligari, P. D. S. 1987. Analysis of competitive ability among genotypes of perennial ryegrass. II Effect upon dry matter production. *Euphytica* 36:109-115.
- Jarosz, A. M., Burdon, J. J., and Mueller, W. J. 1989. Longterm effects of disease epidemics. *J. Appl. Ecol.* 26:725-733.

- Jennings, P. R., and de Jesus, J. Jr. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. *Evolution* 22:119-124.
- Jennings, P. R., and Herrera, R. M. 1968. Studies on competition in rice. II. Competition in segregating populations. *Evolution* 22:332-336.
- Jensen, N. F. 1952. Intra-varietal diversification in oat breeding. *Agron. J.* 44:30-34.
- Johnson, R., Green, G. J., and Samborski, D. J. 1967. The world situation of the cereal rusts. *Annu. Rev. Phytopathol.* 5:183-200.
- Johnson, R. 1984. A critical analysis of durable resistance. *Ann Rev. Phytopathol.* 22:309-330.
- Johnson, T. 1961. Man-guided evolution in plant rusts. *Science* 133:357-362.
- Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. Appl. Ecology* 21:227-243.
- Kilen, T. C., and Keeling, B. L. 1990. Gene frequency changes in soybean bulk populations exposed to *Phytophthora* rot. *Crop Sci.* 30:575-578.
- Klages, K. H. W. 1936. Changes in the proportions of the components of seeded and harvested cereal mixtures in abnormal seasons. *J. Am. Soc. Agron.* 28:935-940.
- Knott, E. A., and Mundt, C. C. 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and non-diseased conditions. *Theor. Appl. Gen.* 80:313-320.
- Knott, R. D. 1972. Using race-specific resistance to manage the evolution of plant pathogens. *J. Environ. Quality*, 1:227-231.
- Leonard, K. J. 1969a. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. *Phytopathology* 59:1845-1850.
- Leonard, K. J. 1969b. Selection in heterogeneous populations of *Puccinia graminis* f. sp. *avenae*. *Phytopathology* 59:1851-1857.

- Leonard, K. J. 1969c. Genetic equilibria in host-pathogen systems. *Phytopathology* 59:1858-1863.
- Leonard, K. J. 1977. Selection pressures and plant pathogens. *Ann. N. Y. Acad. Sci.* 287:207-222.
- Leonard, K. J., and Czocho, R. J. 1980. Theory of genetic interactions among populations of plants and their pathogens. *Annu. Rev. Phytopathol.* 18:337-358.
- Leonard, K. J., and Mundt, C. C. 1984. Methods for estimating epidemiological effects of quantitative resistance to plant diseases. *Theor. Appl. Gen.* 67:219-230.
- Marshall, D. R. 1977. The advantages and hazards of genetic homogeneity. *Ann. N. Y. Acad. Sci.* 287:1-20.
- May, R. M. 1985. Host-parasite associations: Their population biology and population genetics. *In: Ecology and Genetics of Host-Parasite Interactions*, pp. 243-262.
- May, R. M., and Anderson, R. M. 1979. Population biology of infectious diseases: Part II. *Nature* 280:455-461.
- May, R. M., and Anderson, R. M. 1983. Parasite-host coevolution. *In: Coevolution*. D. J. Futuyma and M. Slatkin eds. Sinauer, pp. 186-206.
- McDonald, B. A., Allard, R. W., and Webster, R. K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. *Crop Science* 28:447-452.
- McDonald, B. A., McDermott, J. M., Allard, R. W., and Webster, R. K. 1989. Coevolution of host and pathogen populations in the Hordeum vulgare - Rhynchosporium secalis pathosystem. *Proc. Nat. Acad. Sci.* 86:3924-3927.
- Montgomery, E. G. 1912. Competition in cereals. *Bull. Neb. Agric. Exp. Stn.* No. 127:3-22.
- Mooney, P. R. 1979. Seeds of the Earth. A Private or Public Resource. Published by Inter Pares (Ottawa) for the Canadian Council for Intern. Co-operation and the Intern. Coalition for Development Action (London). Mutual Press Limited, Ottawa.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity

- and cereal rust management. In: The Cereal Rusts Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: effect of genotype unit area. *Phytopathology* 75:607-610.
- Mundt, C. C., and Leonard, K. J. 1985. Effect of host genotype unit area on epidemic development of crown rust following focal and general inoculations of mixtures of immune and susceptible oat plants. *Phytopathology* 75:1141-1145.
- Mundt, C. C., and Leonard, K. J. 1986a. Analysis of factors affecting disease increase and spread in mixtures of immune and susceptible plants in computer simulated epidemics. *Phytopathology* 76:832-840.
- Mundt, C. C., and Leonard, K. J. 1986b. Effect of host genotype unit area on development of focal epidemics of bean rust and common maize rust in mixtures of resistant and susceptible plants. *Phytopathology* 76:895-900.
- Muona, O., and Allard, R. W. 1982. Evolution of resistance to Rhynchosporium secalis (Oud.) Davis in Barley Composite Cross II. *Theor. Appl. Genet.* 61:209-214.
- Murphy, J. P., Hebsel, D. B., Elliott, A., Thro, A. M., and Frey, K. J. 1982. Compositional stability of an oat multiline. *Euphytica* 31:33-40.
- Nitzsche, W., and Hesselbach, J. 1983. Sortenmischungen statt Vielliniensorten. *Z. Pflanzenz.* 90:68-74.
- Norrington-Davies, J., and Hutto, J. M. 1972. Diallel analysis of competition between diploid and tetraploid genotypes of Secale cereale grown at two densities. *J. Agric. Sci. Camb.* 78:251-256.
- Oates, J. D., Burdon, J. J., and Brower, J. B. 1983. Interactions between Avena and Puccinia species II. The pathogens: Puccinia coronata CDA and P. graminis Pers. F. Sp. Avenae Eriks. & Henn. *J. Appl. Ecology* 20:585-596.
- Paul, N. D. 1989. The effects of Puccinia lagenophorae on Senecio vulgaris in competition with Euphorbia peplus. *J. Ecology* 77:552-564.

- Paul, N. D., and Ayres, P. G. 1986. Interference between healthy and rusted groundsel within mixed populations of different densities and proportions. *New Phytol.* 104:257-269.
- Paul, N. D., and Ayres, P. G. 1987. Effects of rust infection of Senecio vulgaris on competition with lettuce. *Weed Res.* 27:431-441.
- Person, C. 1966. Genetic polymorphism in parasitic systems. *Nature (London)* 212:266-267.
- Prakash, C. S., and Heather, W. A. 1988. Antagonisms between races of Melampsora medusae on poplar, resulting in reduced disease expression. *Plant Pathology*
- Stakman, E. C. 1947. Plant diseases are shifting enemies. *Am. Scientist* 35:321-350.
- Stevens, N. E. 1942. How plant breeding programs complicate plant disease problems. *Science* 95,:313-316.
- Suneson, C. A. 1949. Survival of four barley varieties in mixture. *Agron. J.* 41:459-461.
- Suneson, C. A. 1956. An evolutionary plant breeding method. *Agron. J.* 48:188-191.
- Suneson, C. A., and Wiebe, G. A. 1942. Survival of barley and wheat varieties in mixtures. *J. Am. Soc. Agron.* 34:1052-1056.
- Thomas, S. C., and Weiner, J. 1989. Including competitive asymmetry in measures of local interference in plant populations. *Oecologia* 80:349-355.
- Trenbath, B. R. 1977. Interactions among diverse hosts and diverse parasites. *Ann. N. Y. Acad. Sci.* 287:124-150.
- Ullstrup, J. A. 1972. the impact of the southern corn leaf blight epidemics of 1979-1971. *Annu REv. Phytopathol.* 10:37-50.
- Van der Plank, J. E. 1963. *Plant Diseases: Epidemics and Control.* Academic Press, New York.
- Van der Plank J. E. 1968. *Disease Resistance in Plants.* Academic Press, New York.
- van Leur, J. A. G., Ceccarelli, S., and Grando, S. 1989.

- Diversity for disease resistance in barley landraces from Syria and Jordan. *Plant Breeding* 103:324-335.
- Wahl, I. 1970. Prevalence and geographic distribution of resistance to crown rust in Avena sterilis. *Phytopathology* 60:746-749.
- Wahl, I., Anikster, Y., Manisterski, J., and Segal, A. 1984. Evolution at the center of origin. In: The Cereal Rusts Vol. I. W. R. Bushnell and A. P. Roelfs, eds. Academic Press, Orlando, pp. 39-77.
- Webster, R. K., Saghai-Maroo, M. A., and Allard, R. W. 1986. Evolutionary response of Barley Composite Cross II to Rhynchosporium secalis analyzed by pathogenic complexity and by gene-by-race relationships. *Phytopathology* 76:661-668.
- Wolfe, M. S. 1973. Changes and diversity in populations of fungal pathogens. *Ann. Appl. Biol.* 75:132-136.
- Wolfe, M. S. 1978. Some practical implications of the use of cereal variety mixtures. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford, pp. 201-207.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annu. Rev. Phytopathol.* 23:251-273.
- Wolfe, M. S., and Barrett, J. A. 1977. Population genetics of powdery mildew epidemics. *Ann. N. Y. Acad. Sci.* 287:151-163.
- Wolfe, M. S., and Barrett, J. A. 1980. Can we lead the pathogen astray? *Plant Dis.* 64:148-155.
- Wolfe, M. S., Barrett, J. A., and Jenkins, J. E. E. 1981. The use of mixtures for disease control. In: Strategies for the Control of Cereal Diseases. J. F. Jenkyn and R. T. Plumb, eds. Blackwell, Oxford, pp. 73-80.
- Young, L. D., and Hartwig, E. E. 1988. Selection pressure in soybean cyst nematode from soybean cropping sequences. *Crop Science* 28:845-847.

## II. Effects of Plant Competition on Stripe Rust in Wheat Cultivar Mixtures

Maria R. Finckh and Christopher C. Mundt

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

Paper No. \_\_\_\_ of the journal series of the Oregon  
Agricultural Experiment Station.

Supported in part by the USDA STEEP Program and the Oregon  
Wheat Commission.

Accepted for publication 00 00000 0000.



## Abstract

Finckh, M. R., and Mundt, C. C. 1991. Effects of plant competition on stripe rust in wheat cultivar mixtures. *Phytopathology* 81:000-000.

Mixtures of two-to-five winter wheat (Triticum aestivum) cultivars and their component pure stands were either exposed to or protected from two stripe rust (Puccinia striiformis) races at three and two locations in 1986/87 and 1987/88, respectively. Disease severity and yield components were determined on a per-cultivar basis for a subset of the mixtures and also for the pure stands. Disease severity in the mixtures compared to the arithmetic mean of the pure stands was reduced between 6 and 97%. Changes in disease severity could be separated into two effects. First, selection changed frequencies of the cultivars in the mixtures by up to 35% at harvest as compared to the planted frequencies. Reductions in overall disease severity in mixtures due to selection for the more resistant cultivar were as high as 47%, and increases in overall disease severity due to selection for the more susceptible cultivar were as high as 11% over the mean disease severity in the pure stands. Second, the epidemiological effect of host diversity reduced disease severity on individual cultivars below that observed in their pure stands.

Additional keywords: genetic diversity

## Introduction

Intrafield diversification as a means of disease control was first promoted by Jensen (1952) and Borlaug (1959). Jensen (1952) proposed selection of pure lines of oats that were similar for important agronomic traits so they could be grown together, but which possessed genetic diversity for reaction to abiotic and biotic stresses, including disease. In contrast, Borlaug (1959) promoted the development of backcrossed lines that differed in their reaction to rusts but were similar for their remaining genetic background. More recently, attention has turned to the use of cultivar mixtures to attain disease control (Wolfe, 1985). There are several advantages to the use of cultivar mixtures over multilines, including ease of synthesis, additional disease control against the target disease through race non-specific resistance, reduced selection for a superrace (a race virulent on all host components in the mixture), and protection from non-target diseases and abiotic stresses (Mundt and Browning, 1985a; Wolfe, 1985). Some of the mechanisms by which host diversity might reduce disease severity include the dilution of host tissue susceptible to a given pathogen race, a barrier function of resistant hosts, and interactions among different pathogen genotypes (Barrett, 1978; Browning and Frey, 1969; Chin and Wolfe, 1984;

Leonard, 1969a,b; Mundt and Browning, 1985a; Vanderplank, 1968; Wolfe, 1978, 1985).

Mixtures of plant genotypes mostly have been studied for their effects on crop performance (disease control and yield) (Allard, 1960; Allard and Adams, 1969; Barrett, 1978; Borlaug, 1959; Browning and Frey, 1969; Jensen, 1952; Leonard, 1969a; Leonard and Czocho, 1980; Mahmood et al., 1991; Mundt and Browning, 1985a,b; Mundt and Leonard, 1985, 1986a,b; Nitzsche and Hesselbach, 1983; Norrington-Davies and Hutto, 1972; Suneson, 1956; Wolfe, 1978, 1985; Wolfe and Barrett, 1980; Wolfe et al., 1981). Few studies, however, have addressed the reciprocal effects of disease and plant-plant interactions in mixtures (Alexander et al., 1986).

Multilines or cultivar mixtures are usually composed of more than two components. These components are chosen because of good yielding ability in pure stands and for resistance to specific diseases. In agricultural production, these mixtures can be confronted with a mixture of pathogen races, each of which might affect one or more of the mixture components. On the other hand, most studies of disease effects on plant interactions have used a single race of one pathogen and only two host genotypes (Alexander et al., 1986). In addition, host genotypes used in such studies are often not those that would be used in production agriculture.

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

Knott and Mundt (1990) analyzed field trials of inoculated and non-inoculated mixtures of five commercial wheat (Triticum aestivum L.) cultivars that were differentially susceptible to two races of stripe rust (Puccinia striiformis Westend. (=P. glumarum (Schm.) Jacob, Eriksson & Henn.)). The mixing ability of cultivars with respect to yield and disease control was determined with combining ability analysis. An advantage of the analysis is that it did not require the physical separation of the mixture components to evaluate their performance. However, it could not predict the end composition of a mixture at harvest. Therefore, no insight was provided into the interactive effects of disease and plant population dynamics in mixtures. In this paper, we provide an analysis of these effects using data derived from the experiments described by Knott and Mundt (1990). In a separate paper, we analyzed the effects of mixing and disease on yield and yield components (Finckh and Mundt, 1992).

## Materials and Methods

The experiments were superimposed on a field trial designed to screen wheat cultivar mixtures for their performance with respect to yield and disease.

### Cultivars.

Host genotypes were five soft white, club-type winter wheat cultivars with different stripe rust resistances, heights, and chaff colors (Table II. 1). Published records on the cultivar Faro had listed it as susceptible to stripe rust race 5. Our disease assessments revealed, however, that the seed source had consisted of two closely related lines, one resistant and one susceptible to race 5. This finding was confirmed by R. E. Allan (Dept. of Crop Science, Wash. State Univ., Pullman, personal communication).

### Locations.

Experiments were conducted at three locations in Oregon. Pendleton and Moro, located in the semi-arid region of eastern Oregon, receive approximately 450 and 300mm annual precipitation, respectively. Corvallis is located in the Willamette Valley in western Oregon, and receives approximately 1000 mm annual precipitation.

### Experimental design.

All possible two-to-five way combinations of equal proportions of germinable seed of Faro, Jacmar, Moro, Tres, and Tyee (Table II. 2) and their pure stands were planted in the fall of 1986. Plots were arranged in a randomized complete block design with four replications at each location. Plots were 1.5 m by 4.5 m with four rows per plot (38 cm between rows) in Moro and six rows per plot (25 cm between rows) in Pendleton and Corvallis. Plots were adjacent in the narrow dimension and separated by 1.8 m of fallow ground in the long dimension. Seeding rates were those appropriate for commercial wheat production at each site and were 198, 316, and 395 seed/m<sup>2</sup> in Moro, Pendleton, and Corvallis, respectively. In the fall of 1987, six replications of all possible two-to-four way combinations of Faro, Jacmar, Tres, and Tyee (Table II. 2) and their pure stands were planted at Pendleton and Moro in four-row plots, with 38 cm between rows.

Two separate experiments were conducted in each location. One experiment was protected from stripe rust with three-to-four applications of Bayleton (triadimefon) at 284 g a.i. per ha; the other experiment was inoculated with stripe rust. The inoculated experiment was located 12 m downwind from the fungicide-treated experiment at each site. To reduce interplot interference, the area between the experiments was planted to the resistant cultivar

Stephens or to barley (Hordeum vulgare). Fertilizers and herbicides were applied according to standard practices for wheat in the respective regions.

#### Inoculation.

Peat pots (6 cm) containing two-to-three week old seedlings of the winter wheat cultivar Nugaines were inoculated with an equal mixture of uredospores of P. striiformis races CDL 5 and CDL 27 (CDL race designations are those of the USDA Cereal Disease Laboratory, Washington State University, Pullman). Inoculated plants were placed in a dew chamber for 12 h. Upon removal from the dew chamber, plants were placed outdoors to harden off until sporulation. At the onset of sporulation, one pot was transplanted into the center of each plot in the inoculated experiments. In 1986, inoculation took place in late November to early December. In Moro and Pendleton, wooden shingles were used to protect transplants from heavy winds. Because disease occurrence was sporadic in Corvallis by spring, the inoculation was repeated in early April 1987. In 1987, the experiment in Pendleton was inoculated on 28 Nov. Because of a severe fall drought in Moro, the wheat emerged in late Jan. 1988. Therefore, the plots were inoculated on 12 March 1988 when sufficient foliage was available. Because the fall 1987 inoculation had failed in Pendleton, it was repeated on 28 March 1988.



**Disease assessments.**

Assessments were performed before disease had reached 90% severity on the F-1 leaf of the most susceptible cultivar. Assessment dates were 20-23 May 1987 and 30 May-1 June 1988 in Pendleton, 27-31 May 1987 and 12-16 June 1988 in Moro, and 3-6 June 1987 in Corvallis. Subplots containing a minimum of 120 tillers were marked within each plot approximately midway between the inoculation point and the downwind end of the plot. The subplots included sections of equal length of the two center rows of the four-row plots and the four center rows of the six-row plots. As the size of the subplots was determined by tiller density, subplot sizes varied among years and locations and ranged from 30 to 66 cm in length.

Disease was assessed by visually estimating the percentage (using an unaltered scale from 1 to 100%) of the F-1 leaf area that was covered by stripe rust on each headbearing tiller in each subplot. Each tiller that was assessed also was given a numbered tag matched to an identification number on data sheets used to record disease severity. The same person assessed all plants. To limit the duration of assessments to four days per location, only 19 out of 31 treatments were assessed in 1987 and 12 out of 16 treatments in 1988 (Table II. 2).

To determine if there was an effect of tagging on

yield, two plots of the common wheat cultivar Stephens were planted in each block in 1986/87; a duplicate plot of the mixture of Jacmar and Tres was the repeated treatment in 1987/88. One of the repeated plots was left as an untagged control in each block in the inoculated experiments.

### **Harvest.**

Upon maturity, all tillers in each subplot of the inoculated and fungicide-treated experiments were cut with sickles and bagged. Plants were transported to the laboratory and separated by chaff color. The tag numbers were matched to disease notes taken in the field so that mean disease severity could be calculated separately for the brown and white colored components in the mixtures. Brown and white heads were counted to determine tiller frequencies, threshed separately with a stationary plot thresher, and seed weight per plot and 1000-seed weight were recorded. Yield data for both the inoculated and fungicide-treated experiments are reported in more detail elsewhere (Finckh and Mundt, 1992).

### **Data analysis.**

Data were analyzed using SAS (1988). One-way analyses of variance were performed for each experiment in each location. Fisher's non-protected LSD and linear contrasts were used to determine significance of treatment

differences for disease and tiller frequencies. In addition, a two-way analysis was performed on mixture treatment means across locations within each year, using location as replication. The two factors were mixture treatment and inoculation versus fungicide control. Thus, each mixture treatment had three replicates (three locations) in 1987 and two replicates (two locations) in 1988 for both inoculation and fungicide treatments.

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

$$1 - (S_X/S_M) = \text{Total Disease Reduction} \quad (1)$$

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

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

$$([N_{iX}/N_X] \times S_{iM}) + ([N_{jX}/N_X] \times S_{jM}) = S_{MW} \quad (2)$$

where  $N_{ix}$  and  $N_{jx}$  denote the number of tillers of components  $i$  and  $j$  in mixtures,  $S_{im}$  and  $S_{jm}$  are the mean disease severities of components  $i$  and  $j$  in pure stands, and  $S_{Mw}$  represents the weighted pure stand mean. The disease severity relative to the weighted pure stand mean represents the effect of mixing on epidemic development:

$$1 - (S_x/S_{Mw}) = \text{Epidemiological Effect} \quad (3)$$

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

$$\text{Total Reduction} - \text{Epidemiological Effect} = \text{Selection Effect} \quad (4)$$

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

## Results

### Effect of tagging.

There was no significant effect ( $0.16 < P < 0.86$  in the different experiments) of tagging tillers on yield per plot or 1000-seed weight in either season or location.

### Disease severity.

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

### Effect of host diversity on overall disease severity.

Disease severity in all mixtures that were assessed was lower than the mean of the pure stands (Table II. 3). Disease reductions were statistically significant in 38 out of 58 mixtures. Although the percent disease reduction was

often substantial, it was not always statistically significant because disease reduction was based on differences in absolute amount of diseased leaf area. For example, the mean of the disease severities on the pure stands of Faro and Tyee in Corvallis 1987 was 39.1%. The observed severity on the Faro-Tyee mixture was 14.9%. This represents a 62% reduction that was highly significant. In contrast, the mean disease severity on the pure stands of Faro and Tres was 1.7%. The disease severity on the Faro-Tres mixture was 0.3% which is 1.4% less total disease or an 83.5% reduction that was not statistically significant. Thus, disease reduction was significant in 38 out of 43 mixtures that contained at least one highly susceptible component (disease severity in pure stand >30%). Disease reductions were not statistically significant in the 15 mixtures of more resistant components (Table II. 3).

#### Disease severity on mixture components.

For the individual mixture components, disease reduction was greatest on the cultivars that had more than 30% disease severity in pure stands in a given year and location (Table II. 4). Disease reduction was always significant on Jacmar and Tyee in Pendleton and in Moro in both years and on the cultivar Moro in Pendleton 1987. Healthy leaf area on those cultivars was increased between 11.6 to 50.2% in the mixtures over the pure stands. For

Faro in all locations and both years and the cultivar Moro in the Moro site in 1987, mixing increased healthy leaf area only between 1.0 to 10.2%. Disease severity on Tres remained essentially the same, ranging from 0.1% more to 2.1% less healthy leaf area in the mixtures as compared to the pure stands.

#### **Effects of plant competition.**

In most of the mixtures that were evaluated for selection effects, the genotype with superior tillering ability was also the more resistant genotype. Disease reduction through selection for the more resistant genotype ranged from 1 to 47%. In cases where selection favored the more susceptible cultivar, disease was increased between 2 and 11% (Table II. 4).

The cultivars differed somewhat in their tillering abilities in pure stands. Faro produced more tillers than the other cultivars in both years and at all locations. Differences in tillering ability among the other cultivars were usually not significant (Table II. 5).

The proportions of the cultivars in mixtures could not be predicted from their pure stand tiller numbers. In 1987, tiller proportions of the five cultivars at harvest within mixtures were very consistent across locations and inoculation treatments (Table II. 6). Rank order by tiller proportion was Tres > Faro > Moro >= Tyee > Jacmar, except

in the inoculated experiment in Moro 1987 where the ranking of Faro and Tres was reversed. In Pendleton 1988 the ranking was Faro > Tres > Tyee > Jacmar. However, in Moro 1988, Jacmar was present at much higher proportions than in Pendleton 1988 or in Moro and Pendleton in 1987, leading to a rank reversal for Tyee and Jacmar.



## Discussion

Diversity for stripe rust resistance within wheat populations reduced disease severity below the mean of the component pure stands for all of the mixtures. The overall positive effects of the mixtures on disease that were reported by Knott and Mundt (1990) were confirmed by our studies. Although the plots were adjacent and interplot-interference may have increased overall disease severity, differences among the mixtures were considerable, reflecting differences in host composition. Low success of the inoculations of race 5 in Corvallis and race 27 in Moro 1987 resulted in great variability in disease severity, explaining the frequent non-significant reductions in that year.

Both selection effects and epidemiological effects influenced stripe rust severity in the mixtures. If selection favors the more resistant cultivar, then disease severity in a mixture can be reduced below the mean of the pure stands of its components even if disease on the more susceptible cultivar is not reduced in the mixture. Selection can only affect disease if mixture components are differentially susceptible, however. In 1988, for example, the harvested proportions in the mixtures of Jacmar and Tyee were substantially different from the planted frequencies of 50% (Table II. 6). Nevertheless, selection

effects were zero because the disease severity on the two cultivars in pure stand was almost the same (Table II. 4). Epidemiological effects reduced disease beyond that accounted for by selection.

The consistently low tiller frequencies of Jacmar in inoculated and fungicide-treated mixtures in 1987 could have been due to that cultivar's shortness. Poor performance of a cultivar in rice cultivar mixtures has been ascribed to its shortness relative to other mixture components (Jennings and de Jesus, 1968). Moro however, was by far the tallest cultivar, but its tillering ability was not always improved by mixing. The considerably higher tiller frequencies of Jacmar in Moro 1988 than in Pendleton 1988 or in Moro and Pendleton in 1987 were probably due to a severe drought in Moro in the fall and winter of the 1987/88 season. Tres and Tyee produced substantially fewer heads relative to their pure stands in Moro 1988 than in Pendleton 1988 and also less than in Moro and Pendleton in 1987 (Finckh and Mundt, 1992), suggesting that Jacmar was more drought-tolerant than Tres and Tyee.

The effects of cultivar interactions on disease have been elucidated only partially in this paper. An increase or decrease in competition for resources might also directly alter the response of plants to disease. Such effects could have acted on Jacmar at the Moro site under the drought conditions in 1988, which kept the taller

cultivars almost as short as Jacmar. In the inoculated experiment, Jacmar performed considerably better in 1988 than in 1987 (Table II. 6). However, when mixed with Tres, the disease severity on Jacmar was 49% in 1988 but only 21% in 1987 (Table II. 4). One explanation for this counterintuitive result could be that a decrease in competition from Tres could have rendered Jacmar more tolerant to disease, explaining why it produced relatively more tillers in 1988 than in 1987 despite the much higher disease severity. In subsequent experiments, we found that disease severity on cultivars in mixtures was affected not only by selection and epidemiological effects, but also depended on the genotype of the companion cultivar (Finckh and Mundt, unpublished data).

Our study has shown that disease reduction in mixtures can be partitioned into selection and epidemiological effects. Differences in disease reduction between mixtures of a resistant and a susceptible cultivar and mixtures of two differentially susceptible cultivars could be partially ascribed to differential survival and/or tiller production of mixture components. Because in our experiments selection often favored the resistant cultivar in mixtures, the total percent disease reduction was often greater in mixtures of a resistant and a susceptible cultivar than in mixtures of two differentially susceptible cultivars. For the practical use of mixtures for disease control not only

the resistance genes of the prospective mixture components, but also their competitiveness, need to be taken into account.

Table II.1. Wheat cultivars used in field experiments and their chaff colors, heights, and reactions to two stripe rust races

Cultivar	Chaff color	Relative height	Reaction <sup>a</sup> to <u>Puccinia striiformis</u> race	
			5	27
Faro	brown	medium	VAR	R
Jacmar	brown	short	S	R
Moro	brown	tall	S	R
Tres	white	medium	MR	R
Tyee	white	medium	R	S

<sup>a</sup>VAR = reaction variable, approximately one-half of the plants were resistant and one-half susceptible; R = resistant; S = susceptible; MR = moderately resistant.

Table II.2. Wheat populations studied in cultivar mixture experiments in the field in 1986/87 and 1987/88

Population	Season	
	1986/87	1987/88
Faro-Jacmar-Moro-Tres-Tyee	yes	-
Faro-Jacmar-Moro-Tres	yes <sup>x</sup>	-
Faro-Jacmar-Moro-Tyee	yes <sup>x</sup>	-
Faro-Jacmar-Tres-Tyee	yes	yes
Faro-Moro-Tres-Tyee	yes	-
Jacmar-Moro-Tres-Tyee	yes	-
Faro-Jacmar-Moro	yes	-
Faro-Jacmar-Tres	yes <sup>x</sup>	yes <sup>x</sup>
Faro-Jacmar-Tyee	yes <sup>x</sup>	yes <sup>x</sup>
Faro-Moro-Tres	yes <sup>x</sup>	-
Faro-Moro-Tyee	yes <sup>x</sup>	-
Faro-Tres-Tyee	yes	yes <sup>x</sup>
Jacmar-Moro-Tres	yes <sup>x</sup>	-
Jacmar-Moro-Tyee	yes <sup>x</sup>	-
Jacmar-Tres-Tyee	yes	yes <sup>x</sup>
Moro-Tres-Tyee	yes	-
Faro-Jacmar	yes	yes
Faro-Moro	yes	-
Faro-Tres	yes <sup>x</sup>	yes <sup>x</sup>
Faro-Tyee	yes <sup>x</sup>	yes <sup>x</sup>
Jacmar Moro	yes	-
Jacmar-Tres	yes <sup>x</sup>	yes <sup>x</sup>
Jacmar-Tyee	yes <sup>x</sup>	yes <sup>x</sup>
Moro-Tres	yes <sup>x</sup>	-
Moro-Tyee	yes <sup>x</sup>	-
Tres-Tyee	yes	yes
Faro	yes <sup>x</sup>	yes <sup>x</sup>
Jacmar	yes <sup>x</sup>	yes <sup>x</sup>
Moro	yes <sup>x</sup>	-
Tres	yes <sup>x</sup>	yes <sup>x</sup>
Tyee	yes <sup>x</sup>	yes <sup>x</sup>
Jacmar-Tres <sup>y</sup>	-	yes
Stephens <sup>y</sup>	yes <sup>x</sup>	-
Stephens <sup>y</sup>	yes	-

<sup>x</sup>Single tillers were assessed for disease and tagged.

<sup>y</sup>Control treatments for the effect of tagging on yield.

Table II.3. Severity of stripe rust of wheat in pure stands and mixtures and percent reduction in disease severity due to mixing at three locations in 1987 and two locations in 1988

Population	Location					
	Moro		Pendleton		Corvallis	
	Severity <sup>a</sup> (%)	Reduction <sup>b</sup> (%)	Severity (%)	Reduction (%)	Severity (%)	Reduction (%)
1987						
FJMR <sup>c</sup>	12.94	51.4*	20.53	37.1***	1.26	77.1
FJMY	27.02	18.9	30.46	29.7***	7.74	68.0**
FJR	15.30	52.3***	16.69	47.5**	0.19	97.1
FJY	27.18	33.7*	27.34	40.7**	10.78	65.8**
FMR	3.18	63.1	11.13	45.9*	1.45	76.6
FMY	6.70	61.9	10.63	69.5**	16.53	38.3*
FR	6.33	19.1	6.24	53.0	0.27	83.5
FY	10.91	48.7	18.32	47.2**	14.86	62.0**
JMR	7.67	74.7**	11.93	66.3**	0.71	88.6
JMY	17.69	55.0**	21.79	56.2**	18.65	40.2***
JR	6.75	83.3**	14.49	59.3**	1.91	76.7
JY	24.74	54.1**	29.81	47.7**	42.77	6.3
MR	4.47	15.2	4.52	75.9***	0.36	68.1
MY	12.35	34.0	17.71	55.9**	31.93	17.2
F	15.33		24.18		3.29	
J	80.54		68.86		16.37	
M	10.22		35.15		2.21	
R	0.33		2.36		0.02	
Y	27.19		45.24		74.91	

Table II.3. (continued)

Population	Location					
	Moro		Pendleton		Corvallis	
	Severity <sup>a</sup> (%)	Reduction <sup>b</sup> (%)	Severity (%)	Reduction (%)	Severity (%)	Reduction (%)
1988						
FJR	16.23	42.8**	4.88	70.6**		
FJY	28.96	35.6***	13.20	55.3**		
FR	8.76	35.9	3.32	28.3		
FRY	13.38	51.0**	8.66	47.1***		
FY	20.74	46.2**	13.00	46.0**		
JR	24.49	21.9	4.94	76.2**		
JRY	18.58	52.5**	14.35	47.1**		
JY	35.72	36.4**	27.79	30.9**		
F	22.44		8.24			
J	57.81		40.52			
R	4.86		1.04			
Y	54.58		39.88			

<sup>a</sup>Percent of F-1 leaf area covered with stripe rust.

<sup>b</sup>Percent reduction relative to the mean of the pure stands of the mixture components.

<sup>c</sup>F = Faro, J = Jacmar, M = Moro, R = Tres, Y = Tyee.

\*, \*\*, \*\*\* Reduction was significant at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).



Table II.4. Severity of stripe rust in two-way mixtures of wheat cultivars on a per-cultivar basis, on whole plots, or as percent reduction relative to pure stands, and subdivision of percent reduction into selection and epidemiological effects in 1987 and 1988

Mixture components		Disease severity per cultivar <sup>a</sup>				Disease per plot <sup>f</sup>	Reduction (%)	Selection <sup>c</sup> effect	Epidemiological <sup>d</sup> effect
		Brown <sup>*</sup> White		Brown White					
Corvallis 1987									
Faro	Tres	0.7	(3.3)	0.1	(0.02)	0.27	84	5	79
Faro	Tyee	1.8	(3.3)	31.7	(74.9)	14.86	62	5	57
Jacmar	Tres	6.3	(16.4)	0.2	(0.02)	1.91	77	17	60
Jacmar	Tyee	29.6	(16.4)	54.6	(74.9)	42.77	6	-11	17
Moro	Tres	0.8	(2.2)	0.1	(0.02)	0.36	68	5	63
Moro	Tyee	1.8	(2.2)	58.4	(74.9)	31.93	18	- 4	21
Moro 1987									
Faro	Tres	11.8	(15.3)	0.4	(0.3)	6.33	19	- 5	24
Faro	Tyee	11.3	(15.3)	11.6	(27.2)	10.91	49	5	43
Jacmar	Tres	21.1	(80.5)	0.4	(0.3)	6.75	83	10	73
Jacmar	Tyee	39.6	(80.5)	12.4	(27.2)	24.74	54	2	53
Moro	Tres	3.7	(10.2)	3.3	(0.3)	4.47	68	47	20
Moro	Tyee	8.5	(10.2)	19.4	(27.2)	12.35	34	7	27
Pendleton 1987									
Faro	Tres	12.4	(24.2)	1.7	(2.4)	6.24	53	8	45
Faro	Tyee	15.6	(24.2)	20.5	(45.2)	18.32	47	4	43
Jacmar	Tres	47.1	(68.9)	1.7	(2.4)	14.49	59	35	25
Jacmar	Tyee	40.4	(68.9)	22.9	(45.2)	29.81	48	1	46
Moro	Tres	8.2	(35.2)	2.2	(2.4)	4.52	76	9	67
Moro	Tyee	9.0	(35.2)	28.2	(45.2)	17.71	56	1	55

Table II.4. (continued)

Mixture components		Disease severity per cultivar <sup>a</sup>				Disease per plot <sup>f</sup>	Reduction (%)	Selection <sup>c</sup> effect	Epidemiological <sup>d</sup> effect
		Brown <sup>e</sup> White		Brown	White				
Moro 1988									
Faro	Tres	11.2	(22.4)	6.1	(4.9)	8.76	36	- 2	38
Faro	Tyee	15.1	(22.4)	31.6	(54.6)	20.74	46	8	39
Jacmar	Tres	48.8	(57.8)	8.0	(4.9)	24.49	22	15	7
Jacmar	Tyee	41.6	(57.8)	28.9	(54.6)	35.72	36	0	37
Pendleton 1988									
Faro	Tres	5.0	(8.2)	1.5	(1.0)	3.32	29	- 6	35
Faro	Tyee	5.0	(8.2)	22.7	(39.9)	13.00	46	5	41
Jacmar	Tres	13.7	(40.5)	1.8	(1.0)	4.94	76	24	53
Jacmar	Tyee	9.1	(40.5)	40.2	(39.9)	27.79	31	0	31

<sup>a</sup>Percent of F-1 leaf area covered with stripe rust. Disease per cultivar represents the average over all tagged tillers with a given chaff color (between 5 and 10% of the tags were lost in each plot; disease data from untagged tillers could be used to compute the mean disease severity in a plot, however those data were ignored when determining the disease severity on a per-cultivar basis). Numbers in brackets represent disease severity of same cultivar in pure stand.

<sup>b</sup>Percent disease reduction relative to pure stand mean.

<sup>c</sup>Selection effect is the percent decrease or increase in disease severity in a mixture due to changes in frequencies of the mixture components.

<sup>d</sup>Epidemiological effect is the percent reduction in disease severity below the mean of the pure stands weighted by the harvested cultivar frequencies.

<sup>e</sup>Brown and white refers to chaff color.

<sup>f</sup>Disease per plot is based on all assessed tillers regardless if chaff color could be determined.

Table II.5. Number of tillers per plot for wheat cultivars grown in pure stands in the presence and absence of stripe rust in field experiments at three locations in 1987 and at two locations in 1988

Number of tillers per plot <sup>y</sup>		
	Inoculated	Fungicide
Corvallis 1987		
Faro	146.8 a	164.5 a <sup>z</sup>
Jacmar	130.3 ab	141.5 a
Moro	97.0 c	102.3 b
Tres	136.5 a	164.0 a
Tyee	115.5 bc	145.3 a
Moro 1987		
Faro	160.3 a	178.0 a
Jacmar	134.0 ab	117.3 b
Moro	134.7 ab	140.3 ab
Tres	134.7 ab	137.7 ab
Tyee	113.7 b	109.7 b
Pendleton 1987		
Faro	146.0 a	135.5 a
Jacmar	114.0 b	122.3 ab
Moro	124.8 ab	100.0 b
Tres	129.0 ab	115.0 ab
Tyee	108.5 b	127.0 a
Moro 1988		
Faro	163.5 a	152.5 a
Jacmar	134.2 b	144.5 a
Tres	137.3 b	130.2 ab
Tyee	124.3 b	109.0 b
Pendleton 1988		
Faro	132.2 a	131.0 a
Jacmar	92.7 b	111.2 b
Tres	110.7 ab	99.5 b
Tyee	102.8 b	112.2 b

<sup>y</sup>Plot size depended on tiller density and was not the same for all locations and years. See text for details.

<sup>z</sup>Numbers within column followed by the same letter for each site/year combination are not significantly different at  $P < 0.05$  (Fisher's unprotected LSD).

Table II.6. Tiller frequencies<sup>a</sup> of wheat cultivars grown in mixtures in presence and absence of stripe rust in three locations in 1987 and in two locations in 1988

Mixture Brown <sup>b</sup> White		Location					
		Moro		Pendleton		Corvallis	
		Inoc. <sup>c</sup>	Fung. <sup>d</sup>	Inoc.	Fung.	Inoc.	Fung.
1987							
Faro	Tres	0.53	0.45	0.44	0.45	0.46	0.47
Faro	Tyee	0.64	0.61	0.63	0.56	0.56	0.56
Jacmar	Tres	0.33	0.32	0.25	0.35	0.35	0.29
Jacmar	Tyee	0.46	0.46	0.46	0.46	0.43	0.50
Moro	Tres	0.15	0.38	0.33	0.37	0.40	0.39
Moro	Tyee	0.61	0.58	0.58	0.60	0.47	0.49
1988							
Faro	Tres	0.54	0.55	0.57	0.54		
Faro	Tyee	0.64	0.66	0.56	0.53		
Jacmar	Tres	0.42	0.43	0.29	0.29		
Jacmar	Tyee	0.60	0.57	0.37	0.42		

<sup>a</sup>Frequency of brown tillers is listed; white tiller frequency = 1 - brown frequency.

<sup>b</sup>Brown cultivars = Faro, Jacmar, and Moro; white cultivars = Tres and Tyee.

<sup>c</sup>Inoc. = plots inoculated with stripe rust.

<sup>d</sup>Fung. = plots treated with fungicide.

# Literature Cited

- Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition in monocultures and mixtures of two wheat cultivars. *Plant Pathol.* 35:457-465.
- Allard, R. W. 1960. Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1:127-133.
- Allard, R. W., and Adams, J. 1969. Population studies in predominantly self-pollinating species XIII. Intergenotypic competition and population structure in barley and wheat. *Am. Naturalist* 103:620-645.
- Barrett, J. A. 1978. A model of epidemic development in variety mixtures. In: *Plant Disease Epidemiology*. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 129-137.
- Borlaug, N. E. 1959. The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants. *Proc. 1st Int. Wheat Genet. Symp.*, 1958, pp. 12-27.
- Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7:355-382.
- Burdon, J. J., Groves, R. H., Kaye, P. E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. *Oecologia* 64:199-203.
- Chin, K. M., and Wolfe, M. S. 1984. Selection on Erysiphe graminis in pure and mixed stands of barley. *Plant Pathol.* 33:535-546.
- Finckh, M. R., and Mundt, C. C. 1992. Effects of stripe rust and plant competition on yield of wheat cultivar mixtures. *Phytopathology* 82: (submitted as companion paper)
- Jennings, P. R., and De Jesus, J. Jr. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. *Evolution* 22:119-124.
- Jensen, N. F. 1952. Intra-varietal diversification in oat breeding. *Agron. J.* 44:30-34.

- Knott, E. A., and Mundt, C. C. 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and non-diseased conditions. *Theor. Appl. Genet.* 80:313-320.
- Leonard, K. J. 1969a. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. *Phytopathology* 59:1845-1850.
- Leonard, K. J. 1969b. Selection in heterogeneous populations of Puccinia graminis f. sp. avenae. *Phytopathology* 59:1851-1857.
- Leonard, K. J., and Czocho, R. J. 1980. Theory of genetic interactions among populations of plants and their pathogens. *Annu. Rev. Phytopathol.* 18:337-358.
- Mahmood, T., Marshall, D., and McDaniel, M. E. 1991. Effect of winter wheat cultivar mixtures on leaf rust severity and grain yield. *Phytopathology* 81:470-474.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity and cereal rust management. In: *The Cereal Rusts Vol. II.* A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando. pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: Effect of genotype unit area. *Phytopathology* 75:607-610.
- Mundt, C. C., and Leonard, K. J. 1985. Effect of host genotype unit area on epidemic development of crown rust following focal and general inoculations of mixtures of immune and susceptible oat plants. *Phytopathology* 75:1141-1145.
- Mundt, C. C., and Leonard, K. J. 1986. Analysis of factors affecting disease increase and spread in mixtures of immune and susceptible plants in computer-simulated epidemics. *Phytopathology* 76:832-840.
- Mundt, C. C., and Leonard, K. J. 1986. Effect of host genotype unit area on development of focal epidemics of bean rust and common maize rust in mixtures of resistant and susceptible plants. *Phytopathology* 76:895-900.
- Nitzsche, W., and Hesselbach, J. 1983. Sortenmischungen statt Vielliniensorten. *Z. Pflanzenz.* 90:68-74.
- Norrington-Davies, J., and Hutto, J. M. 1972. Diallel

- analysis of competition between diploid and tetraploid genotypes of Secale cereale grown at two densities. J. Agric. Sci. Camb. 78:251-256.
- SAS Institute Inc. 1988. SAS/STAT User's Guide Ed. 6.03. SAS Institute, Cary, NC. 1029 pp.
- Suneson, C. A. 1956. An evolutionary plant breeding method. Agron. J. 48:188-191.
- Vanderplank J. E. 1968. Disease Resistance in Plants. Academic Press, New York.
- Wolfe, M. S. 1978. Some practical implications of the use of cereal variety mixtures. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 201-207.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. Annu. Rev. Phytopathol. 23:251-273.
- Wolfe, M. S., and Barrett, J. A. 1980. Can we lead the pathogen astray? Plant Dis. 64:148-155.
- Wolfe, M. S., Barrett, J. A., and Jenkins, J. E. E. 1981. The use of cultivar mixtures for disease control. In: Strategies for the Control of Cereal Diseases. J. F. Jenkyn and R. T. Plumb, eds. Blackwell, Oxford. pp. 73-80.

III. Effects of Stripe Rust and Plant Competition  
on Yield of Wheat Cultivar Mixtures

Maria R. Finckh and Christopher C. Mundt

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

Paper No. \_\_\_\_ of the journal series of the Oregon  
Agricultural Experiment Station.

Supported in part by the USDA STEEP Program and the Oregon  
Wheat Commission.

Accepted for publication 00 00000 0000.



**Abstract**

Finckh, M. R., and Mundt, C. C. 1991. Effects of stripe rust and plant competition on yield of wheat cultivar mixtures. *Phytopathology* 91:000-000.

Mixtures of two-to-five winter wheat (Triticum aestivum) cultivars and their component pure stands were either exposed to or protected from two stripe rust (Puccinia striiformis) races at three and two locations in 1986/87 and 1987/88, respectively. Yield components were determined on a per-cultivar basis for a subset of the mixtures and also for the pure stands. In the absence of disease, mixtures yielded between 0 and 5% more than the mean of the pure stands. In the presence of disease, mixing increased yield between 8 and 13%. Early competitive advantage of a cultivar in tillering often was counteracted by a reduction in yield per head, indicating that competition among cultivars did not remain constant throughout the season. Environmental conditions influenced the effects of disease on plant performance indirectly by affecting the competitive abilities of the cultivars.

Additional keywords: genetic diversity, ecological combining ability

## Introduction

Recognition of the importance of host-pathogen population dynamics in agricultural systems has led plant pathologists and breeders to develop new approaches and strategies to control plant diseases. A strategy that has been shown to be effective, especially for the control of airborne diseases, is the spatial deployment of cultivars with different resistance genes (Browning and Frey, 1969; Mahmood et al., 1991; Wolfe, 1985). Resistance genes can be deployed by growing mixtures of host cultivars that are similar for important agronomic traits, but which possess diversity for disease resistance.

Mixtures have frequently been reported to increase yield (e.g. Allard, 1960; Allard and Adams, 1969; Borlaug, 1959; Jensen, 1952; Mahmood et al., 1991; Nitzsche and Hesselbach, 1983; Norrington-Davies and Hutto, 1972; Wolfe, 1978; Wolfe et al., 1981). In an experiment with two-way mixtures of four different wheat cultivars, however, Klages (1936) found that yields of mixtures were almost always lower than expected. Yielding ability of a cultivar in a mixture and in pure stand are not necessarily correlated. For example, Suneson and Wiebe (1942) and Suneson (1949) found that the proportion of a barley (Hordeum vulgare) cultivar greatly declined in mixtures, despite the fact that it had a significantly better yield and leaf disease

resistance record in pure stand than the other cultivars tested.

Such contrasting results indicate that interactions among plant genotypes in mixture are complex. This was confirmed by Allard and Adams (1969), who distinguished between neighborhood and competitive effects in mixtures, and introduced the term ecological combining ability. Genotypes possess good ecological combining ability if they are both good competitors (yield higher when bordered by other genotypes than when bordered by themselves) and good neighbors (induce a mean increase in yield on a different, bordering genotype).

Mixtures of plant genotypes mostly have been studied either for their effect on disease (Barrett, 1978; Borlaug, 1959; Browning and Frey, 1969; Leonard, 1969; Mundt and Browning, 1985a,b; Mundt and Leonard, 1985, 1986 a,b, among others) or for their effect on yield (Allard, 1969; Allard and Adams, 1969; Klages, 1936; Nitzsche and Hesselbach, 1983; Norrington-Davies and Hutto, 1972; Suneson, 1949). Of course, when studying one phenomenon the other was usually recognized by the researchers (e.g., Mahmood et al., 1991; Wolfe and Barrett, 1980). However, little or no data are available that separate the contribution of disease control from other factors that influence the yield of mixtures. To gain insight into the effects of disease on interactions among different plant genotypes, and

effects of host genetic composition on disease severity, it is necessary to study the population dynamics of host mixtures in both the absence and presence of disease.

Knott and Mundt (1990) analyzed field trials of inoculated and non-inoculated two-way mixtures of five wheat cultivars (Triticum aestivum L.) that were differentially susceptible to two races of stripe rust (Puccinia striiformis Westend. (=P. glumarum (Schm.) Jacob, Eriksson & Henn.)) with combining ability analysis. Their analysis allowed identification of cultivars that combined well with respect to yielding ability and disease control, but it provided no insight into how the yields of the mixtures were influenced by competition and by neighborhood effects. Also, the composition of the mixtures at harvest could not be predicted. In this paper, we provide a more detailed analysis of the nature of the interactions between different cultivars using data derived from the experiments described by Knott and Mundt (1990). In a separate paper, we analyzed the interactive effects of disease and plant-plant interactions in mixtures (Finckh and Mundt, 1992).

## **Materials and Methods**

The experiments were part of a field trial designed to screen wheat cultivar mixtures for their performance with respect to yield and disease.

### **Cultivars.**

Five soft white, club-type winter wheat cultivars were used. Their characteristics with respect to stripe rust resistance, height, and chaff color are summarized in Table III.1.

### **Locations.**

Experiments were conducted at three locations in Oregon. Pendleton and Moro, located in the semi-arid region of eastern Oregon, receive approximately 450 and 300 mm annual precipitation, respectively. Corvallis is located in the Willamette Valley in western Oregon, and receives approximately 1000 mm annual precipitation.

### **Experimental design.**

The experiments have been described in detail by Finckh and Mundt (1992). In 1986/87, all possible two-to-five way combinations of equal proportions of germinable seed of Faro, Jacmar, Moro, Tres, and Tyee and their pure stands were planted in a randomized complete block design

with four replications in all three locations. In 1987/88, six replications of all possible two-to-four way combinations of Faro, Jacmar, Tres, and Tyee and their pure stands were grown at Pendleton and Moro. Two experiments were conducted in each location. One experiment was protected from stripe rust with three-to-four applications of Bayleton (triadimefon) at 284g a.i. per ha. This provided complete protection from stripe rust in both years and locations. The other experiment was inoculated with stripe rust. The inoculated experiment was located 12 m downwind from the fungicide-treated experiments at each site. The area between experiments was planted to the resistant wheat cultivar Stephens or to barley (Hordeum vulgare) to reduce interplot interference.

#### **Inoculation.**

Plots were inoculated with a mixture of race 5 and race 27 of Puccinia striiformis. Inoculation procedures were described by Finckh and Mundt (1992). Inoculations took place in late fall of each season and, if necessary, they were repeated in early spring. In Corvallis 1987, disease severity on Faro, Jacmar, and Moro was much lower than in Pendleton and Moro despite reinoculation in spring (Table III.2).

**Harvest.**

Subplots containing a minimum of 120 tillers were marked within each plot approximately midway between the center and the end of the plot. Subplots were limited to the two center rows of the four-row plots and the four center rows of the six-row plots. Length of the subplots was determined by tiller density, therefore, subplot sizes varied among years and locations and ranged from 30 to 66 cm in length. Upon maturity, all tillers in each subplot of the inoculated and fungicide-treated experiments were cut with sickles and bagged. Heads were separated by chaff color and heads of each color were counted, threshed separately with a stationary plot thresher, and seed weight per subplot and 1000-seed weight were recorded.

**Data analysis.**

Data were analyzed using SAS (1988). One-way analyses of variance were performed for each experiment in each location. Fisher's non-protected LSD and linear contrasts were used to determine significance of treatment differences for yield components. In Moro and Corvallis 1987, the yield of the resistant cultivar Tres was considerably higher in the fungicide-treated experiments than in the inoculated experiments (Table III.2). Also, the barley in the plots surrounding the experiments grew taller and lusher around the fungicide-treated experiments,

indicating that the soil conditions might have differed between the two experiments. Therefore, no analysis of the effects of disease on total yield of the pure stands was performed across locations. For the mixtures, yield data were expressed relative to the mean of the mixture components within each experiment, thus reducing the effects of differences in soil on yield. This allowed for a two-way analysis of the mixture treatment means across locations within each year, using location as replication. The two factors were mixture treatment and inoculation versus fungicide control. Thus, each treatment had three replications (locations) in 1987 and two replications (locations) in 1988 for both inoculation and fungicide treatments.



## Results

### Yield and yield components of the pure stands,

Pure stands of Faro, Jacmar, Tres, and Tyee did not differ significantly in yield in the fungicide-treated experiments in either year, except in Pendleton 1988 where the yield of Faro was significantly higher than the yield of Jacmar and Tres (Table III.2). The cultivar Moro yielded significantly less than the other cultivars in all three locations in 1987. Faro produced consistently more heads than the other cultivars; this was rarely statistically significant, however. The higher tillering of Faro was counteracted by either a low seed weight or a low number of seed per head compared to the other cultivars.

Differences in yield among the five cultivars were considerably larger when inoculated than when fungicide-treated (Table III.2). In addition, the yields of the most susceptible cultivars (Jacmar and Tyee) were always substantially greater in the fungicide-treated than in the inoculated experiments. The high yield of Jacmar relative to Faro and Tres in the inoculated experiment in Corvallis 1987 could be due to the low disease severity on Jacmar at that site (Table III.2).

Overall differences between inoculated and fungicide-treated plots were usually small for Faro, Moro, and Tres,

and yield was not always higher in the fungicide-treated plots of these cultivars. There was little difference between number of heads produced in the presence and absence of disease. However, the 1000 seed weight and number of seed per head were smaller in the inoculated experiments. Differences between inoculated and fungicide-treated experiments were greater for Jacmar and Tyee than for Faro, Moro, and Tres.

#### **Yield and yield components of mixtures.**

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

Mixtures produced approximately the same number of heads than the mean of the pure stands in both years, but the 1000 seed weight was usually increased in mixtures (Table III.4). No single mixture had a significantly lower seed weight than the mean of the component pure stands. In 1987, 83% of the fungicide-treated mixtures had fewer seed per head than the corresponding pure stands. The differences in number of seed per head between mixtures and

pure stands were significant at  $P < 0.05$  in Moro and Pendleton and at  $P = 0.11$  in Corvallis (Table III.4). In contrast, the number of seed per head was lower than the pure-stand mean in only 23% of the inoculated mixtures. In 1988, the difference in seed per head relative to the pure stand means between the fungicide-treated and the inoculated mixtures were much smaller in both locations.

#### **Competitive interactions among cultivars in mixtures,**

In the presence of Tres, the relative yield of Faro, Jacmar and Moro was significantly lower than in the presence of Tyee in all experiments in both seasons (Table III.5). Similarly, the relative number of heads, seed weight, and number of seed per head of Faro, Jacmar, and Moro were consistently lower when mixed with Tres than when mixed with Tyee, although these effects were not always statistically significant (data not shown). Correspondingly, the relative yield of Tres in mixtures was always significantly higher than the relative yield of Tyee, except in the inoculated experiment in Corvallis 1987 (Table III.5).

The relative yield of Faro was always greater than the relative yield of Jacmar (Table III.5). This trend was consistent, but not always statistically significant, for the number of heads, seed weight, and number of seed per head. Also, the relative yield of Tres and Tyee was lower

in the presence of Faro than in the presence of Jacmar. Again, the yield components were consistently, but not always significantly, lower in the presence of Faro.

A more detailed analysis of the two-way mixtures containing one brown-chaffed and one white-chaffed cultivar (Tables III.6 and III.7) provides additional insight into competitive interactions among the cultivars. The number of tillers produced by a cultivar in mixture relative to its pure stand provided an estimate of interference between cultivars during early development. As overall number of tillers did not differ between mixtures and pure stands, relative yield per head reflected cultivar interactions after tillering rather than effects of density on yield. Relative yield per cultivar provided a cumulative measure of interference effects throughout the season.

Based on relative number of heads produced in two-way mixtures (Tables III.6 and III.7), the rank order of the cultivars was very consistent in all of the experiments in 1987. In general, the ranking was Tres > Moro = Faro > Tyee > Jacmar. The performance of Faro and Moro relative to each other was variable among the sites and inoculation treatments. In 1988, ranking by tillering ability was more ambiguous and not consistent among inoculation treatments and sites. Overall, however, Tres and Faro still appeared to be better tiller-producers than Jacmar and Tyee.

The effects of competition on yield per head were

variable among locations and, to a lesser degree, within locations. Yield per head of Jacmar was affected in a way similar to its number of heads. In contrast, the relative yield per head could not be predicted from the relative number of heads for the other four cultivars.

Fig. III.1 gives an overview of the relative performance of the cultivars in mixtures. Mixtures that fall above the expected line, the majority of the mixtures, yielded more than the mean of their component pure stands. Most mixtures fall in the lower right quadrants, indicating that Tres and Tyee were superior competitors. Also, differences in competitive abilities of the cultivars are evident. For example, mixtures containing Tres usually fall further to the right than mixtures containing Tyee. Similarly, mixtures with Jacmar fall lower than mixtures with Faro and Moro. Correlations between relative yield of mixture components were significant in both years and under diseased and non-diseased conditions ( $P < 0.01$ ) (Fig. III.1).

Although neither the slopes nor the intercepts of the regression lines in Fig. III.1 were significantly different from the expected lines, some distinct trends were discernible. Except for the fungicide-treated experiments in 1988, distance between the regression lines and the expected lines increased with the improvement of the performance of the white cultivars (right quadrants in Fig. III.1), indicating that the corresponding decrease in

relative yield of the brown cultivars was not as strong as the increase in relative yield of the white cultivars. On the other hand, in cases where Faro, Jacmar, and Moro were the better competitors (top quadrants in Fig. III.1), the yield decrease of Tres and Tyee was somewhat stronger than the corresponding increase of Faro, Jacmar, and Moro. In only a few mixtures did both cultivars yield higher than expected (Fig. III.1 upper right quadrants). All of these mixtures contained Tyee. Also, the majority of the mixtures that contained Tyee fall above the regression lines whereas the majority of the mixtures that contained Tres fall below. Thus, Tyee was usually a less aggressive neighbor than Tres.

#### Effects of environment and disease.

The two-way analysis of the two-way mixtures over locations within seasons provides some insight into the interactions among plant genotypes in mixtures, disease, and environment. There were environment effects (caused by the different locations) on the relative yield of Faro and Tyee in 1987 ( $P < 0.05$  and  $P < 0.01$ , respectively) and on the relative yield of Jacmar and Tyee in 1988 ( $P < 0.05$  and  $P = 0.07$ , respectively). Faro, Jacmar, and Moro performed better in mixture in Pendleton and Moro than in Corvallis. Tres performed similarly in mixtures in all three locations, and the yield of Tyee in mixtures relative to

its pure stands was considerably higher in Corvallis than in Moro and Pendleton. In 1988, the relative yield of Jacmar was higher in Moro than in Pendleton. Both Tres and Tyee had relative yields that were lower in Moro than in Pendleton.

In 1987, the cultivar Moro consistently yielded relatively higher in the fungicide-treated than in the inoculated experiments. Except for the Moro site, Faro performed relatively better in the inoculated mixtures than in the fungicide-treated mixtures (Tables III.6 and III.7). Differences between inoculation treatments for Moro and Faro separately were not significant. However, the Faro vs. Moro x inoculation interaction was significant at  $P < 0.05$ . In the inoculated experiments, the relative yield of Faro was slightly higher than Moro. In the fungicide-treated experiments, the relative yield of Faro was between 4 and 24% lower than Moro. Jacmar yielded relatively higher in the inoculated experiment in Moro, but lower in Pendleton and Corvallis. The relative yield of Tres and Tyee was higher in the presence of disease than in the absence of disease ( $P < 0.05$  for Tres,  $P < 0.1$  for Tyee).

In 1988, no significant effects of disease on the relative yields of the cultivars were found. To determine if disease had a different effect in 1987 than in 1988, a two-way analysis was performed on the subset of the 1987 data that included the same locations and mixtures as in

1988. The relative yield of Tres and Tyee in mixture was still 19% ( $P < 0.05$ ) and 13% ( $P < 0.1$ ) higher, respectively, in the presence of disease. Again, there was no effect of disease on the relative yields of Faro and Jacmar. Also, without the Corvallis data in the analysis, there was no environment effect in 1987.



## Discussion

The magnitude of the yield increases in our mixtures over the mean of their pure stands were similar to increases that were observed by others (Allard and Adams, 1969; Mahmood et al., 1991; Nitzsche and Hesselbach, 1983; Wolfe and Barrett, 1980). Although only few mixtures yielded higher than the highest yielding pure stand in a given location and year, no mixture yielded less than the lowest yielding pure stand. Our data support the view of Wolfe and Barrett (1982) and Mahmood et al. (1991) that cultivar mixtures should help reduce risks involved in choosing cultivars because it is usually impossible to predict the best yielding cultivar prior to planting.

The treatments utilized precluded a formal competition analysis as proposed by others (Firbank and Watkinson, 1985; Jolliffe et al., 1984; Spitters, 1983a,b), because no yield-density function was determined for the cultivars. Nevertheless, differences in competitive abilities of the cultivars were evident. Variable competitiveness of the cultivars among locations and years might be partially explained by climatic conditions. By affecting plant competitiveness, climatic conditions also influenced the effect of disease on cultivar performance. For example, in Moro, the yield of Jacmar relative to its pure stand when mixed with Tres in the absence of disease was much higher

in 1988 than in 1987. Also, the relative yield of Tres was lower in 1988 than in 1987 (Table III.7). The increased competitiveness of Jacmar in 1988 could have been due to the greater drought tolerance of Jacmar in contrast to Tres. In the inoculated experiments, disease severity on Jacmar in mixtures with Tres was 21.1% and 48.8% in Moro 1987 and 1988, respectively (Finckh and Mundt, 1992). Despite this higher disease severity, the relative yield of Jacmar was higher and the relative yield of Tres was lower in 1988 than in 1987 (Table III.6).

Disease probably also affected the competitive abilities of the cultivars. Tres was almost disease-free and disease severity on Tyee in mixtures was considerably lower than on Faro and Jacmar in 1987 (Finckh and Mundt, 1992). This may have reduced competition from Faro and Jacmar and increased the relative yield of Tres and Tyee. Effects of disease on the competitive ability of plants in mixtures have been reported in other host-pathogen systems (e.g. Burdon et al., 1984; Paul and Ayres, 1986, 1987).

Despite the presumed effect of disease on their competitive abilities, the yield of Faro and Jacmar relative to their pure stands did not differ between the diseased and the non-diseased mixtures. This may be due to the fact that cultivar performance in mixtures was determined relative to the performance of the cultivars in the pure stands. Such a comparison is straight-forward in

non-diseased mixtures. However, we compared the performance of cultivars in diseased mixtures with their pure stands that were more heavily diseased. For example, in Pendleton and Moro 1987, disease severity on Jacmar in mixtures was reduced from an average of 69% and 81% in pure stands to an average of 47% and 30% in mixtures, respectively (Finckh and Mundt, 1992). Therefore, one might expect a cultivar to perform better in mixture simply because of disease reduction. Thus, the lack of improvement in performance of Jacmar in 1987 may actually indicate competition from Tres and Tyee.

When both mixture components were susceptible, environmental and disease effects on competition could not be readily separated. For example, in the absence of disease, competitive interactions between Jacmar and Tyee were reversed in Moro between 1987 and 1988. Tyee was the stronger competitor in 1987 whereas Jacmar was more competitive in 1988 (Table III.7) which could be due to its greater drought tolerance. Disease severities in Moro 1987 on Tyee and Jacmar were 12.4 and 39.6%, respectively (Finckh and Mundt, 1992), and in the presence of disease, the competitiveness of Tyee was considerably greater in Moro 1987. In contrast, in 1988, disease severities were 41.6 and 28.9% on Jacmar and Tyee, respectively (Finckh and Mundt, 1992), and the competitive ability of Tyee was decreased in the presence of disease (Table III.6). The

smaller difference in disease severity as well as the drought might have contributed to the change in competitive interactions.

Competition among cultivars did not remain constant throughout the season. The competitive advantage of Tres and Tyee was mainly established early in the season through greater tiller production, whereas the yield per head was often less than in the pure stands and less than that of the companion cultivars. In contrast, Faro, Jacmar, and Moro were often less affected in yield per head than in tiller production. Depending on the mixture, location, and treatment, competitive interactions between mixture components were reduced, enhanced, or sometimes even reversed from the early season to the late season (Tables III.6 and III.7).

In common with others (Suneson, 1949; Suneson and Wiebe, 1942), we found that the performance of a cultivar in pure stand was not always indicative of its performance in mixtures. The poor performance of Jacmar in the mixtures could be due to its shortness. No height measurements were taken in 1987, but the pure stands of Jacmar and Moro could be identified without difficulty as the smallest or tallest stands, respectively. In Pendleton 1988, Jacmar was between 11 and 26 cm shorter than the other cultivars, and in Moro 1988 it was between 7 and 16 cm shorter. Poor performance of a cultivar in rice

cultivar mixtures has been ascribed to its shortness relative to other mixture components (Jennings and de Jesus, 1968). However, Moro was by far the tallest cultivar, but its performance was not always improved by mixing.

Only few cultivar combinations possessed good ecological combining ability sensu Allard and Adams (1969), i.e., both components responded with a yield increase in mixtures (Fig. III.1 upper right quadrants). This is consistent with the work of Allard and Adams (1969) who found that good ecological combining ability was common in mixtures of barley lines that had coevolved for many generations, but that it was very rare among cultivars that had been selected as pure lines. Our results indicate that different degrees of competitiveness and neighborhood effects can result in similar effects on the total yield in mixtures. For example, in mixtures that contained Tres, yield increased despite the negative neighborhood effects of Tres on the other cultivars and was mainly due to the competitive ability of Tres. On the other hand, in mixtures with Tyee, yield increases were due to a combination of less negative and sometimes positive neighborhood effects of Tyee and its good competitive ability.

In small grain production, growers often do not purchase new seed every season. Therefore, growers who

want to use cultivar mixtures to stabilize yield and/or control disease need to know how long they can expect the seed harvested from mixtures to contain the mixture components at proportions that still provide the advantages of mixing. Mixtures in which the components perform very unequally will change in composition over time, possibly requiring remixing more often than mixtures of more similar components.

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

Table III.1. Wheat cultivars used in field experiments and their chaff colors, heights, and reactions to two stripe rust races

Cultivar	Chaff color	Relative height	Reaction <sup>a</sup> to <u>Puccinia striiformis</u> race	
			5	27
Faro	brown	medium	VAR	R
Jacmar	brown	short	S	R
Moro	brown	tall	S	R
Tres	white	medium	MR	R
Tyee	white	medium	R	S

<sup>a</sup>VAR = reaction variable, approximately one-half of the plants were resistant and one-half susceptible; R = resistant; S = susceptible; MR = moderately resistant.

Table III.2. Disease severity, yield, and yield components of five wheat cultivars grown as pure lines in the presence and absence of stripe rust in three locations in 1987 and two locations in 1988

Cultivar	Disease severity <sup>w</sup>	Yield per plot (g)				Heads per plot		1000 seed weight		Seed per head							
		Inoc. <sup>x</sup>		Fung. <sup>y</sup>		Inoc.		Fung.		Inoc.		Fung.					
Corvallis 1987																	
Faro	3.29	125.84	a	161.53	a <sup>z</sup>	146.75	a	164.50	a	32.20	ab	31.96	ab	26.65	b	31.02	bc
Jacmar	16.37	110.69	ab	152.65	a	130.25	ab	141.50	a	29.50	b	31.23	ab	28.53	ab	35.40	ab
Moro	2.21	113.31	ab	122.96	b	97.00	c	102.25	b	35.62	a	32.96	ab	33.16	a	36.46	a
Tres	0.02	124.43	a	149.52	a	136.50	a	164.00	a	34.92	a	33.53	a	26.25	b	27.61	c
Tyee	74.91	89.42	b	157.27	a	115.50	bc	145.25	a	28.93	b	30.58	b	27.01	b	35.46	a
Moro 1987																	
Faro	15.33	114.51	a	138.73	a	160.33	a	178.00	a	20.88	a	23.34	ab	34.19	a	33.67	b
Jacmar	80.54	90.09	ab	155.09	a	134.00	ab	117.33	b	21.68	a	29.15	a	31.69	a	45.29	a
Moro	10.22	70.02	b	96.44	b	134.67	ab	140.33	ab	18.55	a	21.13	b	27.99	a	32.55	b
Tres	0.33	91.50	ab	138.30	a	134.67	ab	137.67	ab	21.50	a	28.50	a	31.35	a	35.61	b
Tyee	27.19	81.44	ab	134.77	a	113.67	b	109.67	b	21.63	a	28.74	a	33.53	a	43.20	a
Pendleton 1987																	
Faro	24.18	117.07	ab	117.68	a	146.00	a	135.50	a	28.04	ab	30.22	bc	28.93	bc	28.75	c
Jacmar	68.86	85.91	c	126.97	a	114.00	b	122.25	ab	25.47	ab	28.52	c	29.61	b	36.54	a
Moro	35.15	83.12	c	74.92	b	124.75	ab	100.00	b	24.27	b	25.81	d	26.80	c	29.12	c
Tres	2.36	119.46	a	114.81	a	129.00	ab	115.00	ab	29.60	a	33.65	a	31.57	ab	29.89	bc
Tyee	45.24	94.96	bc	133.13	a	108.50	b	127.00	a	26.76	ab	30.75	b	32.73	a	34.17	ab
Moro 1988																	
Faro	22.44	181.17	a	180.43	a	163.50	a	152.50	a	27.95	a	29.16	ab	39.83	b	40.86	b
Jacmar	57.81	102.93	b	175.52	a	134.17	b	144.50	a	21.87	b	25.07	c	34.97	c	48.80	ab
Tres	4.86	176.14	a	186.07	a	137.33	b	130.17	a	28.25	a	31.47	a	45.77	a	46.02	ab
Tyee	54.58	121.50	b	151.02	a	124.33	b	109.00	a	23.47	b	27.75	bc	41.54	b	50.83	a



Table III.2. (continued)

Cultivar	Disease severity <sup>w</sup>	Yield per plot (g)		Heads per plot		1000 seed weight		Seed per head			
		Inoc. <sup>x</sup>	Fung. <sup>y</sup>	Inoc.	Fung.	Inoc.	Fung.	Inoc.	Fung.		
Pendleton 1988											
Faro	8.24	122.16 a	157.59 a	132.17 a	131.00 a	25.52 b	31.07 b	36.57 a	38.76 b		
Jacmar	40.52	58.77 c	136.18 b	92.67 b	111.17 b	21.45 c	30.14 bc	29.75 b	41.31 ab		
Tres	1.04	142.16 a	134.27 b	110.67 ab	99.50 b	33.94 a	33.68 a	37.96 a	40.80 ab		
Tyee	39.88	92.02 b	145.58 ab	102.83 b	112.17 b	24.30 b	29.35 c	36.94 a	44.24 a		

<sup>w</sup>Percent leaf area of the F-1 leaf covered with stripe rust. Data from (7).

<sup>x</sup>Inoc. = plots inoculated with stripe rust.

<sup>y</sup>Fung. = plots treated with fungicide.

<sup>z</sup>Numbers in column followed by the same letter for each sit/year combination are not significantly different at  $P < 0.05$  (Fisher's unprotected LSD).

Table III.3. Yield of wheat cultivar mixtures relative to the mean of the mixture components in pure stands in the presence and absence of stripe rust in three locations in 1987 and in two locations in 1988

Mixture	Location					
	Moro		Pendleton		Corvallis	
	Fung. <sup>a</sup>	Inoc. <sup>b</sup>	Fung.	Inoc.	Fung.	Inoc.
1987						
FJMY <sup>c</sup>	1.06	1.00	1.01	1.04	0.99	1.15
FJMR	1.03	1.15	1.16*	1.04	0.98	1.16
FJMY	1.01	1.04	1.14	1.11	1.14*	1.21**
FJRY	0.97	1.28**	1.09	1.16*	0.88	1.06
FMY	1.12*	1.36**	1.05	0.98	1.01	1.25**
JMY	0.96	1.21	0.97	1.13	1.06	1.12
FJM	0.90	1.01	1.10	1.02	0.99	0.98
FJR	1.07	1.00	1.05	1.08	1.03	1.09
FJY	1.08	0.90	1.04	1.17*	0.85*	1.37***
FMR	1.14*	0.98	0.97	1.24**	1.01	1.04
FMY	1.04	1.11	1.03	1.17*	1.07	1.25**
FRY	1.12*	1.03	0.94	1.04	1.04	1.03
JMR	1.04	1.09	1.06	1.08	0.99	1.07
JMY	1.16**	1.34**	0.95	1.16*	1.04	1.20*
JRY	1.02	1.06	0.97	1.15	0.99	1.19*
MRY	1.11	1.10	1.04	1.15	0.95	1.40***
FJ	1.03	0.81	1.03	1.00	1.04	0.93
FM	1.17**	1.00	1.16*	0.91	0.95	0.88
FR	0.98	1.10	1.01	1.18*	0.83**	1.19*
FY	0.98	0.92	1.06	1.08	0.90	1.26**
JM	1.03	1.09	0.87	0.88	1.10	0.97
JR	1.03	1.14	1.03	1.19*	0.92	0.98
JY	0.92	1.19	1.07	1.17*	1.12	1.10
MR	0.97	1.21	1.18**	1.11	1.10	1.06
MY	1.03	1.15	0.89	0.94	1.12	1.27**
RY	1.05	1.09	0.88	1.13	0.97	1.29**
MEAN	1.04	1.09	1.03	1.09**	1.00	1.13***

Table III.3 (continued)

Mixture	Location					
	Moro		Pendleton		Corvallis	
	Fung. <sup>a</sup>	Inoc. <sup>b</sup>	Fung.	Inoc.	Fung.	Inoc.
1988						
FJRY	1.05	1.11	1.08	1.11		
FJR	1.07	1.02	1.20**	1.09		
FJY	0.96	1.15*	1.04	1.22*		
FRY	1.17**	1.10	1.06	1.03		
JRY	1.05	1.15*	1.04	1.10		
FJ	1.00	0.99	1.00	1.06		
FR	0.98	1.04	1.01	0.98		
FY	1.20**	1.01	1.03	1.05		
JR	0.98	1.13	1.05	1.26		
JY	1.03	1.10	1.07	1.18		
RY	1.08	1.07	0.97	1.01		
MEAN	1.05	1.08 <sup>+</sup>	1.05 <sup>+</sup>	1.10 <sup>+</sup>		

<sup>a</sup>Inoc. = plots inoculated with stripe rust.

<sup>b</sup>Fung. = plots treated with fungicide.

<sup>c</sup>F = Faro, J = Jacmar, M= Moro, R = Tres, Y = Tyee.

\*, \*\*, \*\*\*Mixture yield is significantly different from the mean of the pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$  (linear contrasts).

<sup>+</sup>, <sup>++</sup>, <sup>+++</sup>Mean yield of mixtures was different from the mean yield of the pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$  respectively (linear contrast).

Table III.4. Yield and yield components for wheat cultivar mixtures and their pure stands in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust

	Location							
	Moro		Pendleton		Corvallis		Mean	
	Fung. <sup>a</sup>	Inoc. <sup>b</sup>	Fung.	Inoc.	Fung.	Inoc.	Fung.	Inoc.
1987								
yield mix <sup>c</sup>	137.71	97.21	116.44	109.03	148.92	127.20	134.36	111.14
yield pure	132.67	89.51	113.50	100.10	148.79	112.74	131.65	100.79
mix/pure <sup>d</sup>	1.04	1.09	1.03	1.09**	1.00	1.13***	1.02	1.10***
#heads mix <sup>e</sup>	141.99	142.13	126.50	126.13	143.02	131.38	137.17	133.21
#heads pure	136.60	135.47	119.95	124.45	143.50	125.20	133.35	128.37
mix/pure	1.04	1.05	1.05	1.01	1.00	1.05**	1.03	1.04*
#sd/hd mix <sup>f</sup>	36.59	32.55	30.32	30.39	31.94	29.05	32.95	30.66
#sd/hd pure	38.06	31.75	31.69	29.93	33.19	28.32	34.31	30.00
mix/pure	0.96**	1.03	0.96**	1.02	0.96	1.03	0.96**	1.02
1000sw mix <sup>g</sup>	26.92	21.08	30.41	28.47	32.77	33.48	30.04	27.68
1000sw pure	26.17	20.85	29.79	26.83	32.05	32.23	29.34	26.64
mix/pure	1.03	1.01	1.02	1.06***	1.02	1.04*	1.02*	1.04**

Table III.4. (continued)

	Location							
	Moro		Pendleton		Corvallis		Mean	
	Fung. <sup>a</sup>	Inoc. <sup>b</sup>	Fung.	Inoc.	Fung.	Inoc.	Fung.	Inoc.
1988								
yield mix	181.77	156.31	150.41	113.06			166.09	134.69
yield pure	173.26	145.44	143.40	103.78			158.33	124.61
mix/pure	1.05	1.07*	1.05*	1.09*			1.05**	1.08***
#heads mix	138.09	141.11	119.05	113.61			128.57	127.36
#heads pure	134.04	139.83	113.46	109.58			123.75	124.71
mix/pure	1.03	1.01	1.05*	1.04			1.04	1.02
#sd/hd mix	46.99	42.04	42.11	36.33			44.55	39.18
#sd/hd pure	46.63	40.52	41.28	35.30			43.95	37.91
mix/pure	1.01	1.04*	1.02	1.03			1.01	1.03
1000sw mix	28.63	26.43	30.23	27.65			29.43	27.04
1000sw pure	28.36	25.38	31.06	26.30			29.71	25.84
mix/pure	1.01	1.04*	0.97**	1.05***			0.99	1.05***

Table III.4. (continued)

<sup>a</sup>Fung. = plots treated with fungicide.

<sup>b</sup>Inoc. = plots inoculated with stripe rust.

<sup>c</sup>Mean yield of all mixtures.

<sup>d</sup>Yield of mixtures relative to the yield of the pure stands.

<sup>e</sup>Mean number of heads per plot of all mixtures.

<sup>f</sup>Mean number of seed per head in all mixtures.

<sup>g</sup>One-thousand seed weight.

\*, \*\*, \*\*\*Mixtures performed different from pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively.

Table III.5. Relative yield<sup>a</sup> of the wheat cultivars Faro, Jacmar, Moro, Tres, and Tyee when grown in mixtures<sup>b</sup> in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust

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

<sup>a</sup>Yield relative to the pure stands.

<sup>b</sup>Mixtures in which at least one cultivar could be separated by chaff color are included.

<sup>c</sup>Brown-chaffed cultivars were Faro (F), Jacmar (J), and Moro (M); White-chaffed cultivars were Tres (R) and Tyee (Y).

<sup>d</sup>Mixtures containing Tres were FJMR, FJR, FMR, FR, JR, MR.

<sup>e</sup>Mixtures containing Tyee were FJMY, FJY, FMY, FY, JY, MY.

<sup>f</sup>Mixtures containing Faro were FRY, FR, FY.

<sup>g</sup>Mixtures containing Jacmar were JRY, JR, JY.

\*, \*\*, \*\*\*Mixtures yielded different from mixtures in line below at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively.

Table III.6. Yield components of five wheat cultivars grown in two-way mixtures in the presence of stripe rust in three locations in 1987 and two locations in 1988

Mixture components			Mixture yield <sup>a</sup>	Rel. number of tillers <sup>b</sup>		Rel. yield per tiller		Rel. yield per cultivar	
Brown <sup>c</sup>	White <sup>d</sup>	Brown		White	Brown	White	Brown	White	
Corvallis 1987									
Faro	Tres	1.19	0.92	1.16	0.80*	1.39**	0.75*	1.62**	
Faro	Tyee	1.26**	1.16	1.15	0.97	1.26*	1.11	1.47*	
Jacmar	Tres	0.98	0.62**	1.11	0.53***	1.38***	0.34***	1.56**	
Jacmar	Tyee	1.10	0.87	1.20**	0.77**	1.40**	0.59***	1.73***	
Moro	Tres	1.06	1.14	1.21**	0.64***	1.12	0.73*	1.36	
Moro	Tyee	1.27**	1.25*	1.18*	0.85	1.25	1.08	1.51**	
Moro 1987									
Faro	Tres	1.10	1.07	1.13	0.85	1.16	0.91	1.33	
Faro	Tyee	0.92	1.30**	1.07	0.76	0.74	0.98	0.83	
Jacmar	Tres	1.14	0.73*	1.46**	0.79	1.15	0.63**	1.64**	
Jacmar	Tyee	1.19	0.93	1.26	0.93	1.23	0.85	1.56*	
Moro	Tres	4.21	0.29**	1.67**	0.97	1.10	0.32***	1.87**	
Moro	Tyee	1.15	1.26*	0.98	1.14	0.91	1.44**	0.91	
Pendleton 1987									
Faro	Tres	1.18*	0.94	1.33**	0.96	1.08	0.91	1.45**	
Faro	Tyee	1.08	1.21*	0.98	1.05	0.86*	1.27*	0.83	
Jacmar	Tres	1.19*	0.55**	1.47***	0.47***	1.25***	0.26***	1.85***	
Jacmar	Tyee	1.17*	1.08	1.32*	0.87	1.05	0.94	1.38*	
Moro	Tres	1.11	0.71**	1.37**	1.11	0.97	0.78	1.35*	
Moro	Tyee	0.94	1.03	0.85	1.32***	0.67***	1.34**	0.58**	



Table III.6. (continued)

Mixture components			Rel. number of tillers <sup>b</sup>		Rel. yield per tiller		Rel. yield per cultivar	
Brown <sup>c</sup>	White <sup>d</sup>	Mixture yield <sup>a</sup>	Brown	White	Brown	White	Brown	White
Moro 1988								
Faro	Tres	1.04	0.95	0.97	1.05	1.09	1.01	1.07
Faro	Tyee	1.01	1.14	0.82	0.97	1.06	1.10	0.87
Jacmar	Tres	1.13	0.91	1.23*	0.92	1.06	0.83	1.30*
Jacmar	Tyee	1.10	1.21	0.85	1.06	1.14	1.26*	0.97
Pendleton 1988								
Faro	Tres	0.98	1.11	1.02	0.97	0.88	1.08	0.89
Faro	Tyee	1.05	0.96	0.98	1.26**	0.86**	1.21	0.85
Jacmar	Tres	1.26**	0.72**	1.43***	0.71**	1.10	0.50***	1.57***
Jacmar	Tyee	1.18*	0.79**	1.26**	1.30**	0.99	1.03	1.27*

<sup>a</sup>Yield is expressed relative to the mean of the component pure stands.

<sup>b</sup>Values are calculated relative to the mean of the pure stands.

<sup>c</sup>Brown-chaffed cultivars were Faro, Jacmar, and Moro.

<sup>d</sup>White-chaffed cultivars were Tres and Tyee.

\*, \*\*, \*\*\*Mixtures or mixture components performed different from pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Table III.7. Yield components of five wheat cultivars grown in two-way mixtures in the absence of stripe rust in three locations in 1987 and two locations in 1988

Mixture components		Mixture yield <sup>a</sup>	Rel. number of tillers <sup>b</sup>		Rel. yield per tiller		Rel. yield per cultivar	
Brown <sup>c</sup>	White <sup>d</sup>		Brown	White	Brown	White	Brown	White
Corvallis 1987								
Faro	Tres	0.83**	0.84*	0.96	0.65***	1.16	0.56***	1.11
Faro	Tyee	0.90	0.94	0.81*	0.93	1.13	0.89	0.91
Jacmar	Tres	0.92	0.54***	1.13	0.45***	1.40***	0.25***	1.60***
Jacmar	Tyee	1.12	0.93	0.92	0.85	1.55***	0.79*	1.51***
Moro	Tres	1.10	1.11	1.07	0.72***	1.25*	0.80**	1.36**
Moro	Tyee	1.12	1.33***	0.98	0.86	1.13	1.15	1.09
Moro 1987								
Faro	Tres	0.98	0.75	1.14	1.11	1.02	0.81	1.15
Faro	Tyee	0.98	1.08	1.12	1.01	0.75**	1.10	0.86
Jacmar	Tres	1.03	0.76	1.39	0.69**	1.17	0.52***	1.61***
Jacmar	Tyee	0.92	0.95	1.16	0.84	0.88	0.78	1.08
Moro	Tres	0.97	0.69	1.16	0.97	1.00	0.71	1.14
Moro	Tyee	1.03	0.97	0.91	1.39***	0.94	1.29	0.85
Pendleton 1987								
Faro	Tres	1.01	0.83	1.21	1.01	0.99	0.84	1.19
Faro	Tyee	1.06	1.18	0.96	1.02	0.97	1.20	0.93
Jacmar	Tres	1.03	0.68***	1.38**	0.83**	1.13*	0.56**	1.55***
Jacmar	Tyee	1.07	0.92	1.05	1.03	1.15**	0.94	1.20
Moro	Tres	1.18**	0.86	1.30*	1.15*	0.99	0.98	1.31*
Moro	Tyee	0.89	1.43***	0.82	1.07	0.64***	1.51***	0.52**

Table III.7. (continued)

Mixture components			Mixture yield <sup>a</sup>	Rel. number of tillers <sup>b</sup>		Rel. yield per tiller		Rel. yield per cultivar	
Brown <sup>c</sup>	White <sup>d</sup>	Brown		White	Brown	White	Brown	White	
Moro 1988									
Faro	Tres	0.98	1.03	0.98	0.97	0.93	1.01	0.94	
Faro	Tyee	1.20**	1.32**	0.98	1.03	1.03	1.36**	1.01	
Jacmar	Tres	0.98	0.76	1.09	0.98	1.08	0.75*	1.19	
Jacmar	Tyee	1.03	0.90	0.90	1.08	1.20**	0.99	1.09	
Pendleton 1988									
Faro	Tres	1.01	1.07	1.19*	0.90	0.90*	0.96	1.07	
Faro	Tyee	1.03	1.06	1.10	0.97	0.96	1.03	1.04	
Jacmar	Tres	1.05	0.54***	1.47***	0.77***	1.14**	0.42***	1.69***	
Jacmar	Tyee	1.07	0.84	1.20	0.88*	1.14**	0.76**	1.36***	

<sup>a</sup>Yield is expressed relative to the mean of the component pure stands.

<sup>b</sup>Values are calculated relative to the mean of the pure stands.

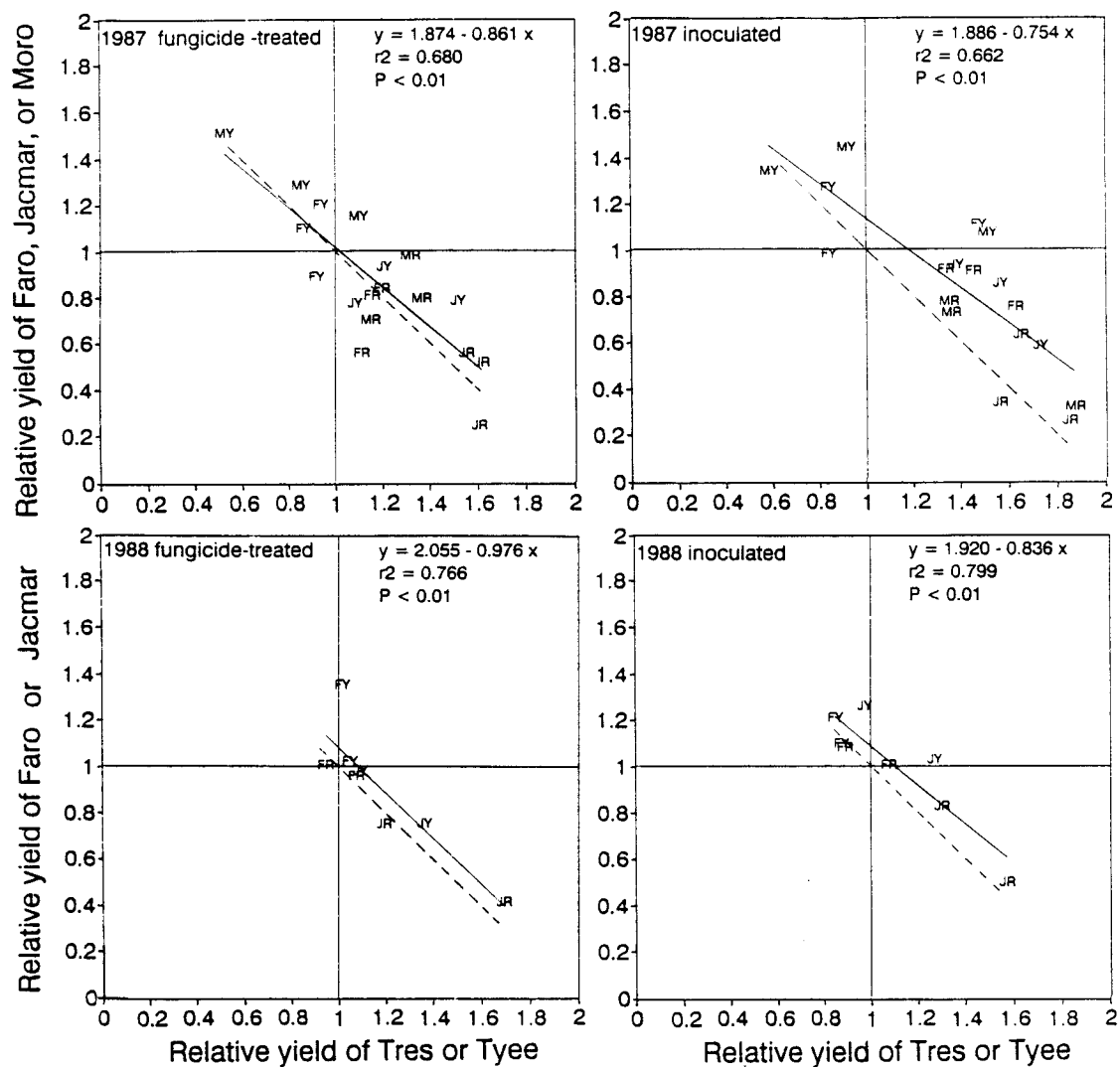
<sup>c</sup>Brown-chaffed cultivars were Faro, Jacmar, and Moro.

<sup>d</sup>White-chaffed cultivars were Tres and Tyee.

\*, \*\*, \*\*\*Mixtures or mixture components performed different from pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Fig. III.1. Correlation of the yield relative to their pure stands of the wheat cultivars Faro (F), Jacmar (J), Moro (M), Tres (R) and Tyee (Y) when grown in two-way mixtures in three locations in 1987 and two locations in 1988 in the presence and absence of stripe rust. The dashed line (-----) represents the expected correlation between brown and white cultivar yield if an increase in yield in one mixture component were compensated for by an equal decrease in yield of the other component, the solid line (——) is the actual regression line. The graph is divided into quadrants in which either none (lower left), one (upper left or lower right), or both (upper right) components yield higher than expected. Mixtures falling below the expected line yielded less than the mean of their pure stands; see Tables III.6 and III.7 for data.

Fig. III.1.



### Literature Cited

- Allard, R. W. 1960. Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1:127-133.
- Allard, R. W., and Adams, J. 1969. Population studies in predominantly self-pollinating species XIII. Intergenotypic competition and population structure in barley and wheat. *Am. Naturalist* 103:620-645.
- Barrett, J. A. 1978. A model of epidemic development in variety mixtures. In: *Plant Disease Epidemiology*. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 129-137.
- Borlaug, N. E. 1959. The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants. *Proc. 1st Int. Wheat Genet. Symp.*, 1958, pp. 12-27.
- Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7:355-382.
- Burdon, J. J., Groves, R. H., Kaye, P. E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. *Oecologia* 64:199-203.
- Finckh, M. R., and Mundt, C. C. 1992. Effects of plant competition on stripe rust in wheat cultivar mixtures. *Phytopathology* 82: (submitted as companion paper)
- Firbank, L. G., and Watkinson, A. R. 1985. On the analysis of competition within two-species mixtures of plants. *J. Appl. Ecol.* 22, 503-517.
- Jennings, P. R., and De Jesus, J. Jr. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. *Evolution* 22:119-124.
- Jensen, N. F. 1952. Intra-varietal diversification in oat breeding. *Agron. J.* 44:30-34.
- Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. Appl. Ecology* 21, 227-243.

- Klages, K. H. W. 1936. Changes in the proportions of the components of seeded and harvested cereal mixtures in abnormal seasons. J. Am. Soc. Agron. 28, 935-940.
- Knott, E. A., and Mundt, C. C. 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and non-diseased conditions. Theor. Appl. Genet. 80:313-320.
- Leonard, K. J. 1969. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. Phytopathology 59:1845-1850.
- Mahmood, T., Marshall, D., and McDaniel, M. E. 1991. Effect of winter wheat cultivar mixtures on leaf rust severity and grain yield. Phytopathology 81:470-474.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity and cereal rust management. In: The Cereal Rusts, Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando. pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: Effect of genotype unit area. Phytopathology 75:607-610.
- Mundt, C. C., and Leonard, K. J. 1985. Effect of host genotype unit area on epidemic development of crown rust following focal and general inoculations of mixtures of immune and susceptible oat plants. Phytopathology 75:1141-1145.
- Mundt, C. C., and Leonard, K. J. 1986a. Analysis of factors affecting disease increase and spread in mixtures of immune and susceptible plants in computer-simulated epidemics. Phytopathology 76:832-840.
- Mundt, C. C., and Leonard, K. J. 1986b. Effect of host genotype unit area on development of focal epidemics of bean rust and common maize rust in mixtures of resistant and susceptible plants. Phytopathology 76:895-900.
- Nitzsche, W., and Hesselbach, J. 1983. Sortenmischungen statt Vielliniensorten. Z. Pflanzenz. 90:68-74.
- Norrington-Davies, J., and Hutto, J. M. 1972. Diallel analysis of competition between diploid and tetraploid genotypes of Secale cereale grown at two densities. J. Agric. Sci. Camb. 78:251-256.

- Paul, N. D., and Ayres, P. G. 1986. Interference between healthy and rusted groundsel within mixed populations of different densities and proportions. *New Phytol.* 104:257-269.
- Paul, N. D., and Ayres, P. G. 1987. Effects of rust infection of Senecio vulgaris on competition with lettuce. *Weed Res.* 27:431-441.
- SAS Institute Inc. 1988. SAS/STAT User's Guide Ed. 6.03. SAS Institute, Cary, NC. 1029 pp.
- Spitters, C. J. T. 1983a. An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. *Neth. J. Agric. Sci.* 31, 1-11.
- Spitters, C. J. T. 1983b. An alternative approach to the analysis of mixed cropping experiments. 2. Marketable yield. *Neth. J. Agric. Sci.* 31:143-153.
- Suneson, C. A. 1949. Survival of four barley varieties in mixture. *Agr. J.* 41:459-461.
- Suneson, C. A., and Wiebe, G. A. 1942. Survival of barley and wheat varieties in mixtures. *J. Am. Soc. Agron.* 34:1052-1056.
- Wolfe, M. S. 1978. Some practical implications of the use of cereal variety mixtures. In: *Plant Disease Epidemiology*. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 201-207.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annu. Rev. Phytopathol.* 23:251-273.
- Wolfe, M. S., and Barrett, J. A. 1980. Can we lead the pathogen astray? *Plant Dis.* 64:148-155.
- Wolfe, M. S., Barrett, J. A., and Jenkins, J. E. E. 1981. The use of cultivar mixtures for disease control. In: *Strategies for the Control of Cereal Diseases*. J. F. Jenkyn and R. T. Plumb, eds. Blackwell, Oxford. pp. 73-80.



IV. Plant competition and disease in genetically  
diverse wheat populations\*

Maria R. Finckh and Christopher C. Mundt

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

Received                      / Accepted for publication

\*Paper No. \_\_\_\_ of the journal series of the Oregon  
Agricultural Experiment Station.

**Abstract**

Replacement series consisting of a susceptible and a resistant wheat (Triticum aestivum) genotype or two wheat genotypes susceptible to different races of stripe rust (caused by Puccinia striiformis) were grown in the presence and absence of the disease. Stripe rust severity, number of seed heads, seed yield, and seed weight were determined separately for each wheat genotype in the mixtures and the pure stands. The frequency of susceptible genotypes in a mixture explained up to 67% of the variation in disease severity. However, competitive interactions among plant genotypes sometimes appeared to alter susceptibility and obscured the relationship. In pure stands of single genotypes, disease severity explained between 52 and 58% of the variation in seed yield. In mixtures, coefficients of determination were 11 and 21%, suggesting a stronger influence of plant-plant interactions than disease on seed yield.

Additional keywords: plant disease, genetic diversity, frequency-dependence, Triticum aestivum, Puccinia striiformis

## Introduction

Much of the work on coevolution has been focussed on theoretical modeling of host-parasite relationships (e.g. Chilvers and Brittain, 1972; Gates et al., 1986; Leonard and Czocho, 1980; May and Anderson, 1983a,b; Mode, 1958, 1961). Interactive effects of the genetic composition of host and pathogen populations have been observed in natural systems (Wahl, 1970) and in agricultural systems (Flor, 1953; Johnson et al., 1967; McDonald et al., 1988, 1989). Epidemic development and, thus, pathogen population size within a diverse host population, are affected by reduction and dispersion of susceptible host tissue. In addition, resistant plants may function as barriers for the dispersal of inoculum. Disease severity on any given genotype should therefore be dependent on the frequency of this genotype in the host population. However, reports on frequency-dependence of disease severity have yielded contradictory results. In some studies, no frequency-dependence was found (Alexander, 1991; Jarosz and Levy, 1988; Parker, 1989) whereas others have found such relationships to occur (Augspurger and Kelly, 1984; Leonard, 1969) (see Burdon and Chilvers, 1982 for review). Effects such as induced resistance (inoculum from avirulent pathogen strains can trigger defense reactions in hosts that are effective against otherwise virulent strains) and other interactions

among pathogens may also influence epidemic development. Mechanisms affecting disease epidemiology in host mixtures have been studied and discussed extensively (Barrett, 1978; Browning and Frey, 1969; Burdon, 1978; Chilvers and Brittain, 1972; Chin and Wolfe, 1984; Leonard, 1969; Mundt, 1989; Mundt and Browning, 1985a,b; Mundt and Leonard 1986; Wolfe, 1985). In addition to these epidemiological effects, plant-plant interactions such as selection for resistant or susceptible genotypes can greatly influence epidemic development in diverse host populations (Finckh and Mundt, 1992a).

Many studies have demonstrated that disease can alter competitive interactions among plant genotypes (Alexander et al., 1986; Burdon et al., 1984; Finckh and Mundt, 1992b; Paul, 1989; Paul and Ayres 1986a, 1987b) and affect the survival and fitness of hosts differentially (Alexander, 1984; Alexander and Burdon, 1984; Augspurger, 1984; Augspurger and Kelly, 1984; Clay, 1984, 1990; Jarosz et al., 1989; Paul and Ayres, 1986b,c, 1987a).

Studies that address single aspects of host-pathogen interactions have been very useful for the development and partial validation of theoretical models of host-pathogen coevolution. However, few attempts have been made to integrate those different aspects (but see McDonald et al., 1989). In order to gain more insight into the mechanisms of coevolution, it is necessary to simultaneously study the

population dynamics of both hosts and pathogens.

In this paper, we describe a study in which we assessed direct and indirect effects of the genetic composition of wheat (Triticum aestivum L.) populations on stripe rust epidemics caused by Puccinia striiformis Westend. (=P. glumarum (Schm.) Jacob, Eriksson & Henn.). We also investigated the effects of disease on competitive interactions among wheat genotypes.

## Materials and Methods

### Experimental design.

Plant genotypes were five cultivated varieties of winter wheat (Triticum aestivum) differing in stripe rust resistance, height, and chaff color (Table IV.1).

Experiments were conducted in the 1988/1989 season in Pendleton, located in north eastern Oregon and in Moro in north central Oregon, which receive approximately 450 and 300 mm annual precipitation, respectively.

A split plot design with four replications at Pendleton and six replications at Moro was employed. Main plots were either inoculated with stripe rust or protected from stripe rust with three applications of the fungicide Bayleton (triadimefon) at 283g active ingredient per ha. Within each main plot, subplots consisted of pure stands of the wheat varieties Faro, Jacmar, Moro, Tres, and Tyee and 21 mixtures of two-to-four varieties of variable proportions (Table IV.2). Seed numbers were adjusted for germination percentage before planting. Twelve of the mixtures consisted of Jacmar or Moro mixed with either Tres or Tyee at proportions of 1:2, 1:1, and 2:1. Together with their respective pure stands, these mixtures represent four different replacement series of either two differentially susceptible genotypes (one genotype susceptible to race 5 and one susceptible to race 27 of stripe rust (Jacmar or

Moro with Tyee)) or a resistant and a susceptible genotype (Jacmar or Moro with Tres).

Subplots were 1.5m by 4.5m with four rows per plot (38 cm between rows) and separated by 1.8m of fallow ground in the long dimension. Seeding rates were those appropriate for commercial wheat production and were 316 and 198 germinable seed/m<sup>2</sup> in Pendleton and Moro, respectively. To reduce interplot-interference due to spore dispersal, subplots were arranged in a checkerboard pattern alternating with subplots of the stripe rust-resistant variety Stephens. In addition, main plots were separated in both dimensions by two subplots of Stephens. Fertilizers and herbicides were applied according to standard practices for wheat in the respective regions.

Disease was established through artificial inoculation. Peat pots (6cm) containing two-to-three week old seedlings of the winter wheat variety Nugaines were inoculated with an equal mixture of uredospores of P. striiformis races CDL 5 and CDL 27 (CDL race designations are those of the USDA Cereal Disease Laboratory, Washington State University, Pullman). Inoculated plants were placed in a dew chamber for 12 h. Upon removal from the dew chamber, plants were placed outdoors to harden off until sporulation. At the onset of sporulation, one pot was transplanted into the center of each subplot in the inoculated main plots. Plots were inoculated on 20 Nov.

1988 in Moro and on 21 Nov. in Pendleton. Due to an unusually severe winter, most of the infected leaf tissue in the plots was killed and inoculation was repeated on 5 and 6 April 1989 in Moro and Pendleton, respectively.

#### **Disease assessments.**

Assessments were performed before disease had reached 90% severity on the most susceptible variety Jacmar. Assessment dates were 26-31 May and 7-11 June 1989 in Pendleton and Moro, respectively. Miniplots containing a minimum of 120 tillers were marked within each subplot approximately midway between the inoculation point and the downwind end of the plot. Miniplots consisted of sections of the two center rows of 41 cm and 56 cm in Pendleton and Moro, respectively.

Disease was assessed by visually estimating the percentage of the leaf below the flag leaf that was covered by stripe rust lesions on each tiller that produced a flower head in the miniplots. Each tiller that was assessed also was given a numbered tag matched to an identification number on data sheets used to record disease severity. One person assessed all plants. Disease was assessed on all two-way mixtures that contained a brown-chaffed and a white-chaffed genotype and on all pure stands (Table IV.2). To limit assessment duration to four days, only four out of six replications were assessed in Moro.



Seed yield data of the same four replications were used in the analyses.

To determine if tagging affected yield, a duplicate subplot of the 1:1 mixture of Jacmar-Tres was planted in each main plot. One of the repeated subplots was left as an untagged control in each of the inoculated main plots. There was no effect of tagging on the number of seed heads, seed yield, or seed weight ( $0.22 < P < 0.97$ ).

#### **Harvest.**

Tillers in the miniplots were cut with sickles, bagged, transported to the laboratory, and separated by chaff color. The tag numbers were matched to disease notes taken in the field so that mean disease severity could be calculated separately for the brown and white colored components in the mixtures. Brown and white seed heads were counted, threshed in bulk with a stationary plot thresher, and seed yield per miniplot and weight of two replicates of 150 seed each were recorded.

#### **Data analyses.**

Data were analyzed using SAS (SAS Inst., 1986). Fisher's non-protected LSD and linear contrasts were used to determine significance of treatment differences for disease severity, number of seed heads, seed yield, and seed weight.

Total disease reduction (or increase) in mixtures was calculated by dividing the mean disease severity in mixtures by the mean of the disease severities on the mixture components in pure stands. The mean of the pure stands was weighted by the respective planting frequencies for each mixture. Planted and harvested frequencies of the genotypes in the mixtures often differed considerably, however. Therefore, the total reduction was separated into a selection effect and an epidemiological effect for each mixture. The selection effect is the difference in expected disease severity due to frequency changes from planting to harvesting of wheat genotypes, whereas the epidemiological effect is the difference between the total reduction and the selection effect (Finckh and Mundt, 1992a). Positive selection effects indicate selection for the more resistant genotype in a mixture, while selection for the more susceptible genotype results in negative selection effects.

The relationship between disease severity on the susceptible genotypes Jacmar, Moro, and Tyee and their frequency in the replacement series was examined by plotting the disease severity on a genotype versus its frequency. With increasing frequency of a genotype, disease severity approached the severity in the pure stands asymptotically. The disease severity data were therefore transformed and the following equation was employed to

perform a linear regression:

$$\ln \frac{100}{100 - S_i} = \beta_0 + \beta_1 * f_i \quad (1)$$

(Richards, 1969) where  $\ln$  is the natural logarithm and  $S_i$  and  $f_i$  are the percent disease severity on plant genotype  $i$  and its frequency, respectively.  $\beta_0$  and  $\beta_1$  are, respectively, the intercept and slope of the regression line. The residual plots appeared random for all of the regressions that were significant.

The effects of disease severity on seed yield of pure stands, mixtures, and the susceptible genotypes in the replacement series were analyzed using simple linear regression of seed yield per subplot on untransformed disease severity data.

Competitive interactions between genotypes in the replacement series were analyzed graphically by plotting the observed and expected seed yields of the mixture components for all four genotype combinations, inoculated and fungicide-treated, in Moro and Pendleton (Figs. IV.1 and IV.2). To determine if the actual seed yield of the genotypes was different in mixtures than in pure stands, the observed lines were examined for non-linearity. A linear model for the replacement series can be written as:

$$y = \beta_0 + \beta_1 x^\alpha \quad (2)$$

where  $y$  and  $x$  are yield and frequency of the mixture component.  $\beta_0$  must be zero by definition, as at zero frequency there can be no yield. The equation is linear if  $\alpha$  equals one. Omitting  $\beta_0$  and taking the natural logarithm yields:

$$\ln y = \ln \beta_1 + \alpha \ln x \quad (3)$$

T-tests for the slope,  $\alpha$ , were used to determine if  $\alpha$  differed from one. Simple linear regressions were performed on the log-transformed data for each mixture component in all of the replacement series. The lines were forced through the logarithm of the mean of the respective genotype's pure stand yield. Slopes greater than one indicate a concave curvature of the yield line (i.e., below the expected line) and slopes smaller than one indicate a convex curvature (above the expected line).

## Results

### Disease severity in pure stands and mixtures.

The wheat genotypes differed in their degree of susceptibility to stripe rust. Averaged over both locations, disease severity ranged from 87.8% on Jacmar to 1.6% on Tres (Table IV.3). Disease severity readings on Faro have to be considered with caution, as our seed source had consisted of two differentially susceptible lines (Finckh and Mundt, 1992a). Disease severity was less than 1% on an average of 53% (range = 22 to 64%) of the tillers in the pure stands of Faro. Except for one pure stand in Pendleton, where disease had developed poorly, the disease severity on the susceptible Faro tillers ranged from 33.9 to 90.1%.

Disease reductions in mixtures ranged from 17 to 92% and were significant in 17 out of 28 mixtures (Table IV.3). Disease was reduced below the mean of the pure stands in all mixtures that were assessed, except for the Faro-Tres mixture in Pendleton. The mean severity of the pure stands of Faro and Tres in Pendleton was 10.1%. The observed severity in the mixtures was 12.8%, a small increase that, when expressed as percentage, appears large.

Effects of selection on disease severity were most pronounced in the mixtures of Jacmar with Tres, reflecting the superior tillering ability of Tres in the presence of

Jacmar (Table IV.3). Tres also increased in proportion in most mixtures with Moro; the effect was not as strong as in the mixtures with Jacmar, however. In contrast, there were almost no proportional changes in the Faro-Tres mixtures in either location. Tyee decreased in proportion in all mixtures with Faro, Jacmar, or Moro in the Moro site, except in the 1:1 mixture with Moro. As Jacmar was more susceptible than Tyee, negative selection effects indicate a proportional increase of Jacmar in mixtures with Tyee whereas positive selection effects in mixtures of Tyee with Moro and Faro indicate proportional increases of the latter two genotypes. In Pendleton, disease severity was affected by the proportional decrease of Tyee in the 1:1 mixtures with Jacmar and Faro. Although the frequency of Tyee increased in the mixtures with Moro, this was not reflected in measurable selection effects on disease, because disease severities on the two genotypes in pure stands were very similar.

#### **Disease severity on mixture components.**

Disease reductions were most pronounced on the more susceptible genotypes in the two locations. The calculated increase in disease severity on Faro in mixtures versus in pure stands in Pendleton appeared disproportionately great due to poor disease development in one of the pure stands, which lowered the pure stand mean considerably. Disease

severities on Faro in the three replicates were 26.3, 26.4, and 3.0%, respectively. Excluding the plot with low disease from the analysis raised the least squares mean for disease severity on the Faro pure stands to 22.3%. Even with this adjustment, disease severity on Faro was still slightly higher in the mixture than in the pure stand, however. The adjusted overall disease increase in the mixture was 7% due to a negative epidemiological effect of 16% and a positive selection effect (selection for the more resistant variety Tres) of 9%.

There appeared to be an effect of the companion genotype in the mixtures on the relationship between disease severity and frequency. The relationship between disease severity and genotype frequency was significant for Jacmar and Moro in both locations. For Tyee, the relationship was only significant in Moro when mixed with Jacmar (Table IV.4). Frequency-dependence of disease on Jacmar was greater when it was mixed with Tyee than when it was mixed with Tres in both locations. This was also the case for the genotype Moro in the Moro site. Also, frequency-dependence of disease was greater on Tyee when mixed with Jacmar than when mixed with Moro in both locations.

The companion genotypes in the mixtures also affected disease severity on the wheat varieties. For example, in Moro at harvest, Jacmar was present at a frequency of 0.37

in one mixture with Tres and in one mixture with Tyee (Table IV.3). The disease severity on Jacmar was 61.9% in the presence of Tres and only 32.1% in the presence of Tyee. The difference was statistically significant at  $P < 0.05$  (Fisher's unprotected LSD). Similarly, in Pendleton, at a frequency of Jacmar of approximately 0.55, disease severity on Jacmar was 87.0% when mixed with Tres and 55.9% when mixed with Tyee. In a second set of mixtures where Jacmar occurred at a frequency of approximately 0.33, disease severity on Jacmar was 62.6% in the presence of Tres and 18.8% in the presence of Tyee (Table IV.3). In both cases in Pendleton, the differences in disease severity on Jacmar were statistically significant at  $P < 0.05$  (Fisher's unprotected LSD).

#### Effects of disease on tiller number and yield.

Pure stands. There were considerable effects of disease on the performance of the genotypes in pure stands. In the absence of stripe rust, differences in seed yield, number of seed heads, and number of seed per head were not significant for Faro, Jacmar, Tres, and Tyee in either location. Moro yielded significantly less than Faro, Tres, and Tyee, however. The genotypes varied for seed weight in Pendleton (Table IV.5).

In the presence of disease, Faro and Tres outperformed the other three genotypes. Yield reductions through



disease were due to varying degrees of reduction in all seed yield components. In Moro, the greatest effect of disease was on the number of seed per head, which was significantly reduced for Faro, Jacmar, and Tyee. In Pendleton, on the other hand, the greatest effect of disease was on the seed weight for all genotypes except Tres (Table IV.5). There was a clear linear relationship between seed yield per miniplot and disease severity in the pure stands. The  $r^2$ -values were 0.58 and 0.52 in Pendleton and Moro, respectively with  $P < 0.01$  in both locations.

Mixtures. The number of heads in the mixtures was within the same range as the pure stands and ranged from 100-157 in Moro and from 107-154 in Pendleton (Data not shown).

When stripe rust was prevented through fungicide application, 30 out of 40 mixtures yielded higher than the mean of their pure stands (Table IV.6). In the presence of disease, 26 out of 40 mixtures yielded higher than their inoculated pure stands to give an average 10 and 13% yield increase over all mixtures in Moro and Pendleton, respectively. It was not possible to statistically compare the yield of each individual mixture with the mean of its pure stands because of a lack of degrees of freedom. Also, because the set of mixtures did not include all possible genotype combinations, statistical comparisons between all

of the mixtures and the pure stands would have been biased.

The yield of the inoculated mixtures was significantly lower than the yield of the fungicide-treated mixtures in both locations ( $P < 0.01$ ). The effect of disease on yield was variable among mixtures and locations, however (Table IV.6). Many more inoculated mixtures yielded higher than the mean of their components in fungicide-treated pure stands in Moro than in Pendleton. Most of the higher yielding mixtures in Moro contained the genotype Moro, whereas mixtures with Jacmar usually yielded lower than the pure stands. In Pendleton, only two inoculated mixtures yielded slightly higher than their fungicide-treated pure stands. Again, those were mixtures containing the genotype Moro (Table IV.6).

Although there was a significant linear relationship between disease severity and seed yield in the mixtures in Moro ( $P < 0.05$ ) and in Pendleton ( $P < 0.01$ ), the coefficients of determination were only 0.10 and 0.21 in Moro and Pendleton, respectively. As with the frequency-dependence of disease severity, the relationship of disease and seed yield of a given genotype in mixtures was affected by the companion genotype (Table IV.7). There was a significant effect of disease on the relative yield of Jacmar in mixtures with Tyee, but not in mixtures with Tres in both locations. For the variety Moro, there appeared to be no direct effect of disease on seed yield in any mixture. The

yield per head of Tyee was more affected by disease in Pendleton than in Moro. However, the disease effect was only statistically significant when mixed with the variety Moro in Pendleton.

#### Competitive interactions in mixtures.

Figs. IV.1 and IV.2 show the observed and expected seed yields of the mixture components and the total seed yields in the replacement series. Overall, Tres was the strongest competitor in the mixtures. The yield lines of Tres were always convex (above the expected line). The deviations were significant in five of the eight replacement series. On the other hand, yield lines of Jacmar and Moro were significantly concave (below the expected lines) in seven of the eight series (Fig. IV.1).

When mixed with Tyee, Jacmar and Moro often yielded more than expected. However, the deviations of the yield lines from the straight lines were rarely statistically significant (Fig. IV.2).

The response of Tyee to mixing with Jacmar and Moro was variable (Fig. IV.2). In Pendleton, in the absence of disease, the response of Tyee to mixing was significantly non-linear and s-shaped. When mixed with either Jacmar or Moro, Tyee yielded higher than expected if the companion genotype was planted at low frequencies and lower than expected when the companion genotype was planted at high

frequencies. In Moro, the yield line of Tyee also was s-shaped in mixtures with Jacmar, however, it was not significantly non-linear. In the presence of disease, the yield of Tyee in mixture was almost always greater than expected. However, the deviations from the expected lines were usually statistically non-significant.

#### Effects of disease on competitive interactions.

To avoid the introduction of a bias by comparing diseased mixtures with their more diseased pure stands, the fungicide-treated pure stands were used as a reference for all comparisons. In mixtures with Tres, Jacmar yielded significantly less in the presence of disease than in the absence of disease ( $P < 0.01$ ) in both locations (Table IV.8). When mixed with Tyee in Moro, Jacmar yielded similarly in the presence and absence of disease. In contrast, in Pendleton, yield of Jacmar was significantly reduced by Tyee in the presence of disease ( $P < 0.01$ ). There was no clear effect of disease on competitiveness of Moro in the presence of Tres or Tyee in either location. Disease did not significantly affect the yield of Tres in any of the replacement series. In contrast, yield of Tyee in the presence of Jacmar or Moro was always reduced by disease below its yield in the fungicide-treated mixtures ( $P < 0.1$  in mixtures with Jacmar in Pendleton, all other cases  $P < 0.01$ ).

## Discussion

Severity of stripe rust was reduced in 27 out of 28 mixtures that were composed of either a resistant and a susceptible or two differentially susceptible cultivated wheat varieties. Consistent with an earlier study (Finckh and Mundt, 1992a), we found that selection for the more competitive genotype and also epidemiological interactions contributed to disease reduction in the mixtures.

Disease severity on a genotype was often dependent on that genotype's frequency in our study. However, frequency-dependence of disease was in some cases greatly affected by the companion genotype in the mixture. This was due to plant-plant interactions other than selection effects. These results could help explain why research on frequency-dependence of disease has yielded contradictory results.

The increased disease severity on Jacmar when mixed with Tres as compared to equal-proportioned mixtures with Tyee could have been due to at least three factors. First, although the frequencies of Jacmar at harvest were comparable between the mixtures with Tres and the mixtures with Tyee, the planted frequencies had been different (Table IV.3). Thus, disease could have increased in a density-dependent manner early in the season, before tillering substantially affected the frequencies. On the

other hand, disease on Moro did not seem to be affected by its companion cultivar, although Moro was also subject to considerable frequency shifts. Second, Jacmar suffered more from competition by Tres than by Tyee. This could have rendered Jacmar more susceptible to stripe rust. Effects of plant-plant interactions on susceptibility have been suggested by Clay (1990). Finally, interactions between the two rust races could also have affected disease severity. Spores of race 27 that were virulent on Tyee but avirulent on Jacmar could have induced some resistance to race 5 on Jacmar. Induced resistance has been reported in many systems (Ouchi, 1983). Reports for stripe rust are contradictory, however. Johnson (1978) found evidence for weak induced resistance whereas Brown and Sharp (1970) found that a wheat variety could be rendered susceptible to an avirulent stripe rust race by preinoculating with a virulent race. No differences in disease severity on Moro were apparent between mixtures with Tres and mixtures with Tyee.

Clay (1990) noted that the evaluation of competitive interactions among plant genotypes in the presence of disease is complicated through epidemiological interactions. The effects of disease on competitive interactions in mixtures can only be quantified if disease severity on a given mixture component is constant over all mixture proportions and pure stands.

Our experiment cannot be used to quantitatively separate intra- and inter-genotypic competition as has been done by others (Firbank and Watkinson, 1985; Jolliffe et al., 1984; Spitters, 1983), because data on the yield-density relationships of the wheat varieties were not collected. Comparison of the pure stands and the mixtures is still useful in providing information on the relative competitive abilities of the genotypes and the effects of disease on competition. The apparent lack of effect of disease on competitiveness (measured in relative yield) of Tres in mixtures with Jacmar (Table IV.8) could be due to asymmetry in competitive interactions. An alternative explanation might be that the decrease in seed yield of Jacmar below its yield in the non-diseased mixtures was not only due to increased competition by Tres, but also to the direct effect of stripe rust. However, the lack of a significant slope in the disease-yield relationship for Jacmar in mixtures with Tres (Table IV.7) does not support this hypothesis. It is important to realize that, although the total yield of Tres was not changed through disease on Jacmar, the harvested proportion, and thus the relative fitness of Tres, was increased. This illustrates the difference between the effects of disease on competitive ability and reproduction of plants in mixtures that was pointed out by Burdon (1982).

Yield compensation may have obscured the effects of

disease severity on total mixture yield. As disease severities on the individual genotypes in mixtures often differed (Table IV.3), healthy genotypes could have compensated for the lowered yield of diseased genotypes. The lack of s-shaped yield lines of Tyee in the presence of disease could be due to an overall decrease in plant-interference due to disease.

Our study has elucidated some of the interactions among genetically diverse hosts and pathogens. We found that disease severity was changed through epidemiological interactions and through selection for the more competitive wheat genotype in the mixed populations and was generally frequency-dependent. However, it appeared that by affecting plant susceptibility, plant-plant interactions other than selection influenced this frequency-dependence. Although disease generally weakened the susceptible genotypes in their competitive abilities, this did not necessarily improve the performance of the more resistant companion genotypes in the mixtures. The low correlation between disease severity and seed yield in mixtures demonstrate that yield-loss relationships derived from pure stands are of limited value to predict yield losses in mixtures.



Table IV.1. Wheat genotypes used in field experiments and their chaff colors, heights, and reactions to two stripe rust races

Genotype	Chaff color	Relative height	Reaction <sup>a</sup> to <u>Puccinia striiformis</u> race	
			5	27
Faro	brown	medium	VAR	R
Jacmar	brown	short	S	R
Moro	brown	tall	S	R
Tres	white	medium	MR	R
Tyee	white	medium	R	S

<sup>a</sup>VAR = reaction variable, approximately one-half of the plants were resistant and one-half susceptible; R = resistant; S = susceptible; MR = moderately resistant.

Table IV.2. Pure stands and mixtures of wheat genotypes studied in the presence and absence of stripe rust at two locations

Population <sup>a</sup>	Planted proportions	Assessment <sup>b</sup>
Faro	Pure stand	yes
Jacmar	Pure stand	yes
Moro	Pure stand	yes
Tres	Pure stand	yes
Tyee	Pure stand	yes
Jacmar:Tres	1:2, 1:1, 2:1	yes
Jacmar:Tyee	1:2, 1:1, 2:1	yes
Moro:Tres	1:2, 1:1, 2:1	yes
Moro:Tyee	1:2, 1:1, 2:1	yes
Faro:Tres	1:1	yes
Faro:Tyee	1:1	yes
Jacmar:Moro:Tres:Tyee	1:1:1:1	no
Jacmar:Moro:Tres	1:1:1	no
Jacmar:Moro:Tyee	1:1:1	no
Jacmar:Tres:Tyee	1:1:1	no
Moro:Tres:Tyee	1:1:1	no
Tres:Tyee	1:1	no

<sup>a</sup>All plots were planted with the same number of germinable seed.

<sup>b</sup>Disease was assessed on single tillers in miniplots within each subplot (see text).

Table IV.3. Severity of stripe rust of wheat in pure stands and in two-way mixtures, percent reduction relative to pure stands, and subdivision of percent reduction into selection and epidemiological effects in two locations

Location/ Mixture components		Frequencies				Disease severity (%) <sup>a</sup>			Disease reduction (%)		
		Planted		Harvested							
GT1 <sup>b</sup>	GT2	GT1	GT2	GT1	GT2	GT1	GT2	Total	Total <sup>c</sup>	Sel <sup>d</sup>	Epid <sup>e</sup>
<hr/>											
Moro											
Jacmar	Tres	.67	.33	.47	.53	59.0**	4.9	29.6***	48	23	24
		.50	.50	.37	.63	61.9**	2.3	24.5**	43	19	24
		.33	.67	.16	.84	48.9***	2.5	10.2**	66	32	34
Jacmar	Tyee	.67	.33	.74	.26	72.2	33.2**	62.6*	17	-2	19
		.50	.50	.62	.38	51.2***	41.8*	47.4***	36	-2	38
		.33	.67	.37	.63	32.1***	45.2	41.7***	42	-1	42
Moro	Tres	.67	.33	.51	.49	19.4	2.4	11.2	48	9	40
		.50	.50	.48	.52	18.8	3.3	7.3	43	6	37
		.33	.67	.23	.77	14.8*	3.9	6.6	46	20	26
Moro	Tyee	.67	.33	.71	.29	16.5	51.1	26.5*	38	3	35
		.50	.50	.44	.56	14.1*	63.0	39.9	18	-3	20
		.33	.67	.36	.64	3.8***	42.8*	29.9***	45	1	44
Faro	Tres	.50	.50	.57	.43	19.5	2.8	10.6	34	1	33
Faro	Tyee	.50	.50	.64	.36	19.8	43.0*	28.3**	40	6	34
Faro		1.0						29.2			
Jacmar		1.0						83.3			
Moro		1.0						31.0			
Tres		1.0						2.7			
Tyee		1.0						66.0			

Table IV.3. (continued)

Location/ Mixture components		Frequencies				Disease severity (%) <sup>a</sup>			Disease reduction (%)		
		Planted		Harvested							
GT1 <sup>b</sup>	GT2	GT1	GT2	GT1	GT2	GT1	GT2	Total	Total <sup>c</sup>	Sel <sup>d</sup>	Epid <sup>e</sup>
Pendleton											
Jacmar	Tres	.67	.33	.53	.47	87.0	0.9	48.2	19	20	-2
		.50	.50	.31	.69	62.6**	1.6	21.5**	52	33	19
		.33	.67	.26	.74	35.7***	0.6	8.7**	71	10	61
Jacmar	Tyee	.67	.33	.63	.37	86.2	18.3**	62.2	17	1	16
		.50	.50	.55	.45	55.9**	25.8*	41.9***	39	-2	41
		.33	.67	.30	.70	18.8***	26.3*	22.7***	63	0	63
Moro	Tres	.67	.33	.54	.46	3.5***	1.2	1.4**	96	0	96
		.50	.50	.26	.74	5.8***	0.9	2.2**	91	8	83
		.33	.67	.19	.81	4.2***	0.7	1.3	92	5	87
Moro	Tyee	.67	.33	.61	.39	12.0**	29.7	19.8***	57	0	58
		.50	.50	.47	.53	11.9**	55.9	34.1	27	0	28
		.33	.67	.26	.74	1.3***	40.1	29.3*	39	0	39
Faro	Tres	.50	.50	.45	.55	23.2	2.9	12.8	-27	0	-27
Faro	Tyee	.50	.50	.62	.38	20.4	23.2**	22.2	35	7	27
Faro		1.0						18.6			
Jacmar		1.0						87.8			
Moro		1.0						44.7			
Tres		1.0						1.6			
Tyee		1.0						49.5			

Table IV.3. (continued)

<sup>a</sup>Percent of leaf area of the leaf below the flag leaf covered with stripe rust. Disease per genotype represents the average over all tagged tillers with a given chaff color (between 5 and 10% of the tags were lost in each plot); data from all tillers were used to compute the total mean disease severity in a plot.

<sup>b</sup>GT = genotype.

<sup>c</sup> Total disease reduction =  $1 - \frac{\text{total mean disease severity in mixture plot}}{\text{pure stand mean weighted by the planted frequencies}}$

<sup>d</sup>Selection effect is the percent decrease or increase in disease severity in a mixture due to changes in frequencies of mixture components with different levels of resistance.

<sup>e</sup>Epidemiological effect is the percent reduction in disease severity below the mean of the pure stands weighted by the harvested genotype frequencies.

\*, \*\*, \*\*\* Disease severity on the individual genotypes was significantly different from their respective pure stands and total disease severity in the mixtures was significantly different from the mean of the pure stands at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Table IV.4. Coefficients of determination ( $r^2$ ) and significance of slopes (P) for regressions of stripe rust severity<sup>a</sup> on genotypes in mixtures on their frequency for wheat genotypes grown in replacement series<sup>b</sup> in two locations

Replacement series	Location					
	Moro			Pendleton		
	slope	$r^2$	P	slope	$r^2$	P
Jacmar with Tres	1.48	0.36	0.014	2.02	0.36	0.040
Jacmar with Tyee	2.43	0.52	0.002	3.02	0.67	0.001
Moro with Tres	0.31	0.26	0.052	0.77	0.51	0.013
Moro with Tyee	0.45	0.41	0.007	0.89	0.48	0.012
Tyee with Jacmar	1.51	0.36	0.024	0.72	0.22	0.121
Tyee with Moro	0.35	0.01	0.687	0.11	0.00	0.864

<sup>a</sup>See Eqn.1 for regression equation.

<sup>b</sup>Replacement series consisted of two genotypes at proportions of 1:0, 2:1, 1:1, 1:2, and 0:1; the regression for each genotype included all mixtures and its pure stand.

Table IV.5. Seed yield, number of heads, number of seed per head, and mean weight per seed for wheat genotypes grown as pure lines in the presence and absence of stripe rust in two locations

Genotype	Location			
	Moro		Pendleton	
	Fungicide <sup>y</sup>	Inoculated <sup>y</sup>	Fungicide	Inoculated
Seed yield per miniplot (g)				
Faro	171 a	152 ab	210 a	164 ab <sup>z</sup> **
Jacmar	145 ab	87 c **	172 ab	94 d ***
Moro	108 b	110 bc	138 b	116 cd
Tres	157 a	181 a	210 a	192 a
Tyee	157 a	101 bc **	216 a	132 bc ***
Number of heads per miniplot				
Faro	150 a	155 a	152 a	154 a
Jacmar	115 ab	89 b	133 ab	108 b
Moro	105 b	102 b	120 b	111 b
Tres	119 ab	149 a *	139 ab	140 ab
Tyee	115 ab	84 b	152 a	116 b **
Number of seed per head				
Faro	40.2 a	35.3 a *	37.2 ab	33.2 a
Jacmar	41.4 a	34.9 a **	38.5 ab	32.7 a *
Moro	38.3 a	37.3 a	33.0 b	32.9 a
Tres	41.1 a	40.0 a	39.4 a	35.7 a
Tyee	43.8 a	40.0 a *	40.1 a	36.8 a
Mean weight per seed (g)				
Faro	0.0297 ab	0.0292 a	0.0371 ab	0.0322 b ***
Jacmar	0.0310 ab	0.0284 a	0.0338 c	0.0272 c ***
Moro	0.0277 b	0.0287 a	0.0349 bc	0.0316 b ***
Tres	0.0328 a	0.0314 a	0.0384 a	0.0324 a
Tyee	0.0320 a	0.0296 a	0.0356 bc	0.0310 b ***

<sup>y</sup>Fungicide: plots were protected from stripe rust;  
inoculated: plots were inoculated with stripe rust.

<sup>z</sup>Numbers within a column followed by the same letter for each dependent variable are not significantly different (Fisher's unprotected LSD).

\*, \*\*, \*\*\* Yield or yield components of genotypes were different in the presence of disease than in the absence of disease at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Table IV.6. Seed yield of miniplots of wheat genotype mixtures and their components relative to their fungicide-treated pure stands at two locations

Mixture <sup>b</sup> / location	Relative seed yield <sup>a</sup>					
	Fungicide			Inoculated		
	Total	Brown	White <sup>c</sup>	Total	Brown	White
Moro						
JJR	1.11	0.86	1.56	0.74	0.45	1.29
JJY	0.85	0.92	0.72	0.80	0.91	0.61
JR	1.11	0.99	1.22	0.94	0.58	1.27
JY	1.17	0.99	1.30	0.90	1.08	0.74
JRR	1.00	0.75	1.12	1.00	0.39	1.29
JYY	1.10	1.15	1.07	0.81	1.00	0.72
MMR	1.22	0.93	1.63	1.15	0.86	1.55
MMY	1.13	0.82	1.55	1.14	1.42	0.76
MR	1.07	0.92	1.19	1.06	0.94	1.14
MY	1.29	1.16	1.39	0.85	0.90	0.81
MRR	1.16	1.51	1.04	1.04	0.66	1.17
MYY	1.12	1.32	1.04	0.90	1.17	0.81
FR	1.01	0.96	1.07	0.84	0.85	0.83
FY	0.97	1.04	0.90	0.74	0.89	0.58
JMRY	1.13	1.03	1.20	1.08	0.84	1.27
JMR	1.10	0.84	1.49	1.07	0.93	1.29
JMY	1.23	1.08	1.47	1.08	1.01	1.23
JRY	1.07	0.82	1.18	1.01	0.67	1.16
MRY	1.16	0.91	1.24	1.04	0.72	1.15
RY	1.16		1.16	1.04		1.04
Mean (mix)	1.08			0.94***		
F	1.00			0.89		
J	1.00			0.60		
M	1.00			1.02		
R	1.00			1.15		
Y	1.00			0.64		
Mean (pure)	1.00			0.86		



Table IV.6. (continued)

Relative seed yield<sup>a</sup>

Mixture <sup>b</sup> / location	Fungicide			Inoculated		
	Total	Brown	White <sup>c</sup>	Total	Brown	White
Pendleton						
JJR	1.06	0.84	1.42	0.81	0.36	1.55
JJY	0.90	1.06	0.65	0.68	0.55	0.89
JR	0.95	0.81	1.07	0.85	0.23	1.36
JY	1.01	1.06	0.97	0.67	0.66	0.67
JRR	1.13	0.83	1.26	0.77	0.38	0.93
JYY	1.04	0.93	1.09	0.75	0.77	0.72
MMR	1.04	0.95	1.17	1.00	0.81	1.27
MMY	0.85	0.99	0.67	0.92	1.11	0.66
MR	1.05	1.01	1.08	1.07	0.61	1.38
MY	1.08	1.41	0.87	0.78	1.21	0.51
MRR	0.97	0.50	1.12	1.03	0.62	1.17
MYY	1.16	1.27	1.13	0.70	0.74	0.69
FR	1.04	0.94	1.13	0.88	0.64	1.11
FY	0.95	1.00	0.91	0.82	1.02	0.63
JMRY	1.10	0.96	1.20	0.95	0.71	1.13
JMR	1.20	0.83	1.76	0.88	0.51	1.44
JMY	0.98	1.04	0.89	0.74	0.69	0.82
JRY	1.03	1.01	1.03	0.77	0.47	0.89
MRY	1.07	1.39	0.97	0.78	0.51	0.86
RY	0.95		0.95	0.94		0.94
Mean (mix)	1.02			0.83***		
F	1.00			0.78		
J	1.00			0.55		
M	1.00			0.84		
R	1.00			0.91		
Y	1.00			0.61		
Mean (pure)	1.00			0.74		

<sup>a</sup>Seed yield of each mixture and genotype was expressed relative to the seed yield of its fungicide-treated pure stand weighted by the planted frequency of that genotype in mixture.

<sup>b</sup>Mixture components were Faro (F), Jacmar (J), Moro (M), Tres (R), and Tyee (Y); variable planting proportions of genotypes are denoted with variable lettering: e.g., JJR indicates a 2:1 planting mixture of Jacmar with Tres.

<sup>c</sup>Brown components were Faro, Jacmar, and Moro; white components were Tres and Tyee.

\*\*\* Yield in the inoculated mixtures was significantly lower than the yield in the fungicide-treated mixtures at  $P < 0.01$  (linear contrasts).

Table IV.7. Coefficients of determination ( $r^2$ ) and significance of slopes (P-values) for regressions of stripe rust severity on seed yield of wheat genotypes<sup>a</sup> in replacement series

Replacement series	Location					
	Moro			Pendleton		
	slope	$r^2$	P	slope	$r^2$	P
Jacmar with Tres	0.000	0.00	0.975	0.001	0.03	0.572
Jacmar with Tyee	-0.008	0.26	0.052	-0.004	0.31	0.062
Moro with Tres	0.009	0.13	0.183	0.003	0.12	0.290
Moro with Tyee	-0.001	0.00	0.806	-0.001	0.00	0.846
Tyee with Jacmar	-0.003	0.11	0.247	-0.004	0.20	0.164
Tyee with Moro	-0.003	0.04	0.172	-0.004	0.41	0.025

<sup>a</sup>Seed yield of each genotype was expressed relative to the seed yield of its fungicide-treated pure stand weighted by the planted frequency of that genotype in mixture before performing the regressions.

<sup>b</sup>Replacement series consisted of two genotypes at proportions of 1:0, 2:1, 1:1, 1:2, and 0:1; the regression for each genotype included all mixtures and its pure stand.

Table IV.8. Seed yield of single wheat genotypes relative to their fungicide-treated pure stands<sup>a</sup> in replacement series in the presence and absence of stripe rust in two locations

			Location			
			Moro		Pendleton	
			Mixture component			
Mixture	Disease treatment	Jacmar or Moro	Tres or Tyee	Jacmar or Moro	Tres or Tyee	
Jacmar Tres	Fungicide	0.87	1.30	0.82	1.25	
Jacmar Tres	Inoculated	0.47**	1.28	0.32***	1.28	
Jacmar Tyee	Fungicide	1.02	1.03	1.02	0.90	
Jacmar Tyee	Inoculated	1.00	0.69***	0.66***	0.76*	
Moro Tres	Fungicide	1.12	1.29	0.82	1.12	
Moro Tres	Inoculated	0.82*	1.28	0.68	1.27	
Moro Tyee	Fungicide	1.10	1.33	1.22	0.89	
Moro Tyee	Inoculated	1.16	0.79***	1.02*	0.62***	

<sup>a</sup>Seed yield of each genotype was expressed relative to the seed yield of the fungicide-treated pure stands times the planted frequency of the genotype in mixture. For each genotype combination, data are pooled from the 1:2, 1:1, and 2:1 mixtures.

\*, \*\*, \*\*\* Seed yield of a genotype in inoculated mixture was significantly different from its seed yield in fungicide-treated mixture at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Fig. IV.1. Seed yield (g/miniplot) of wheat genotypes Jacmar and Moro in replacement series experiments with Tres in two sites, Moro and Pendleton. Solid triangles (Jacmar and Moro) and hollow symbols (Tres) represent the least squares means of the component yields; filled squares represent the least squares means of the total yield. Lines without symbols represent the expected yield if there were no intergenotypic interactions. Numbers in graphs are the probabilities that the observed component yield lines were linear (see Materials and methods for statistics).

Fig. IV.1.

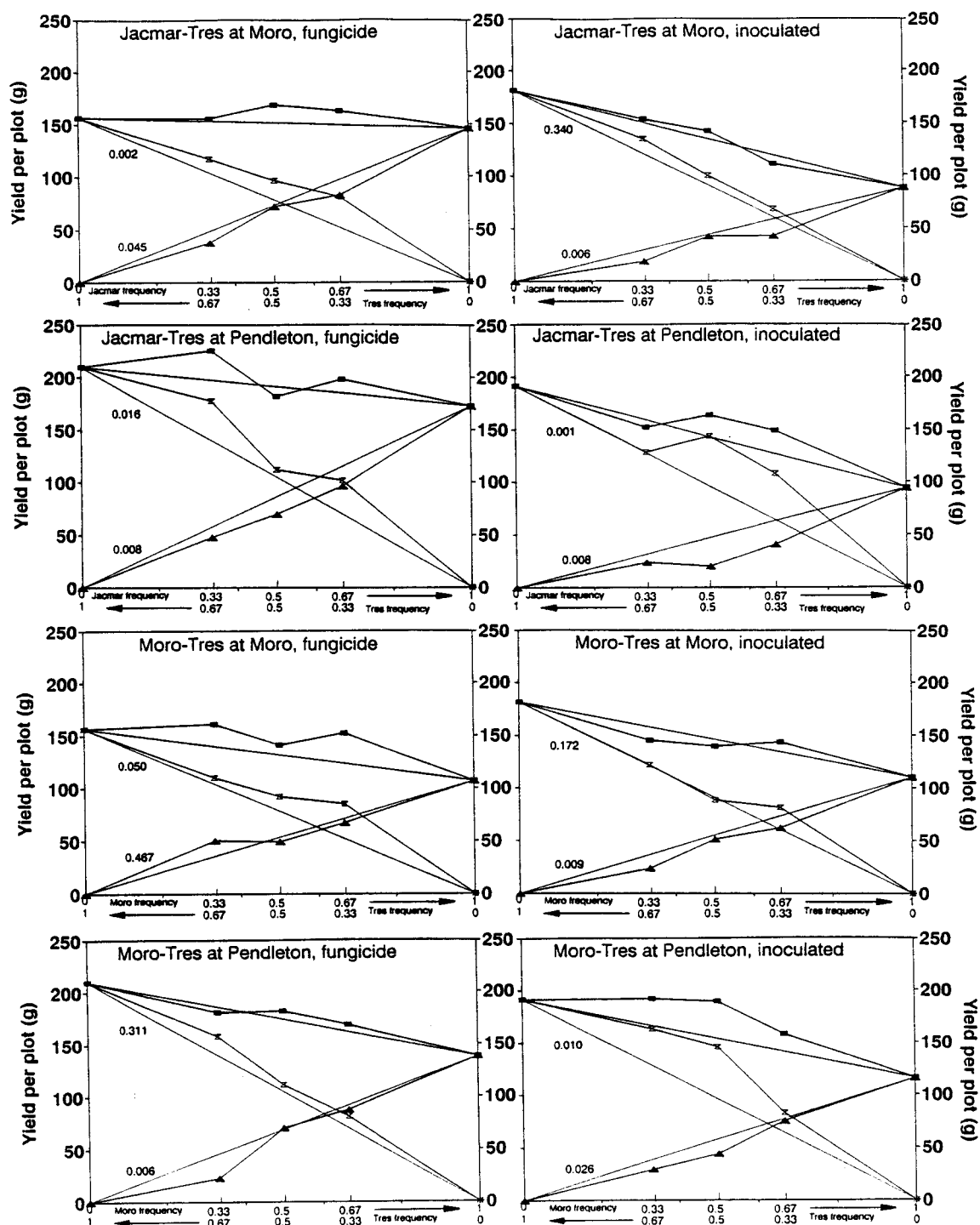
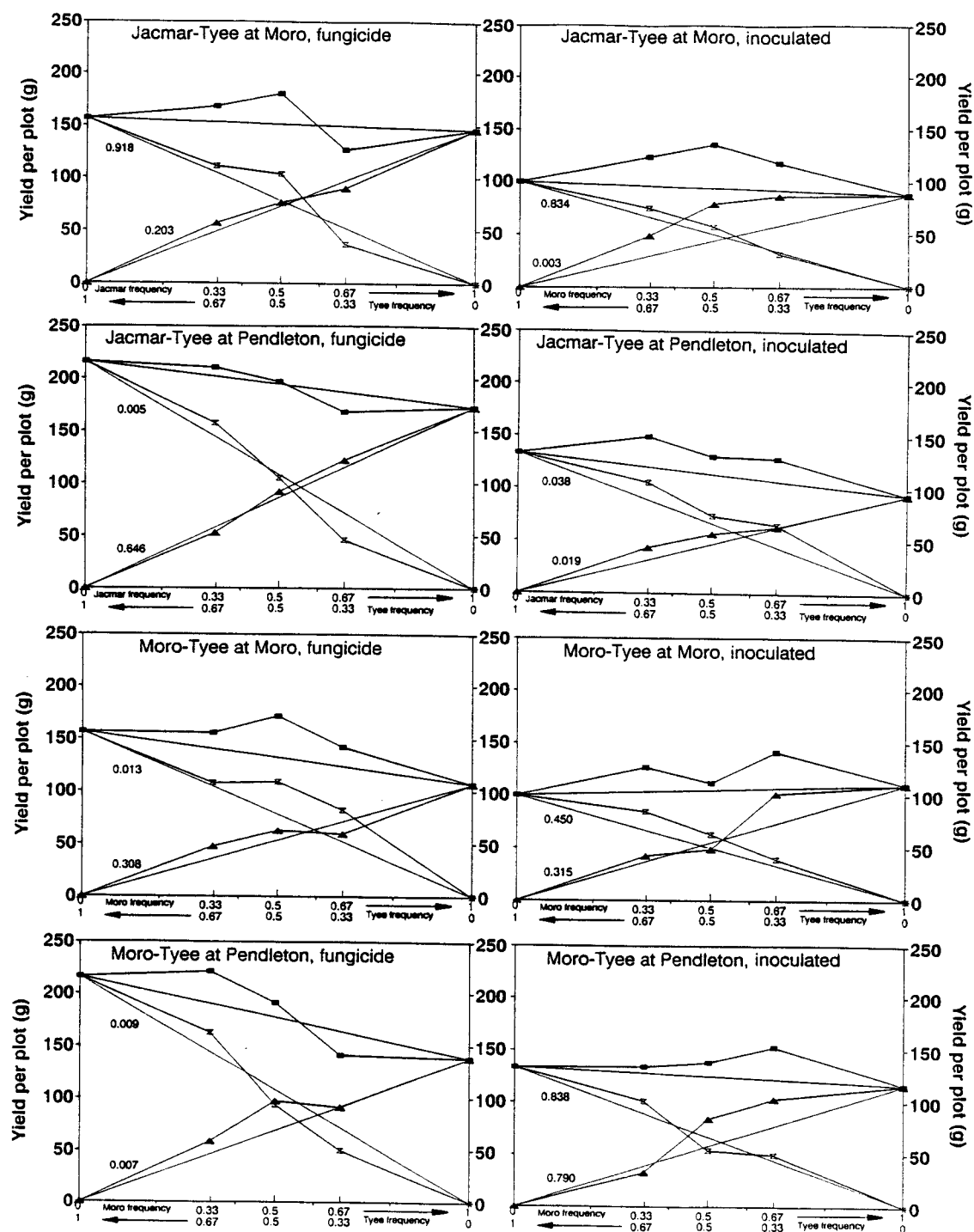


Fig. IV.2. Seed yield (g/miniplot) of wheat genotypes Jacmar and Moro in replacement series experiments with Tyee in two sites, Moro and Pendleton. Solid triangles (Jacmar and Moro) and hollow symbols (Tyee) represent the least squares means of the component yields; filled squares represent the least squares means of the total yield. Lines without symbols represent the expected yield if there were no intergenotypic interactions. Numbers in graphs are the probabilities that the observed component yield lines were linear (see Materials and methods for statistics).

Fig. IV.2.



## Literature Cited

- Alexander, H. M. 1991. Plant population heterogeneity and pathogen and herbivore levels: a field experiment. *Oecologia* 86:125-131.
- Alexander, H. M. 1984. Spatial patterns of disease induced by Fusarium moniliforme var. subglutinans in a population of Plantago lanceolata. *Oecologia* 62:141-143.
- Alexander, H. M., and Burdon, J. J. 1984. The effect of disease induced by Albugo candida (white rust) and Peronospora parasitica on the survival and reproduction of Capsella bursa-pastoris. *Oecologia* 64:314-318.
- Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition in monocultures and mixtures of two wheat cultivars. *Plant Pathol.* 35:457-465.
- Augspurger, C. K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-1712.
- Augspurger, C. K., and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211-217.
- Barrett, J. A. 1978. A model of epidemic development in variety mixtures. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford, pp. 129-137.
- Brown, J. F., and Sharp, E. L. 1970. The relative survival ability of pathogenic types of Puccinia striiformis in mixtures. *Phytopathology* 60:529-533.
- Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7:355-382.
- Burdon, J. J. 1978. Mechanisms of disease control in heterogeneous populations - an ecologists view. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford, pp. 193-200.
- Burdon, J. J. 1982. The effect of fungal pathogens on plant communities. In: The Plant Community as a



- Working Mechanism. E. I. Newman, ed. Blackwell, Oxford, pp 66-112.
- Burdon, J. J., and Chilvers, G. A. 1982. Host density as a factor in plant disease ecology. *Annu. Rev. Phytopathol.* 20:143-166.
- Burdon, J. J., Groves, R. H., Kaye, P.E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. *Oecologia* 64:199-203.
- Chilvers, G. A., and Brittain, E. G. 1972. Plant competition mediated by host-specific parasites - a simple model. *Aust. J. Biol. Sci.* 25:749-756.
- Chin, K. M., and Wolfe, M. S. 1984. Selection on Erysiphe graminis in pure and mixed stands of barley. *Plant Pathol.* 33:535-546.
- Clay, K. 1984. The effect of the fungus Atkinsonella hypoxylon (Clavicipitaceae) on the reproductive system and demography of the grass Danthonia spicata. *New. Phytol.* 98:165-175.
- Clay, K. 1990. The impact of parasitic and mutualistic fungi on competitive interactions among plants. *In: Perspectives on Plant Competition.* J. B. Grace and D. Tilman, eds. Academic Press, London, New York, pp 391-412.
- Connell, J. H. 1990. Apparent versus "real" competition in plants. *In: Perspectives on Plant Competition.* J. B. Grace and D. Tilman, eds. Academic Press, London, New York, pp 9-26.
- Finckh, M. R., and Mundt, C. C. 1992a. Effects of plant competition on stripe rust in wheat cultivar mixtures. *Phytopathology* 82:submitted.
- Finckh, M. R., and Mundt, C. C. 1992b. Effects of stripe rust and plant competition on yield of wheat cultivar mixtures. *Phytopathology* 82:submitted.
- Firbank, L. G., and Watkinson, A. R. 1985. On the analysis of competition within two-species mixtures of plants. *J. Appl. Ecol.* 22:503-517.
- Flor, H. H. 1953. Epidemiology of flax rust in the North Central States. *Phytopathology* 43:624-628.

- Gates, D. J., Westcott, M., Burdon, J. J., and Alexander, H. M. 1986. Competition and stability in plant mixtures in the presence of disease. *Oecologia* 68:559-566.
- Jarosz, A. M., Burdon, J. J., and Mueller, W. J. 1989. Longterm effects of disease epidemics. *J. Appl. Ecol.* 26:725-733.
- Jarosz, A. M., and Levy, M. 1988. Effects of habitat and population structure on powdery mildew epidemics in experimental phlox populations. *Phytopathology* 78:358-362.
- Johnson, R. 1978. Induced resistance to fungal disease with special reference to yellow rust of wheat. *Ann. Appl. Biol.* 89:107-110.
- Johnson, T., Green, G. J., and Samborski, D. J. 1967. The world situation of the cereal rusts. *Annu. Rev. Phytopathol.* 5:183-200.
- Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. Appl. Ecology* 21:227-243.
- Leonard, K. J. 1969. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. *Phytopathology* 59:1845-1850.
- Leonard, K. J., and Czocho, R. J. 1980. Theory of genetic interactions among populations of plants and their pathogens. *Annu. Rev. Phytopathol.* 18:337-358.
- May, R. M., and Anderson, R. M. 1983a. Epidemiology and genetics in the coevolution of parasites and hosts. *Royal Soc. London, Proc. Ser. B* 219:281-313.
- May, R. M., and Anderson, R. M. 1983b. Parasite-host coevolution. *In: Coevolution.* D. J. Futuyma and M. Slatkin, eds. Sinauer, pp.186-206.
- McDonald, B. A., Allard, R. W., and Webster, R. K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. *Crop Sci.* 28:447-452.
- McDonald, B. A., McDermott, J. M., Allard, R. W., and Webster, R. K. 1989. Coevolution of host and pathogen populations in the Hordeum vulgare - Rhynchosporium secalis pathosystem. *Proc. Nat. Acad. Sci.* 86:3924-3927.

- Mode, C. J. 1958. A mathematical model for the co-evolution of obligate parasites and their hosts. *Evolution* 12:158-165.
- Mode, C. J. 1961. A generalized model of a host-pathogen system. *Biometrics*, 17:386-404.
- Mundt, C. C. 1989 Modeling disease increase in host mixtures. *In*: Plant Disease Epidemiology Vol II. K. J. Leonard and W. Fry, eds. McGraw-Hill, New York, pp. 150-181.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity and cereal rust management. *In*: The Cereal Rusts Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: Effect of genotype unit area. *Phytopathology* 75:607-610.
- Mundt, C. C., Leonard, K. J. 1986. Effect of host genotype unit area on development of focal epidemics of bean rust and common maize rust in mixtures of resistant and susceptible plants. *Phytopathology* 76:895-900.
- Ouchi, S. 1983. Induction of resistance and susceptibility. *Annu. Rev. Phytopathol.* 21:289-315.
- Parker, M. A. 1989. Disease impact and local genetic diversity in the clonal plant Podophyllum peltatum. *Evolution* 43:540-547.
- Paul, N. D. 1989. The effects of Puccinia lagenophorae on Senecio vulgaris in competition with Euphorbia peplus. *J. Ecol.* 77:552-564.
- Paul, N. D., and Ayres, P. G. 1986a. Interference between healthy and rusted groundsel within mixed populations of different densities and proportions. *New Phytol.* 104:257-269.
- Paul, N. D., and Ayres, P. G. 1986b. The impact of a pathogen (Puccinia lagenophorae) on populations of groundsel (Senecio vulgaris) overwintering in the field; I. Mortality, vegetative growth and the development of size hierarchies. *J. Ecol.* 74:1069-1084.

- Paul, N. D., and Ayres, P. G. 1986c. The impact of a pathogen (Puccinia lagenophorae) on populations of groundsel (Senecio vulgaris) overwintering in the field; II. Reproduction. J. Ecol. 74:1085-1094.
- Paul, N. D., and Ayres, P. G. 1987a. Survival, growth and reproduction of groundsel (Senecio vulgaris) infected by rust (Puccinia lagenophorae) in the field during summer. J. Ecol. 75:61-71.
- Paul, N. D., and Ayres, P. G. 1987b. Effects of rust infection of Senecio vulgaris on competition with lettuce. Weed Res. 27:431-441.
- Richards, F. J. 1969. The quantitative analysis of growth. In: Plant Physiology, Vol 5A. F. C. Steward, ed. Academic Press New York, pp. 3-76.
- SAS Institute Inc. 1988. SAS/STAT User's Guide Ed. 6.03. SAS Institute, Cary, NC. 1029 pp.
- Spitters, C. J. T. 1983. An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. Neth. J. Agric. Sci. 31:1-11.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. Annu. Rev. Phytopathol. 23:251-273.

V. Effects of Stripe Rust on the Evolution of  
Genetically Diverse Wheat Populations\*

Maria R. Finckh and Christopher C. Mundt

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

Received                    / Accepted for publication

Communicated by

\*Paper No.            of the journal series of the Oregon  
Agricultural Experiment Station.

## Abstract

Eighteen populations, that were mixtures of four wheat (Triticum aestivum) genotypes were grown for one-to-three generations at two locations. Populations were either exposed to two stripe rust (Puccinia striiformis) races, protected from stripe rust, or exposed to alternating years of diseased and disease-free conditions. Regression of the logit of a genotype's frequency versus generation number was used to calculate the relative fitness of each genotype in each population. These analyses suggest that the relative fitnesses of the wheat genotypes were affected by disease and geographic location and were constant over time. However, frequency-changes of genotypes in the mixtures were negatively correlated with their planting frequencies ( $0.0001 < P < 0.085$  in 14 out of 16 cases), suggesting that fitnesses were frequency-dependent in both the presence and absence of disease. We hypothesize that failure to detect frequency-dependence of fitness in the logit analyses was due to a limited number of generations and a limited range of initial genotype frequencies. This is supported by data from longer term studies in the literature that provide evidence for frequency-dependence of fitness in plant mixtures. Analyses of currently available field data suggest that stable equilibria may be a more likely outcome for mixtures of genotypes that are

more closely related and/or more uniformly adapted to the environment in which they are grown.

Key words. - equilibrium frequencies, evolution, frequency-dependence, host diversity, pathogens

## Introduction

Plant host-pathogen systems have been studied with respect to several aspects of coevolutionary processes. It has been demonstrated that in diverse host populations epidemic development and, thus, pathogen population size are affected by reduction and dispersion of susceptible host tissue. In addition, resistant plants may function as barriers for the dispersal of inoculum (e.g., Browning and Frey, 1969; Chin and Wolfe, 1984; Leonard, 1969a; Mundt and Browning, 1985a,b; Wolfe, 1985). This should result in dependence of disease severity of a given host genotype on the frequency of this genotype in the host population (i.e., with increasing frequency disease severity increases). However, reports on frequency-dependence of disease severity have yielded contradictory results (Alexander, 1991; Augspurger and Kelly, 1984; Jarosz and Levy, 1988; Leonard, 1969a; Parker, 1989) (see Burdon and Chilvers, 1982 for review). We have recently shown that frequency-dependent effects can be obscured by plant-plant interactions in heterogeneous host populations (Finckh and Mundt, 1992c).

Disease also has been shown to affect plant-plant interactions by altering competitive interactions among plant genotypes within a season (Alexander et al., 1986; Burdon et al., 1984; Finckh and Mundt, 1992a,b,c; Paul,



1989; Paul and Ayres 1986a, 1987b) and by affecting the survival and fitness of hosts differentially (Alexander, 1984; Alexander and Burdon, 1984; Augspurger, 1984; Augspurger and Kelly, 1984; Clay, 1984; Jarosz et al., 1989; Paul and Ayres, 1986b,c, 1987a). In the intermediate or long term, the frequency of resistant host plants can be significantly increased by disease pressure (Burdon et al., 1981, Kilen and Keeling, 1990; Wahl, 1970; Webster et al., 1986). However, if resistance is linked to unfavorable traits, it may be selected against even in the presence of strong disease pressure (Parker, 1991).

Although there is observational evidence that host and pathogen genetic composition affect each other in natural (Wahl, 1970) and agricultural ecosystems (Flor, 1953; Johnson et al., 1967; McDonald et al., 1988, 1989), most of the work on host-pathogen coevolution has been focussed on theoretical modeling (e.g. Chilvers and Brittain, 1972; Gates et al., 1986; Leonard and Czocho, 1980; May and Anderson, 1983a,b; Mode, 1958, 1961). These models assume that disease severities of given genotypes are frequency-dependent and that disease is a major selective force in the system. The simpler models have allowed for only limited differences in plant fitness such as the fitness of one healthy versus one diseased genotype (Chilvers and Brittain, 1972; Leonard and Czocho, 1980). Mode (1958, 1961) and Gates et al. (1986) on the other hand, allowed

for plant fitnesses to be frequency-dependent in the presence of disease. Plant fitnesses in the absence of disease were assumed to be constant, so as to simplify the models. By differentiating between interspecific and intraspecific competition among plant genotypes, competition analysis has shown, however, that competitive abilities and thus the fitnesses of plants should usually be frequency-dependent even in the absence of disease (e.g., Firbank and Watkinson, 1985; Jolliffe et al., 1984; Spitters, 1983a,b).

Few data are available separating the contribution of disease from the contribution of plant-plant interactions to the population dynamics of plant host populations. If disease is an important selective force, it should have a detectable effect on the population dynamics in addition to the already existing selective forces.

In this paper, we report on a study that was conducted over three seasons, involving mixtures of four wheat (Triticum aestivum L.) genotypes that were grown in a variety of diseased and non-diseased environments. Because cultivated wheat inbreeds almost exclusively, gene frequencies are practically identical with genotype frequencies. We used two independent models to determine fitnesses and frequency-dependent interactions in the populations and compared our results to published results on the population dynamics of small grain mixtures.

## Materials and methods

### Host Genotypes, Locations, and Experimental Designs.

We used four soft white, club-type winter wheat (Triticum aestivum L.) varieties with different stripe rust resistances, heights, chaff colors, and reactions to a phenol-based seed stain (Table V.1). During the first year, we found that our seed source for Faro had consisted of two near-isogenic lines, one susceptible and one resistant to race 5 (Finckh and Mundt, 1992a). An average of 53% of the Faro tillers in pure stands had disease severities equal or less than 1% (range = 22 to 64%). Disease severity on the other tillers was usually between 20 and 99%. Mixed populations and pure stands of the four varieties were included as treatment plots in a series of field trials that we conducted from 1986 to 1989 (see Finckh and Mundt, 1992a,b,c). Experimental locations were Moro and Pendleton in north eastern Oregon, which receive approximately 300 and 450mm annual precipitation annually, respectively. In all years each experimental unit (plot) was 1.5 by 4.5m. In 1986/87 and in 1987/88, we conducted two separate experiments in each location, one experiment inoculated with stripe rust (Puccinia striiformis Westend. (= P. glumarum (Schm.) Jacob, Eriksson & Henn.) races CDL 5 and CDL 27 (CDL race designations are those of the USDA Cereal Disease Laboratory, Washington State University,

Pullman) and one protected from stripe rust with three-to-four applications of Bayleton (triadimefon) at 284g a.i. per ha. Experiments were arranged in randomized complete blocks with four replications in 1986/87 and six replications in 1987/88 in both locations. In 1988/89, a split plot design was employed with disease treatment as the main plots and the different wheat populations as 1.5 by 4.4m experimental units. In the following text experimental units will be referred to as plots. We inoculated each plot by transplanting spreader plants that were infected with stripe rust races 5 and 27 in the center of each plot in late fall or early spring of each year. Inoculation procedures and experimental layout and designs have been described in more detail elsewhere (Finckh and Mundt, 1992a,c).

### Populations.

From 1986 to 1989 we created a total of 18 mixed populations, ten in Pendleton, and eight in Moro, that differed with respect to age (one-to-three generations), location of evolution, and exposure to stripe rust (Table V.2). In 1986, a mixture of equal proportions of germinable seed of the four varieties was planted in each of the inoculated and fungicide-treated experiments in Pendleton and Moro. For the second generation in 1987/88, populations were either exposed to the same (continuous

carryover) or to the contrasting disease treatment (alternating carryover), thus, creating a total of four second-generation populations per location. In addition, new first-generation populations with newly mixed seed were created in 1987/88. In 1988/89, continuous and alternating carryover were continued for each of the four second-generation populations in both locations and for the first-generation populations in Pendleton. Due to spatial constraints, the alternating carryover of the first-generation populations had to be omitted in Moro 1989 (Table V.2). Another set of newly mixed populations was created in 1988/89.

#### **Disease Assessments.**

In late May or early June of each year, we assessed disease severity in each population and in the pure stands of the cultivars by visually estimating the percentage of the leaf area that was covered with stripe rust lesions. Each plot was assessed by two persons, each estimating disease severity on one half of the plot and the estimates were averaged. Due to unusually hot weather in Moro in 1989, the plants had senesced by late May to a degree that prevented acquisition of disease severity data.

In 1989, in addition to the whole-plot assessments, disease severity was estimated on individual tillers in each mixed population and in the pure stands to allow for

the determination of changes in disease severity on each genotype separately. We marked miniplots containing a minimum of 120 tillers approximately midway between the center (inoculation point) and the downwind end of each plot. Miniplots consisted of 41cm (Pendleton) and 56cm (Moro) sections of the center rows of the plots. Disease was assessed by visually estimating the percentage of the leaf below the flag leaf that was covered with stripe rust lesions. Each tiller that was assessed also was given a numbered tag matched to an identification number on data sheets used to record disease severity.

As part of concurrent experiments, we also did single-tiller assessments on the pure stands in 1987 and 1988 (Finckh and Mundt, 1992a). Those data were therefore available in all three years and allowed for a qualitative comparison of the two assessment methods in all three seasons.

#### **Harvest and Laboratory Procedures.**

Each year, seed heads from each miniplot (miniplots were located within plots as described above) were hand-harvested and transported to the laboratory for determination of genotype frequencies. Miniplots ranged from 30 to 66cm in length depending on year and location. The remainder of the plots was combine-harvested and the mixture seed saved for the next generation.

Seed heads harvested in 1987 and 1988 were separated and threshed by chaff color with a stationary plot thresher and total seed yield and 1000-kernel weight were measured. We used 150 seed from the white- (Tres and Tyee) and brown-chaffed (Faro and Jacmar) seed heads to determine the seed frequencies of the varieties. We planted the seed from the Tres-Tyee mix and from the pure stands of Tres and Tyee in the greenhouse and inoculated them with stripe rust race 27 to determine the frequencies of the two varieties based on their differential reaction to the rust race (Table V.1). Tyee plants from the pure stands served as controls to assure that inoculations had been effective, and Tres plants were used as checks for contamination by rust race(s) virulent on Tres. A seed staining procedure was used to determine the frequencies of Faro and Jacmar. Seed was soaked in hot water for at least 10 minutes and then placed embryo-up on filter paper soaked with a 1% phenol solution. Within 60 to 90 min., Jacmar seed turned uniformly black whereas Faro seed remained uniformly white for at least 4h (the methodology was adopted from the Oregon State University seed certification laboratory). Seed from the pure stands of Faro and Jacmar were again included as checks.

To determine if the ratios obtained through the differential tests and phenol tests were biased by differences in viability of the harvested seed, 150 seeds

of each mixture and pure stand were planted in the greenhouse. Germination rates were >97% in 210 out of 216 samples, the remaining six samples had germination rates >87%. Therefore, the genotype frequencies determined from the differential tests and phenol tests should closely reflect the actual frequencies.

For 1989 samples, each individual seed head was threshed with a single-head thresher, and the seed counted and weighed. Differential tests with race 27 and the phenol assays were performed as described above on five seedlings from each white-chaffed and brown-chaffed head, respectively. The tags were used to match the identities and the yield data to the single-tiller disease notes that had been taken earlier in the field.

#### Data Analyses.

Data were analyzed using SAS (SAS Inst., 1986). Fisher's non-protected LSD was used to determine statistical significance of differences among the pure stands, and linear contrasts were used to determine statistical significance of differences in disease among the mixtures and between mixtures and pure stands.

Total disease reduction in mixtures was determined by dividing the disease severity in mixtures by the mean of the pure stands that was weighted by the respective planting frequencies for each mixture. The frequency of



susceptibility to stripe rust race 27 in our experiments was identical to the frequency of Tyee. To determine if disease severity on Tyee was dependent on the frequency of Tyee in the populations, we transformed the disease severity on Tyee to  $[100/(100 - \% \text{ disease severity})]$  (Finckh and Mundt, 1992c) and regressed the transformed data on the frequency of Tyee. As Jacmar and Faro differed in their susceptibility and Faro was contaminated with a resistant line, no such analysis was possible for disease caused by race 5.

Selection coefficients for the four genotypes were calculated using the following equation:

$$\frac{p_n}{1 - p_n} = (1-s)^n \frac{p_0}{1 - p_0} \quad (1)$$

where  $p_n$  is the frequency at which the genotype occurred after  $n$  generations,  $p_0$  is the initial frequency, and  $s$  is the selection coefficient (Leonard 1969b, 1977). Taking logarithms of eqn. 1 yields a linear equation with slope  $b = \ln(1-s)$  and intercept  $\ln(p_0/[1-p_0])$ . From the slope of this equation the selection coefficient is derived as:

$$s = 1 - e^b \quad (2)$$

and the fitness  $w = 1 - s$ . Selection coefficients were determined for the populations in 1989 that had been

exposed to the different carryover treatments for three successive generations.

Regressions that are based on three generations may not reveal non-linearity due to frequency-dependent selection. To determine if there were frequency-dependent changes in the populations, we regressed the changes in frequency of a genotype on its initially planted frequencies. If the slope is negative, the intercept with the x-axis is the equilibrium point at which a genotype will neither increase nor decrease in frequency. This procedure has been used to determine equilibrium frequencies for genes that are subject to forward and back mutations (Falconer, 1981). Frequency changes in all three years were used for the analysis. For example, regressions on fungicide-treated populations were performed on the data from the f, ff, fff, if, and ifi populations that were harvested in 1987, 1988, or 1989 (Table V.2).

## Results

### Disease severity in pure stands and in mixtures.

Disease severity on the pure stands ranged from 2.5% on Tres to 84.0% on Jacmar in the whole plots (Table V.3). Although the single-tiller assessments differed from the whole-plot data (Table V.3), they resulted in similar differences in susceptibility among the four varieties. Thus, the single-tiller data from Moro 1989 provide evidence that disease levels in Moro 1989 were comparable to the levels in 1987 and 1988.

In the mixed populations, disease severity was significantly reduced below the mean of the pure stands in all years ( $P < 0.01$ , linear contrasts). Disease reduction was between 29 and 82% (Table V.3). In Pendleton 1989, there appeared to be an effect of host population age on disease severity. Disease severity on the 1<sup>st</sup> generation population was significantly higher than on the 2<sup>nd</sup> and 3<sup>rd</sup> generation populations ( $P < 0.05$ , linear contrast). These differences were due to decreasing frequencies of the more susceptible genotypes Jacmar and/or Tyee over time (Table V.6). Disease reductions that were calculated based on the planted frequencies differed only little, demonstrating the effects of frequency changes in the host populations on disease. There were no differences in disease severity between the 2<sup>nd</sup> and 3<sup>rd</sup> generation populations in Pendleton

1989 or between generations in 1988.

When disease severities were determined for each variety separately in 1989, reductions were greatest on the two most susceptible varieties, Jacmar and Tyee (Table V.4). Reductions on Faro were often small, however, as the frequencies of susceptible and resistant tillers of Faro were variable, the data cannot be easily interpreted. Disease severity on Tres was often increased in the mixtures, however, the increases were never statistically significant. The means of the single-tiller assessments in Pendleton and Moro 1989 exhibited similar differences among the generations as the whole-plot assessments (Tables 3 and 4). Disease severity was lower in the 3<sup>rd</sup> generation than in the 1<sup>st</sup> generation ( $P < 0.01$  and  $P = 0.075$  in Pendleton and Moro, respectively). There was no detectable effect of frequency of Tyee on its disease severity,  $P = 0.35$  and  $P = 0.39$  in Moro and Pendleton, respectively (data not shown).

#### Performance of the Varieties in Pure Stands and in Mixtures.

Fungicide applications effectively prevented rust infection in all years. In the absence of disease, there were no statistically significant differences in yield per plot among the four varieties in pure stands except for Pendleton 1988 where Faro and Tyee outyielded Jacmar and Tres (Table V.5). In the presence of disease, Faro and

Tres often yielded significantly higher than Jacmar and Tyee. Variation in yield was not always reflected in the number of seed heads. Faro consistently produced the greatest number of seed heads (not always statistically significant, data not shown) but it did not always yield highest. The cultivars often differed considerably in seed weight (Table V.5) and therefore in the number of seed per plot.

Despite their similar performance in pure stands, the varieties differed greatly in mixtures. In mixtures, Faro and Tres increased in frequency while Jacmar and Tyee decreased (Fig. V.1, Table V.6). Disease generally lowered the frequency of Jacmar and Tyee in the mixtures even further. In response, Faro and Tres usually increased in frequency in the presence of disease.

We used the populations that had gone through three generations of selection to calculate the relative fitnesses of the four varieties in the different disease treatments (Fig. V.2). The slopes were non-significant in only two out of 32 regressions ( $P=0.16$  for Faro in Moro, alternating carryover, start fungicide-treated, and  $P=0.12$  for Tyee in Pendleton, continuous carryover, fungicide-treated). Slopes were significant at  $P<0.05$  in 27 cases and at  $P<0.1$  in three cases (data not shown). Jacmar and Tyee always had negative and Faro and Tres always had positive slopes. Excluding the non-significant

regressions, the coefficients of determination ranged from 0.654 to 0.998.

Tres had a higher relative fitness (measured as differences in slopes) than Faro in six populations. The differences were statistically significant ( $P < 0.05$ ) in Moro, continuous carryover, fungicide-treated and in Pendleton, continuous carryover, inoculated (Fig. V.2). Tres was slightly less fit than Faro in two populations (Moro, continuous carryover, inoculated and Moro, alternating carryover, start inoculated), however, the differences were not statistically significant ( $0.55 < P < 0.82$ ). Differences between Tyee and Jacmar were more consistent, with Tyee always being fitter than Jacmar ( $0.0001 < P < 0.06$ ). The relative fitnesses of the genotypes were affected by location and disease. Jacmar was more fit in Moro than in Pendleton (Fig. V.2). Disease lowered the relative fitnesses of Jacmar and Tyee in both locations and, in response, the relative fitnesses of Tres and Faro were higher in the presence of disease.

The frequency changes of the genotypes were inversely correlated to their respective planting frequencies in the presence and absence of disease. The slopes were significantly negative at  $0.001 < P < 0.085$  in 14 out of 16 cases (Table V.7, Fig. V.3) and the sums of the predicted equilibrium frequencies for the genotypes ranged from 0.97 to 1.08 (Table V.7). Disease affected the predicted

equilibrium frequencies in both locations. In Moro, both Jacmar and Tyee were predicted to be present in lower frequencies in the diseased populations than in the disease-free populations. The equilibrium frequency of Faro was predicted to be substantially higher in the diseased populations. In Pendleton, the predicted equilibria in the diseased and non-diseased populations differ mainly in that, in the presence of disease, Jacmar is predicted to disappear from the population.

## Discussion

Our experiments provide insight into the population dynamics of heterogeneous wheat populations and how they are influenced by different locations, years, and disease. Populations that were started in different years, exhibited similar dynamics in their first generation in both locations under diseased and non-diseased conditions (Table V.6). The effects of location and disease became evident only over time. Disease lowered the fitness of Jacmar in both locations and Jacmar was overall more fit in Moro than in Pendleton.

Although the four wheat genotypes were similar in yielding ability in pure stands in the absence of disease, they differed considerably in the presence of disease and when grown in mixtures. The differences in competitiveness among the cultivars were consistent with the ranking in competitiveness that we had derived from two-component mixtures (Finckh and Mundt, 1992b,c).

By introducing the same pathogen population every year we did not allow concurrent evolutionary changes in the pathogen population. Thus, although the mixed populations were effective in reducing stripe rust severity caused by race 5 and 27 in all three years, no prediction can be made about their performance if they were confronted with a changing pathogen population. For example, stripe rust



race 41, which is virulent on Tres, was not prevalent in eastern Oregon when we started our experiments in 1986. However, by 1990 it frequently attacked Tres in the wheat growing areas around Pendleton and Moro (personal observation). Considering that Tres greatly increased in frequency over time (Fig. V.1, Table V.6) the vulnerability of the mixtures to stripe rust race 41 would also have increased. Because the pathogen population was constant, however, the effects of disease on the host population dynamics could be separated from the effects of plant-plant interactions through comparison of the relative fitnesses among the populations (Fig. V.2)

Our failure to detect frequency-dependence of disease severity on Tyee may be due to at least two factors. First, interactions among the genotypes in the mixtures might have affected disease severity on the different genotypes. In experiments with two-way mixtures, we found that the companion genotype can have a profound effect on the disease severity of a genotype in mixtures if the competitive abilities of the genotypes are very different (Finckh and Mundt, 1992c). Second, the frequencies at which Tyee was present in the mixtures ranged from 6 to 27%. This range might have been too small to detect effects of frequency on disease.

The low fitness of Jacmar in mixtures was probably due in part to its shortness, as was found with a rice cultivar

in mixtures (Jennings and de Jesus, 1968). The higher relative fitnesses of Jacmar in Moro than in Pendleton are consistent with earlier results, which had shown that Jacmar generally was more competitive in Moro than in Pendleton (Finckh and Mundt, 1992b,c). In Pendleton, the plants grew taller and denser because of the higher precipitation, and competition for light was likely more important in Pendleton than in Moro.

Leonard's (1969b, 1977) model for relative fitnesses and the negative slopes for the regression of frequency changes on planted frequencies would not be expected to occur for the same data set. If frequency-dependent selection occurs, selection coefficients change over time and straight lines should not result when transforming frequency data. The lack of obvious non-linearities in our data (Fig. V.2) may be due to the limited number of generations studied.

We performed regressions of frequency changes on planted frequencies (Fig. V.3, Table V.7) to determine if frequency-dependent selection was occurring in our populations independent from the number of generations. However, when evaluating frequency changes, it is important to bear in mind that a genotype that was planted at low frequencies, e.g. 5% cannot change as much in one generation as when planted at intermediate frequencies, e.g. 25%. At high frequencies, the changes will again be

small as the companion genotypes must be present at low frequencies. Therefore, frequency changes should follow a sine shaped curve. The frequencies of the different genotypes in the populations did not range over more than 30% (Fig. V.3). The limited range in frequencies and the small number of data points (eight in Moro and nine in Pendleton) are probably responsible for the lack of pattern in the deviations from the straight lines in Fig. V.3.

A few studies have been conducted on the population dynamics of small grain mixtures over several generations. Harlan and Martini (1938) conducted experiments with a mixture of 11 barley (Hordeum vulgare) varieties in 10 locations over two-to-twelve generations. Blijenburg and Snee (1975) grew a mixture of eight barley varieties over six generations and Murphy et al. (1982) followed a mixture of five near-isogenic oat (Avena sativa) lines over four generations in the presence and absence of oat crown rust (caused by Puccinia coronata). We used data from those three studies to test Leonard's (1969, 1977) model (Table V.8). Although the regressions were usually significant with high coefficients of determination, visual examination of scatter plots for populations that were studied for five or more generations suggested specific non-linear trends in 40 out of 88 plots. Sixteen plots appeared random and only 32 plots followed straight lines.

The non-linear plots fell into six general curve types

(Fig. V.4). Straight lines ((1) in Fig. V.4) with positive or negative slopes indicating positive or negative selection coefficients, respectively, should result if intergenotypic and intragenotypic plant-plant interactions were equal but genotypes differed in their innate seed producing capacity. On the other hand, if genotypes differ in their competitive abilities, their relative fitnesses will depend on the type and amount of other genotypes present in the population. A strong competitor and good seed producer might exhibit a pattern such as curve (2). When present at low and intermediate frequencies and competing mostly against weaker genotypes, its fitness will be high. With an increase in its own frequency, it will compete against itself and its relative fitness will decrease. Similarly, the relative fitness of the corresponding weak competitor will increase (curve (3)). If competitive ability and seed production are not correlated, then curves (4) and (5) could result. For example, genotype a might produce many more seed than genotype b in pure stands. However, genotype b may be a strong competitor with respect to a and therefore, in mixtures a may produce only few more seed than b. Over time, b will nevertheless decrease in frequency and with relaxed competitive pressure the relative fitness of a should increase.

Discrepancies between competitiveness of plants and

their reproductive output or allocation have been reported in cultivated plant varieties (Hamblin, 1975; Jennings and de Jesus, 1968; Suneson, 1949; Suneson and Wiebe, 1942) and they may arise when cultivated plant varieties are selected as pure lines in early generations from crosses.

Typically, they are not exposed to intergenotypic competition throughout the breeding and selection process. In natural populations, on the other hand, intergenotypic and intragenotypic competitive interactions play a role as selective forces and patterns such as curves (4) and (5) may not usually be observed. Curve (6) may arise if genotypes with low fitness disappear from the population after a few generations. Intermediate genotypes will have a positive fitness as long as there are less fit genotypes in the population. Once the latter have disappeared, the relative fitnesses of the other genotypes will change and previously positive selection coefficients may become negative. Equilibria at which several genotypes coexist could occur if they followed curves (2) and (3) and reach plateaus, i.e.  $\underline{s}=0$ . If genotypes are identical in their reproductive and competitive abilities they may also coexist, however, this would not be a stable equilibrium.

The results from the analysis of the data from the literature (Table V.8, Fig. V.4) suggest that fitnesses in general might be frequency-dependent and that a more flexible model for the evaluation of fitnesses over time

needs to be adopted.

Attempts to predict equilibrium frequencies were made for the populations of Harlan and Martini (1938) in the six locations where they had been grown for at least seven generations. In Aberdeen, the predicted frequencies of the varieties were very close to the observed frequencies after twelve generations and their sum was 1.02. However, for all other locations the model did not fit. For the Ithaca data, the sum of the predicted frequencies deviated greatly from one (1.33). For the Moccasin, Moro, North Platte, and St. Paul locations, one or two varieties were so much superior in yielding ability in mixtures to all the other varieties that they always increased in frequency. Consequently, the slopes of the regressions were positive for the superior variety making the calculation of equilibrium frequencies impossible. Those superior varieties either followed the straight (1) or the curved (4) lines with positive slopes in Fig. V.4. Lines (1) and (4) exclude the existence of equilibrium frequencies, as fitnesses are constant or increase over time. The eight-component mixture of Blijenburg and Snee (1975) also contained one variety that was highly superior to all other varieties. Although its increase in frequency was significantly affected by its planted frequency (slope = -0.15,  $P < 0.01$ ), the line intercepted the x-axis only at 1.31, indicating that the variety should exclude all other

mixture components over time.

In contrast to the barley variety mixtures of Blijenburg and Sneepe (1975) and Harlan and Martini (1938), frequency changes in the mixture of near-isogenic oat lines (NILs) that Murphy et al. (1982) studied were relatively small and no single line dominated the populations. This was probably due to the close relatedness of the NILs that had been backcrossed four or five times and selected for phenotypic similarity to the recurrent parent for agronomic traits. Blijenburg and Sneepe (1975) and Harlan and Martini (1938) selected their barley varieties because they were dissimilar enough for separation of the varieties but not necessarily because they were adapted to the same environmental conditions. The wheat varieties that we chose for our experiments are closely related, but not as close as NILs (Zwer, 1989), and were all bred for the semi-arid wheat growing environments in the Pacific Northwest. This could help explain why our experimental populations appeared to tend towards equilibrium frequencies, whereas almost none of the described barley mixtures tended towards an obvious equilibrium.

Our study has demonstrated that disease can act as a selective force in diverse plant populations and that it might affect equilibrium frequencies. However, only continuation of our experiments over more generations and the addition of populations starting at different genotype

frequencies could provide more definite answers to questions such as if there is frequency-dependence, if equilibrium frequencies exist, and how equilibrium frequencies will be affected by disease.



Table V.1. Wheat varieties used to create mixed populations, their chaff colors, heights, reactions to two stripe rust races, and reactions to a phenol stain

Variety	Chaff color	Relative height	Phenol stain <sup>b</sup>	Reaction <sup>a</sup> to <u>Puccinia striiformis</u> race	
				5	27
Faro	brown	tall	white	VAR	R
Jacmar	brown	short	black	S	R
Tres	white	tall	white	MR	R
Tyee	white	tall	mixed	R	S

<sup>a</sup>VAR = reaction variable, approximately one-half of the plants were resistant and one-half susceptible; R = resistant; S = susceptible; MR = moderately resistant.

<sup>b</sup>Reaction of seed to exposure to 1% phenol solution.

Table V.2. Mixed populations of the wheat varieties Faro, Jacmar, Tres, and Tyee grown<sup>a</sup> in Pendleton and Moro in three winter wheat seasons

Population	Season		
	1986/87	1987/88	1988/89
I	f <sup>b</sup>	f	f
II	i <sup>c</sup>	i	i
III	f	i	f
IV	i	f	i
V		f	f
VI		i	i
VII		f	i <sup>d</sup>
VIII		i	f <sup>d</sup>
IX			f
X			i

<sup>a</sup>e.g., population III treated with fungicide in 1986/87; seed harvested, replanted, and inoculated in 1987/88; and harvested, replanted, and treated with fungicide in 1988/89.

<sup>b</sup>f = not inoculated with stripe rust, protected from disease with fungicide.

<sup>c</sup>i = inoculated with stripe rust.

<sup>d</sup>Populations not included in Moro.

Table V.3. Stripe rust severity of whole plots and on single tillers in pure stands and in mixed populations of four wheat genotypes in two locations and three years

Location/ Year	Assessment	Pure stands					Mixtures <sup>c</sup>				
		Faro	Jacmar	Tres	Tyee	Mean	i	ii	iii	fi	ifi
Moro 1987	Plot <sup>a</sup>	16.75	69.25	3.25	38.25	31.88	16.25				
	Tiller <sup>b</sup>	15.33	80.54	0.33	27.19		(49) <sup>d</sup>				
Pendleton 1987	Plot	27.00	65.50	12.75	63.00	42.06	22.25				
	Tiller	24.18	68.86	2.36	45.24		(47)				
Moro 1988	Plot	10.50	42.50	4.50	47.33	26.21	14.67	12.83	14.50		
	Tiller	22.44	57.81	4.86	54.58		(44)	(35)	(29)		
Pendleton 1988	Plot	11.00	53.8.	2.50	60.67	32.00	11.00	8.17	11.33		
	Tiller	8.24	40.52	1.04	39.88		(66)	(63)	(53)		
Moro 1989	Plot	- <sup>e</sup>	-	-	-	-	-	-	-	-	-
	Tiller	29.17	83.34	2.66	66.02						
Pendleton 1989	Plot	6.67	84.00	2.13	65.00	39.45	12.67	6.00	4.27	2.33	5.33
	Tiller	18.56	87.77	1.60	49.47		(68)	(74)	(82)	(82)	(72)

<sup>a</sup>Plot: assessments were done on whole plots (see Materials and methods for details).

<sup>b</sup>Tiller: assessments were done on single tillers within miniplots (see Materials and methods for details).

<sup>c</sup>i = inoculated with stripe rust, f = fungicide treated; more than one letter indicates the sequence of treatments over generations; see Table V.2 for description of populations.

<sup>d</sup>Numbers in brackets indicate the percent reduction in mixtures relative to the mean of the pure stands weighted by the planted genotype frequencies.

<sup>e</sup>No whole-plot data were collected in Moro 1989.

Table V.4. Stripe rust severity on four wheat varieties in pure stands and when grown in mixtures based on single-tiller assessments in two locations in 1989

Pop. <sup>a</sup>	Variety				Mean <sup>b</sup>	Disease reduction <sup>c</sup>
	Faro	Jacmar	Tres	Tyee		
Moro						
Pure	29.2	83.3	2.7	66.2	45.4	
i	18.8	39.7**	4.7	14.9***	17.9	0.53
ii	25.9	16.1***	5.0	32.8***	12.7	0.62
iii	12.7*	15.0***	2.9	21.1***	9.8	0.60
ifi	18.3	43.0**	2.0	5.9***	13.9	0.56
Pendleton						
Pure	18.6	87.8	1.6	49.5	39.4	
i	16.4	53.9**	4.1	10.1***	19.3	0.40
ii	9.9	28.5***	5.5	4.2***	7.6	0.61
fi	8.8*	48.5**	7.5	6.7***	9.2	0.63
iii	5.5**	16.2***	0.7	2.8***	2.9	0.82
ifi	16.0	34.0***	3.9	5.8***	9.0	0.57

<sup>a</sup>i: inoculated with stripe rust, f: fungicide treated; more than one letter indicates the sequence of treatments over generations; see also Table V.2 for explanation of population names.

<sup>b</sup>The mean disease severity is based on the actual tiller frequencies of the varieties in the populations.

<sup>c</sup>Disease reduction =  $1 - \frac{\text{observed disease severity}}{\text{expected disease based on tiller frequencies}}$

\*, \*\*, \*\*\* disease severity was significantly different in mixture from the severity in pure stand on the same variety at  $P < 0.1$ ,  $P < 0.05$ , and  $P < 0.01$ , respectively (linear contrasts).

Table V.5. Yield per miniplot<sup>x</sup> and 1000 seed weight of four wheat varieties in pure stands in two locations and three years

		Location			
		Moro		Pendleton	
Year	Variety	Fungicide <sup>y</sup>	Inoculated	Fungicide	Inoculated
Yield per miniplot (g)					
1987	Faro	138.73 a	114.51 a	117.68 a	117.07 ab <sup>z</sup>
	Jacmar	155.09 a	90.09 a	126.97 a	85.91 c
	Tres	138.30 a	91.50 a	114.81 a	119.46 a
	Tyee	134.77 a	81.44 a	133.13 a	94.96 bc
1988	Faro	180.43 a	181.17 a	157.59 a	122.16 a
	Jacmar	175.52 a	102.93 b	136.18 b	58.77 c
	Tres	186.07 a	176.14 a	134.27 b	142.16 a
	Tyee	151.02 a	121.50 b	145.58 ab	92.02 b
1989	Faro	171.28 a	152.12 ab	209.64 a	163.82 ab
	Jacmar	145.25 a	87.45 c	172.47 a	94.43 d
	Tres	156.94 a	180.92 a	210.02 a	191.84 a
	Tyee	156.99 a	100.64 bc	216.36 a	132.21 bc
1000 seed weight					
1987	Faro	23.34 a	20.88 a	30.22 bc	28.04 ab
	Jacmar	29.15 a	21.68 a	28.52 c	25.47 ab
	Tres	28.50 a	21.50 a	33.65 a	29.60 a
	Tyee	28.74 a	21.63 a	30.75 b	26.76 b
1988	Faro	29.16 ab	27.95 a	31.07 b	25.52 b
	Jacmar	25.07 c	21.87 b	30.14 bc	21.45 c
	Tres	31.47 a	28.25 a	33.68 a	33.94 a
	Tyee	27.75 bc	23.47 b	29.35 c	24.30 b
1989	Faro	29.73 a	29.23 a	37.09 ab	32.19 b
	Jacmar	30.98 a	28.43 a	33.81 c	27.27 c
	Tres	32.80 a	31.35 a	8.37 a	38.24 a
	Tyee	31.96 a	29.61 a	35.58 bc	31.10 b

<sup>x</sup>Plot size varied from year to year; see methods for details.

<sup>y</sup>Inoculated: plots were inoculated with stripe rust; fungicide: plots not inoculated protected from stripe rust.

<sup>z</sup>Numbers within a column and year followed by the same letter are not significantly different at  $P < 0.05$  (Fisher's unprotected LSD).

Table V.6. Genotype seed frequencies in populations composed of four wheat varieties that were continuously exposed to stripe rust, continuously protected from stripe rust, or exposed and protected in alternating seasons for one-to-three generations in two locations

Location/ Year of Pop <sup>a</sup> harvest			Harvested seed frequencies			
Trt <sup>b</sup>			Faro	Jacmar	Tres	Tyee
<hr/>						
Moro						
I	1987	f	0.30	0.17	0.35	0.18
	1988	ff	0.26	0.18	0.36	0.20
	1989	fff	0.31	0.09	0.41	0.20
II	1987	i	0.28	0.14	0.39	0.19
	1988	ii	0.40	0.08	0.40	0.12
	1989	iii	0.44	0.07	0.39	0.10
III	1987	f	0.30	0.17	0.35	0.18
	1988	fi	0.22	0.16	0.47	0.14
	1989	fif	0.41	0.08	0.36	0.15
IV	1987	i	0.28	0.14	0.39	0.19
	1988	if	0.28	0.14	0.36	0.22
	1989	ifi	0.44	0.10	0.32	0.14
V	1988	f	0.37	0.17	0.32	0.14
	1989	ff	0.33	0.19	0.29	0.18
VI	1988	i	0.34	0.12	0.36	0.18
	1989	ii	0.40	0.10	0.34	0.17
IX	1989	f	0.34	0.14	0.31	0.21
X	1989	i	0.31	0.17	0.33	0.20
Pendleton						
I	1987	f	0.28	0.12	0.39	0.22
	1988	ff	0.32	0.11	0.42	0.15
	1989	fff	0.35	0.04	0.40	0.22
II	1987	i	0.30	0.09	0.40	0.21
	1988	ii	0.34	0.03	0.52	0.11
	1989	iii	0.34	0.01	0.51	0.15
III	1987	f	0.28	0.12	0.39	0.22
	1988	fi	0.43	0.06	0.38	0.13
	1989	fif	0.43	0.05	0.46	0.06

Table V.6. (continued)

Location/ Pop <sup>a</sup>	Year of harvest	Trt <sup>b</sup>	Harvested seed frequencies			
			Faro	Jacmar	Tres	Tyee
Pendleton						
IV	1987	i	0.30	0.09	0.40	0.21
	1988	if	0.34	0.03	0.43	0.20
	1989	ifi	0.34	0.03	0.41	0.22
V	1988	f	0.39	0.09	0.32	0.19
	1989	ff	0.37	0.10	0.34	0.19
VI	1988	i	0.35	0.10	0.38	0.18
	1989	ii	0.38	0.01	0.40	0.21
VII	1988	f	0.39	0.09	0.32	0.19
	1989	fi	0.35	0.04	0.34	0.27
VIII	1988	i	0.35	0.10	0.38	0.18
	1989	if	0.34	0.10	0.37	0.20
IX	1989	f	0.30	0.17	0.31	0.22
X	1989	i	0.41	0.13	0.29	0.18

<sup>a</sup>Pop=population, see Table V.2 for descriptions. All populations were composed of equal proportions of germinable seed for the initial planting.

<sup>b</sup>Trt=treatment; i=inoculated with stripe rust, f=fungicide-treated;

Table V.7. Statistics for regressions of frequency change on the planted frequency and the predicted equilibrium frequencies of four wheat varieties in mixed populations that were either exposed to or protected from stripe rust for one-to-three generations at two locations

Location / Treatment <sup>a</sup>	Cultivar	Slope	P	r <sup>2</sup>	Predicted Frequencies at Equilibrium <sup>b</sup>	
Moro fungicide	Faro	-1.43	0.013	0.67	0.31	(0.97)
	Jacmar	-0.78	0.085	0.41	0.13	
	Tres	-0.77	0.004	0.78	0.35	
	Tyee	-1.02	0.006	0.75	0.19	
Moro inoculated	Faro	-0.21	0.685	0.03	0.55	(1.08)
	Jacmar	-0.57	0.009	0.71	0.08	
	Tres	-0.79	0.039	0.54	0.39	
	Tyee	-0.35	0.047	0.51	0.06	
Pendleton fungicide	Faro	-0.51	0.038	0.48	0.38	(1.01)
	Jacmar	-0.64	0.005	0.70	0.06	
	Tres	-0.49	0.035	0.49	0.43	
	Tyee	-0.40	0.320	0.16	0.15	
Pendleton inoculated	Faro	-1.06	0.009	0.65	0.35	(1.00)
	Jacmar	-0.58	0.000	0.92	0.00	
	Tres	-0.44	0.071	0.39	0.46	
	Tyee	-0.96	0.057	0.43	0.18	

<sup>a</sup>Fungicide: data from all populations that were protected from stripe rust in each of three years are included, i.e. the f ff, fff, if, and fif populations that were harvested in 1987, 1988, or in 1989 (see Table V.2). Corresponding data were included in the inoculated sets.

<sup>b</sup>Predicted equilibrium frequencies are the intercepts of the regression lines with the X-axis. Numbers in brackets are the sum of the equilibrium frequencies of all four genotypes in the mixed populations.



Table V.8. Analysis of data from published papers on population dynamics in small grain mixtures using Leonard's (1969, 1977) model to determine individual relative fitnesses

Source of data/ Location	Gen <sup>a</sup>	Regressions with $P < 0.05$ <sup>b</sup>	Number non-linear regressions <sup>c</sup>
Harlan and Martini (1938), 11 barley varieties <sup>d</sup>			
Aberdeen	12	10/10	3
Arlington	3	8/9 <sup>e</sup>	- <sup>f</sup>
Davis	4	7/10	- <sup>f</sup>
Fargo	5	8/10	6
Ithaca	12	8/10	5
Moccasin	12	7/10	7
Moro	7	6/10	9
North Platte	7	9/10	6
Pullman	2	8/10	- <sup>f</sup>
St. Paul	9	8/10	6
Blijenburg and Sneepe (1975), 8 barley varieties			
Netherlands	6	6/8	5
Murphy et al. (1982), 5 near isogenic oat lines			
Iowa, no rust	4	2/5	4
Iowa, rusted	4	2/5	4

<sup>a</sup>Number of generations that a population was evaluated.

<sup>b</sup>Number of significant regressions ( $P < 0.05$ ) / total number of regressions performed.

<sup>c</sup>Number of curves that clearly showed non-linear trends by visual examination.

<sup>d</sup>Harlan and Martini (1938) used 11 barley varieties. However, two varieties were indistinguishable and were treated as one composite variety. Therefore, only 10 regressions were performed in each location.

<sup>e</sup>One variety disappeared from the mixture in Arlington within one generation. Therefore, fitnesses were calculated for only nine.

<sup>f</sup>Too few generations for appropriate evaluation of non-linear trends.

Fig. V.1. Dynamics of populations composed of four wheat genotypes over three generations in two locations, Moro and Pendleton. Populations were either continuously protected from stripe rust by fungicide applications (designated by f) or inoculated with stripe rust (designated by i) or exposed to stripe rust in alternating years. Populations were all started at equal proportions of the genotypes Faro, Jacmar, Tres, and Tyee (Start). The first generation is designated with one letter, the second with two, etc. For example, ifi indicates inoculated, fungicide-treated, and inoculated in the first, second, and third generations, respectively.

Fig. V.1.

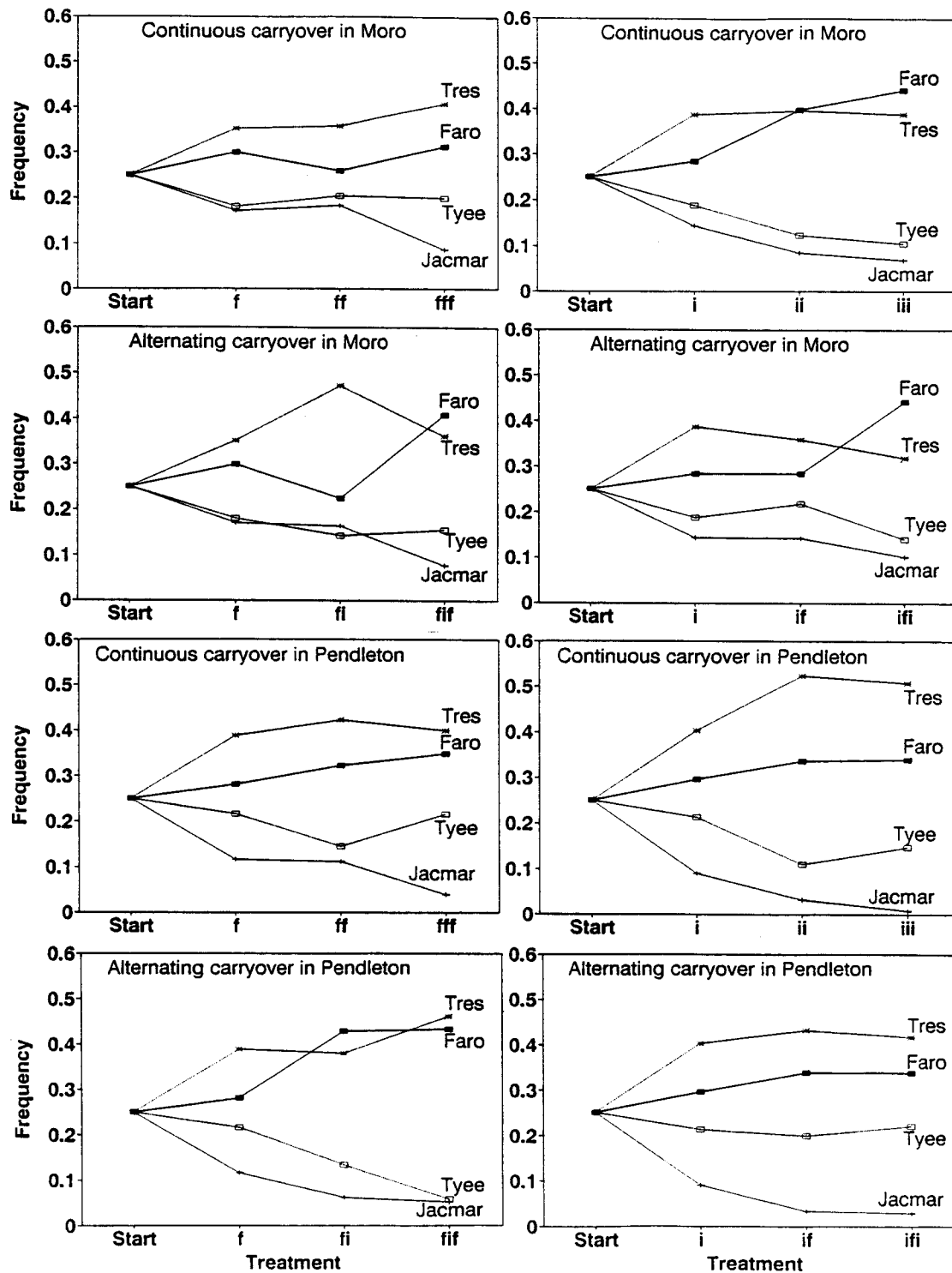


Fig. V.2. Rates of change in frequency of four wheat genotypes grown in mixed populations at two locations for three generations. Populations either carried over from season to season inoculated with stripe rust each year, or fungicide-treated each year, or inoculated and fungicide-treated in alternating years (see Table V.2 for details). Data are plotted as logits of the frequencies  $p$  ( $\ln[p/(1-p)]$ ) versus the number of generations.  $w$  denotes the fitness of each genotype which is calculated as  $(1-[1-e^b])$  where  $b$  is the slope of the regression line (see Materials and methods for details of calculations).

Fig. V.2.

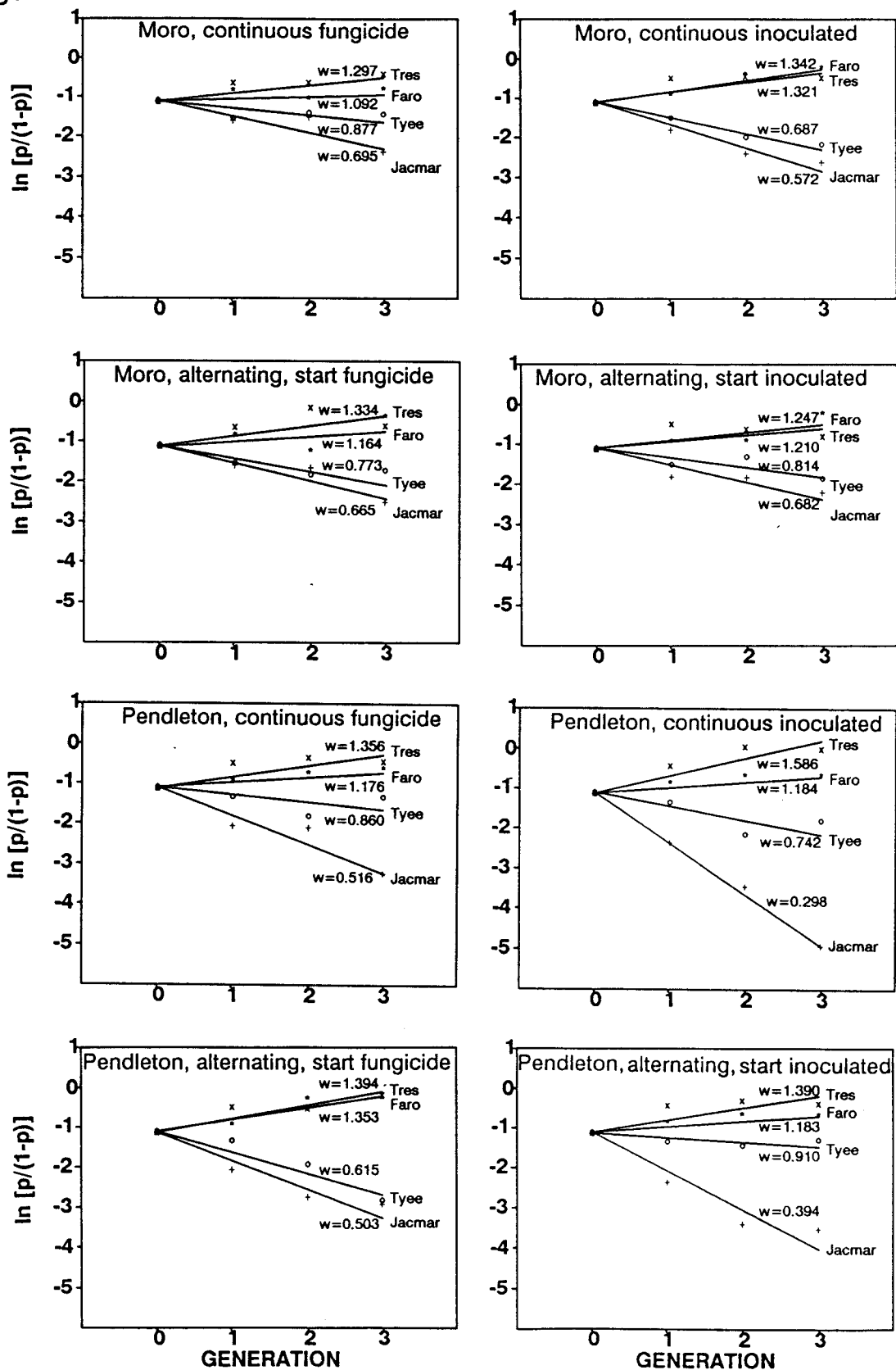


Fig. V.3. Frequency changes of four wheat genotypes grown in mixed populations in two locations versus their planted frequencies. Data from all populations that were protected from stripe rust in each of three years are included in the graphs titled fungicide-treated, and all populations that were inoculated with stripe rust in each of three years are included in the graphs titled inoculated. Data points for each genotype are denoted with letters: F=Faro, J=Jacmar, R=Tres, and Y=Tyee.

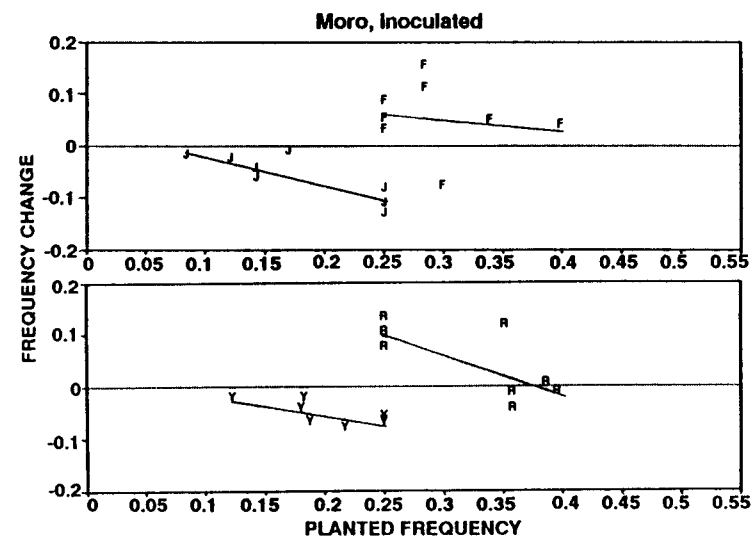
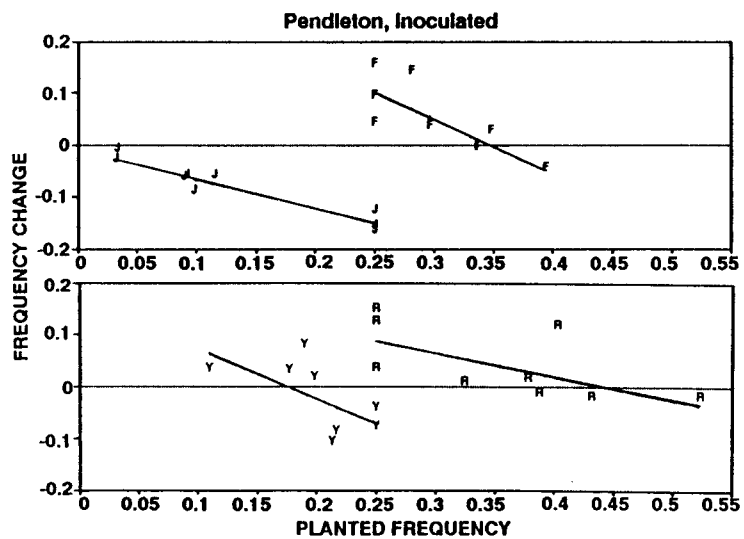
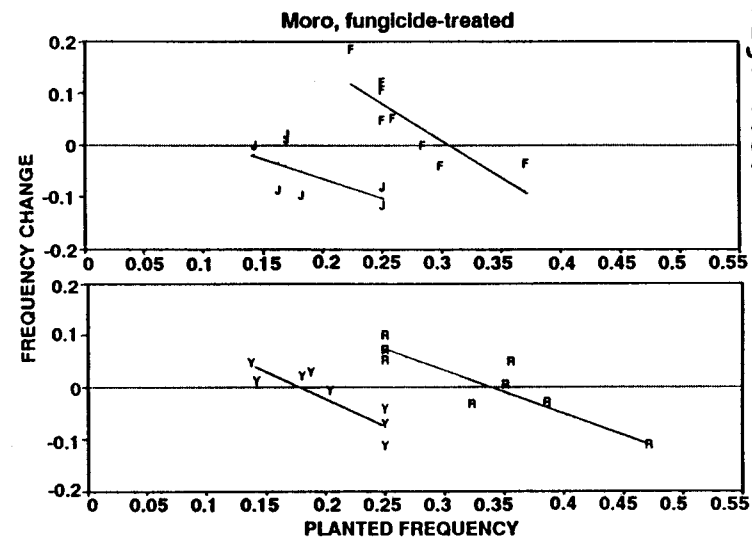
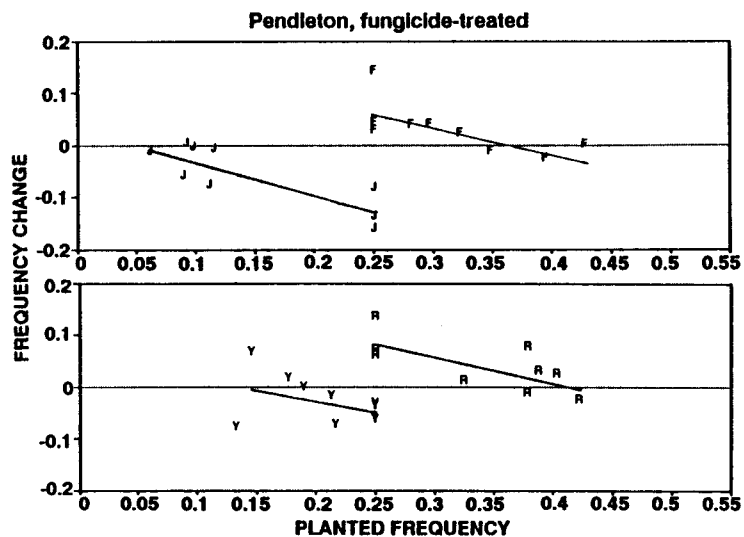


Fig. V.3.

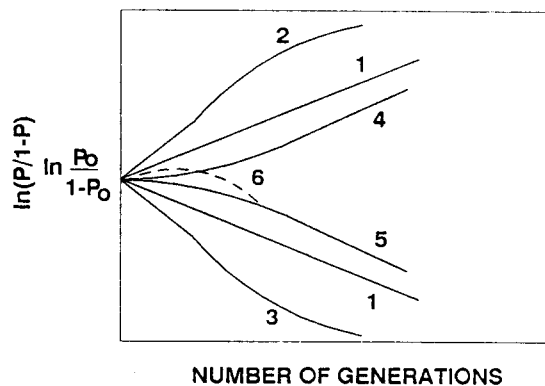


Fig. V.4. Types of curves resulting from plotting logits of the frequencies of plant genotypes ( $p$ ) ( $\ln[p/(1-p)]$ ) versus the number of generations for data of Blijenburg and Snee (1975), Harlan and Martini (1938), and Murphy *et al.* (1982). All populations were started at equal proportions of all genotypes. See text for explanations.



### Literature Cited

- Alexander, H. M. 1991. Plant population heterogeneity and pathogen and herbivore levels: a field experiment. *Oecologia* 86:125-131.
- Alexander, H. M. 1984. Spatial patterns of disease induced by Fusarium moniliforme var. subglutinans in a population of Plantago lanceolata. *Oecologia* 62:141-143.
- Alexander, H. M., and Burdon, J. J. 1984. The effect of disease induced by Albugo candida (white rust) and Peronospora parasitica on the survival and reproduction of Capsella bursa-pastoris. *Oecologia* 64:314-318.
- Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition in monocultures and mixtures of two wheat cultivars. *Plant Pathol.* 35:457-465.
- Augspurger, C. K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-1712.
- Augspurger, C. K., and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211-217.
- Blijenburg, J. G., and Snee, J. 1975. Natural selection in a mixture of eight barley varieties grown in six successive years. 1. Competition between the varieties. *Euphytica* 24:305-315.
- Browning, J.A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* 7:355-382.
- Burdon, J. J., and Chilvers, G. A. 1976. Controlled environment experiments on epidemics of barley mildew in different density host stands. *Oecologia* 26:61-72.
- Burdon, J. J., and Chilvers, G. A. 1982. Host density as a factor in plant disease ecology. *Annu. Rev. Phytopathol.* 20:143-166.
- Burdon, J. J., Groves, R. H., and Cullen, J. M. 1981. The impact of biological control on the distribution and abundance of Chondrilla juncea in south-eastern

- Australia. J. Appl. Ecol. 18:957-966.
- Burdon, J. J., Groves, R. H., Kaye, P.E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. Oecologia 64:199-203.
- Chilvers, G. A., and Brittain, E. G. 1972. Plant competition mediated by host-specific parasites - a simple model. Aust. J. Biol. Sci. 25:749-756.
- Chin, K. M., and Wolfe, M. S. 1984. Selection on Erysiphe graminis in pure and mixed stands of barley. Plant Pathol. 33:535-546.
- Clay, K. 1984. The effect of the fungus Atkinsonella hypoxylon (Clavicipitaceae) on the reproductive system and demography of the grass Danthonia spicata. New. Phytol. 98:165-175.
- Falconer, D. S. 1981. Introduction to Quantitative Genetics. Second edition. Longman Scientific & Technical, Wiley, New York. 340 pp.
- Finckh, M. R., and Mundt, C. C. 1992a. Effects of plant competition on stripe rust in wheat cultivar mixtures. Phytopathology 82:submitted.
- Finckh, M. R., and Mundt, C. C. 1992b. Effects of stripe rust and plant competition on yield of wheat cultivar mixtures. Phytopathology 82:submitted.
- Finckh, M. R., and Mundt, C. C. 1992c. Plant competition and disease in genetically diverse wheat populations. Oecologia: submitted.
- Finckh, M. R., and Mundt, C. C. 1991. The influence of stripe rust on coevolving wheat populations. Phytopathol. 81:(abstr.) in press.
- Firbank, L. G., and Watkinson, A. R. 1985. On the analysis of competition within two-species mixtures of plants. J. Appl. Ecol. 22:503-517.
- Flor, H. H. 1953. Epidemiology of flax rust in the North Central States. Phytopathology 43:624-628.
- Gates, D. J., Westcott, M., Burdon, J. J., and Alexander, H. M. 1986. Competition and stability in plant mixtures in the presence of disease. Oecologia 68:559-566.

- Hamblin, J. 1975. Effect of environment, seed size, and competitive ability on yield and survival of Phaseolus vulgaris (L.) genotypes in mixtures. *Euphytica* 24:435-445.
- Harlan, H. V., Martini, M. I. 1938. The effect of natural selection in a mixture of barley varieties. *J. Agric. Res.* 57:189-199.
- Jarosz, A. M., Burdon, J. J., and Mueller, W. J. 1989. Longterm effects of disease epidemics. *J. Appl. Ecol.* 26:725-733.
- Jarosz, A. M., and Levy, M. 1988. Effects of habitat and population structure on powdery mildew epidemics in experimental phlox populations. *Phytopathology* 78:358-362.
- Jennings, P. R., and de Jesus, J. Jr. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. *Evolution* 22:119-124.
- Johnson, T., Green, G. J., and Samborski, D. J. 1967. The world situation of the cereal rusts. *Annu. Rev. Phytopathol.* 5:183-200.
- Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. Appl. Ecology* 21:227-243.
- Kilen, T. C., and Keeling, B. L. 1990. Gene frequency changes in soybean bulk populations exposed to *Phytophthora* rot. *Crop Sci.* 30:575-578.
- Leonard, K. J. 1969a. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. *Phytopathology* 59:1845-1850.
- Leonard, K. J. 1969b. Selection in heterogeneous populations of Puccinia graminis f. sp. avenae. *Phytopathology* 59:1851-1857.
- Leonard, K. J. 1977. Virulence, temperature optima, and competitive abilities of isolines of races T and O of Bipolaris maydis. *Phytopathology* 67:1273-1279.
- Leonard, K. J., and Czocho, R. J. 1980. Theory of genetic interactions among populations of plants and their pathogens. *Annu. Rev. Phytopathol.* 18:337-358.

- May, R. M., and Anderson, R. M. 1983a. Epidemiology and genetics in the coevolution of parasites and hosts. Royal Soc. London, Proc. Ser. B 219:281-313.
- May, R. M., and Anderson, R. M. 1983b. Parasite-host coevolution. In: Coevolution. D. J. Futuyma and M. Slatkin, eds. Sinauer, pp.186-206.
- McDonald, B. A., Allard, R. W., and Webster, R. K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. Crop Sci. 28:447-452.
- McDonald, B. A., McDermott, J. M., Allard, R. W., and Webster, R. K. 1989. Coevolution of host and pathogen populations in the Hordeum vulgare - Rhynchosporium secalis pathosystem. Proc. Nat. Acad. Sci. 86:3924-3927.
- Mode, C. J. 1958. A mathematical model for the coevolution of obligate parasites and their hosts. Evolution 12:158-165.
- Mode, C. J. 1961. A generalized model of a host-pathogen system. Biometrics, 17:386-404.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity and cereal rust management. In: The Cereal Rusts Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: Effect of genotype unit area. Phytopathology 75:607-610.
- Murphy, J. P., Hebsel, D. B., Elliott, A., Thro, A. M., and Frey, K. J. 1982. Compositional stability of an oat multiline. Euphytica 31:33-40.
- Parker, M. A. 1989. Disease impact and local genetic diversity in the clonal plant Podophyllum peltatum. Evolution 43:540-547.
- Parker, M. A. 1991. Nonadaptive evolution of disease resistance in an annual legume. Evolution 45:1209-1217.
- Paul, N. D. 1989. The effects of Puccinia lagenophorae on Senecio vulgaris in competition with Euphorbia peplus. J. Ecol. 77:552-564.

- Paul, N. D., and Ayres, P. G. 1986a. Interference between healthy and rusted groundsel within mixed populations of different densities and proportions. *New Phytol.* 104:257-269.
- Paul, N. D., and Ayres, P. G. 1986b. The impact of a pathogen (*Puccinia lagenophorae*) on populations of groundsel (*Senecio vulgaris*) overwintering in the field; I. Mortality, vegetative growth and the development of size hierarchies. *J. Ecol.* 74:1069-1084.
- Paul, N. D., and Ayres, P. G. 1986c. The impact of a pathogen (*Puccinia lagenophorae*) on populations of groundsel (*Senecio vulgaris*) overwintering in the field; II. Reproduction. *J. Ecol.* 74:1085-1094.
- Paul, N. D., and Ayres, P. G. 1987a. Survival, growth and reproduction of groundsel (*Senecio vulgaris*) infected by rust (*Puccinia lagenophorae*) in the field during summer. *J. Ecol.* 75:61-71.
- Paul, N. D., and Ayres, P. G. 1987b. Effects of rust infection of *Senecio vulgaris* on competition with lettuce. *Weed Res.* 27:431-441.
- SAS Institute Inc. 1988. SAS/STAT User's Guide Ed. 6.03. SAS Institute, Cary, NC. 1029 pp.
- Spitters, C. J. T. 1983. An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. *Neth. J. Agric. Sci.* 31:1-11.
- Suneson, C. A. 1949. Survival of four barley varieties in mixture. *Agron. J.* 41:459-461.
- Suneson, C. A., Wiebe, G. A. 1942. Survival of barley and wheat varieties in mixtures. *J. Am. Soc. Agron.* 34:1052-1056.
- Wahl, I. 1970. Prevalence and geographic distribution of resistance to crown rust in *Avena sterilis*. *Phytopathology* 60:746-749.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annu. Rev. Phytopathol.* 23:251-273.
- Zwer, P. K. 1989. History of club wheat cultivars in the Pacific Northwest. Special report 840. *Agric. Exp. Stn. Oregon State University*, pp. 35-39.

## VI. Bibliography

- Adams, M. W., Ellingboe, A. H., and Rossman, E. C. 1971. Biological uniformity and disease epidemics. *Bioscience* 21:1067-1070.
- Alexander, H. M. 1984. Spatial patterns of disease induced by Fusarium moniliforme var. subglutinans in a population of Plantago lanceolata. *Oecologia* 62:141-143.
- Alexander, H. M. 1988. Spatial heterogeneity and disease in natural populations. In: Spatial components of epidemics. M. J. Jeger, ed. Prentice-Hall, Englewood Cliffs, NJ, pp. 144-164.
- Alexander, H. M. 1991. Plant population heterogeneity and pathogen and herbivore levels: a field experiment. *Oecologia* 86:125-131.
- Alexander, H. M., and Burdon, J. J. 1984. The effect of disease induced by Albugo candida (white rust) and Peronospora parasitica on the survival and reproduction of Capsella bursa-pastoris. *Oecologia* 64:314-318.
- Alexander, H. M., Antonovics, J., and Rausher, M. D. 1984a. Relationship of phenotypic and genetic variation in Plantago lanceolata to disease caused by Fusarium moniliforme var. subglutinans. *Oecologia* 65:89-93.
- Alexander, H. M., Burdon, J. J., and Roelfs, A. P. 1984b. Applications of competition models to studies of yield in mixtures: need for yield data on a per-component basis. Handout from poster presented at 1984 Am. Phytopathol. Soc. meeting, Guelph, Ontario.
- Alexander, H. M., Roelfs, A. P., and Cobbs, G. 1986. Effects of disease and plant competition in monocultures and mixtures of two wheat cultivars. *Plant Pathol.* 35:457-465.
- Allard, R. W. 1960. Relationship between genetic diversity and consistency of performance in different environments. *Crop Sci.* 1:127-133.
- Allard, R. W., and Adams, J. 1969. Population studies in predominantly self-pollinating species XIII. Intergenotypic competition and population structure in barley and wheat. *Am. Naturalist* 103:620-645.

- Anderson, R. M., and May, R. M. 1986. The invasion, persistence and spread of infectious diseases within animal and plant communities. *Phil. Trans. R. Soc. Lond. B.* 314:533-570.
- Anikster, Y., and Wahl, I. 1979. Coevolution of the rust fungi on Gramineae and Liliaceae and their hosts. *Ann. Rev. Phytopathol.* 17:367-403.
- Anonymous, 1972. Genetic vulnerability of major crops. National Academy of Sciences, Washington, D. C.
- Antonovics, J., and Alexander, H. M. 1987. The concept of fitness in plant-pathogen interactions in natural populations. *In: Plant Disease Epidemiology Vol. II.* K. J. Leonard and W. Fry, eds. McGraw-Hill, New York, pp. 185-214.
- Antonovics, J., and Levin, D. A. 1980. The ecological and genetical consequences of density-dependent regulation in plants. *Annu. Rev. Ecol. Syst.* 11:411-452.
- Antonovics, J., Clay, K., and Schmitt, J. 1987. The measurement of small-scale environmental heterogeneity using clonal transplants of Anthoxanthum odoratum and Danthonia spicata. *Oecologia* 71:601-607.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705-1712.
- Augsburger, C. K., and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings. Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211-217.
- Barrett, J. A. 1978. A model of epidemic development in variety mixtures. *In: Plant Disease Epidemiology.* P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 129-137.
- Barrett, J. A. 1981. The evolutionary consequences of monoculture. *In: Genetic Consequences of Man Made Change.* J. A. Bishop and L. M. Cook, eds. Academic Press, New York, pp. 209-248.
- Blijenburg, J. G., and Sneep, J. 1975. Natural selection in a mixture of eight barley varieties grown in six successive years. 1. Competition between the varieties. *Euphytica* 24:305-315.
- Borlaug, N. E. 1959. The use of multilineal or composite

- varieties to control airborne epidemic diseases of self-pollinated crop plants. Proc. 1st Int. Wheat Genet. Symp., 1958, pp. 12-27.
- Borlaug, N. E. 1981. Increasing and stabilizing food production. In: Plant Breeding II, K. J. Frey, ed. Iowa State University Press, Ames Iowa, pp. 467-492.
- Browder, L. E., and Eversmeyer, M. G. 1977. Pathogenicity associations in Puccinia recondita f. sp. tritici. Phytopathology 67:766-771.
- Brown, J. F., and Sharp, E. L. 1970. The relative survival ability of pathogenic types of Puccinia striiformis in mixtures. Phytopathology 60:529-533.
- Browning, J. A. 1974. Relevance of knowing about natural ecosystems to development of pest management programs in agroecosystems. Proc. Am. Phytopathol. Soc. 1:191-199.
- Browning, J. A., and Frey, K. J. 1969. Multiline cultivars as a means of disease control. Annu. Rev. Phytopathol. 7:355-382.
- Browning, J. A., Simons, M. D., Frey, K. J., and Murphy, H. C. 1969. Regional deployment for conservation of oat crown rust resistance genes. Spec. Rep.-Iowa Agric. Home Econ. Exp. Stn. 64:49-56.
- Burdon, J. J. 1978. Mechanisms of disease control in heterogeneous populations - an ecologists view. In: Plant Disease Epidemiology. P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford, pp. 193-200.
- Burdon, J. J. 1982. The effect of fungal pathogens on plant communities. In: The Plant Community as a Working Mechanism. E. I. Newman, ed. Blackwell, Oxford, pp. 66-112.
- Burdon, J. J., and Chilvers, G. A. 1976. Controlled environment experiments on epidemics of barley mildew in different density host stands. Oecologia 26:61-72.
- Burdon, J. J., and Chilvers, G. A. 1982. Host density as a factor in plant disease ecology. Annu. Rev. Phytopathol. 20:143-166.
- Burdon, J. J., and Shattock, R. C. 1980. Disease in plant communities. Appl. Biol. 5:145-219.



- Burdon, J. J., Groves, R. H., and Cullen, J. M. 1981. The impact of biological control on the distribution and abundance of Chondrilla juncea in south-eastern Australia. *J. Appl. Ecol.* 18:957-966.
- Burdon, J. J., Groves, R. H., Kaye, P. E., and Speer, S. S. 1984. Competition in mixtures of susceptible and resistant genotypes of Chondrilla juncea differentially infected with rust. *Oecologia* 64:199-203.
- Burdon, J. J., Oates, J. D., and Marshall, D. R. 1983. Interactions between Avena and Puccinia species I. The wild hosts: Avena barbata Pott ex Link, A. Fatua L., A. Ludoviciana Durieu. *J. Appl. Ecology* 20:571-584.
- Chilvers, G. A., and Brittain, E. G. 1972. Plant competition mediated by host-specific parasites. A simple model. *Aust. J. Biol. Sci.* 25:749-756.
- Chin, K. M., and Wolfe, M. S. 1984. Selection on Erysiphe graminis in pure and mixed stands of barley. *Plant Pathol.* 33:535-546.
- Clay, K. 1984. The effect of the fungus Atkinsonella hypoxylon (Clavicipitaceae) on the reproductive system and demography of the grass Danthonia spicata. *New. Phytol.* 98:165-175.
- Clay, K. 1990. The impact of parasitic and mutualistic fungi on competitive interactions among plants. In: *Perspectives on Plant Competition*. J. B. Grace and D. Tilman, eds. Academic Press, London, New York, pp 391-412.
- Clay, R. E., and Allard, R. W. 1969. A comparison of the performance of homogeneous and heterogeneous barley populations. *Crop. Sci.* 9:407-412.
- Connell, J. H. 1990. Apparent versus "real" competition in plants. In: *Perspectives on Plant Competition*. J. B. Grace and D. Tilman, eds. Academic Press, London, New York, pp 9-26.
- Dinoor, A., and Eshed, N. 1984. The role and importance of pathogens in natural plant communities. *Annu. Rev. Phytopathol.* 22:443-466.
- Donald, C. M. 1968. The breeding of crop ideotypes. *Euphytica* 17:385-403.

- Falconer, D. S. 1981. Introduction to Quantitative Genetics. Second edition. Longman Scientific & Technical, Wiley, New York. 340 pp.
- Finckh, M. R., and Mundt, C. C. 1991. The influence of stripe rust on coevolving wheat populations. *Phytopathol.* 81:(abstr.) in press.
- Finckh, M. R., and Mundt, C. C. 1992a. Effects of plant competition on stripe rust in wheat cultivar mixtures. *Phytopathology* 82:submitted.
- Finckh, M. R., and Mundt, C. C. 1992b. Effects of stripe rust and plant competition on yield of wheat cultivar mixtures. *Phytopathology* 82:submitted.
- Finckh, M. R., and Mundt, C. C. 1992c. Plant competition and disease in genetically diverse wheat populations. *Oecologia*: submitted.
- Firbank, L. G., and Watkinson, A. R. 1985a. On the analysis of competition within two-species mixtures of plants. *J. Appl. Ecol.* 22:503-517.
- Firbank, L. G., and Watkinson, A. R. 1985b. A model of interference within plant monocultures. *J. Theor. Biol.* 116:291-311.
- Flor, H. H. 1953. Epidemiology of flax rust in the North Central States. *Phytopathology* 43:624-628.
- Flor, H. H. 1956. The complementary genic systems in flax and flax rust. *Adv. Genet.* 8:29-54.
- Frey, K. J. 1982. Multiline breeding. In: Plant Improvement and somatic cell genetics. I. K. Vasil, W. R. Scowcroft, and K. J. Frey, eds. Academic Press, New York, pp. 43-72.
- Frey, K. J., and Maldonado, U. 1967. Relative productivity of homogeneous and heterogeneous oat cultivars in optimum and suboptimum environments. *Crop Sci.* 7:532-535.
- Frey, K. J., Browning, J. A., and Simons, M. D. 1977. Management systems for host genes to control disease loss. *Ann. N. Y. Acad. Sci.* 287:255-274.
- Frey, K. J., Browning, J. A., and Simons, M. D. 1973. Management of host resistance genes to control diseases. *Z. Pflanzenkr. Pflanzenschutz* 80:160-180.

- Gates, D. J., Westcott, M., Burdon, J. J., and Alexander, H. M. 1986. Competition and stability in plant mixtures in the presence of disease. *Oecologia* 68:559-566.
- Gause, G. F. 1934. The struggle for existence. Hafner publishing Co., New York.
- Giles, B. E. 1990. The effects of variation in seed size on growth and reproduction in the wild barley Hordeum vulgare ssp. spontaneum. *Heredity* 64:239-250.
- Grafius, J. E. 1966. Rate of change of lodging resistance, yield, and test weight in varietal mixtures of oat. *Crop Sci.* 6:369-370.
- Hamblin, J. 1975. Effect of environment, seed size, and competitive ability on yield and survival of Phaseolus vulgaris (L.) genotypes in mixtures. *Euphytica* 24:435-445.
- Hamblin, J., and Donald, C. M. 1974. The relationship between plant form, competitive ability and grain yield in a barley cross. *Euphytica* 23:535-542.
- Harlan, H. V., and Martini, M. I. 1929. A composite hybrid mixture. *J. Am. Soc. Agron.* 21:487-490.
- Harlan, H. V., Martini, M. I. 1938. The effect of natural selection in a mixture of barley varieties. *J. Ag. Res.* 57:189-199.
- Harlan, J. R. 1972. Genetics of disaster. *J. Environ. Qual.* 1:212-215.
- Harlan, J. R. 1975. Our vanishing genetic resources. *Science* 188:618-621.
- Harlan, J. R. 1976. Disease as a factor in plant evolution. *Annu. Rev. Phytopathol.* 14:31-51.
- Harper, J. L. 1977. *Population Biology of Plants.* Academic Press, New York.
- Hasan, S., and Ayres, P. G. 1990. The control of weeds through fungi: principles and prospects. *New Phytol.* 115:201-222.
- Hill, J., Mather, K., and Caligari, P. D. S. 1987. Analysis of competitive ability among genotypes of perennial ryegrass. II Effect upon dry matter production. *Euphytica* 36:109-115.

- Jarosz, A. M., and Levy, M. 1988. Effects of habitat and population structure on powdery mildew epidemics in experimental phlox populations. *Phytopathology* 78:358-362.
- Jarosz, A. M., Burdon, J. J., and Mueller, W. J. 1989. Longterm effects of disease epidemics. *J. Appl. Ecol.* 26:725-733.
- Jennings, P. R., and de Jesus, J. Jr. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. *Evolution* 22:119-124.
- Jennings, P. R., and Herrera, R. M. 1968. Studies on competition in rice. II. Competition in segregating populations. *Evolution* 22:332-336.
- Jensen, N. F. 1952. Intra-varietal diversification in oat breeding. *Agron. J.* 44:30-34.
- Johnson, R. 1978. Induced resistance to fungal disease with special reference to yellow rust of wheat. *Ann. Appl. Biol.* 89:107-110.
- Johnson, R. 1984. A critical analysis of durable resistance. *Ann Rev. Phytopathol.* 22:309-330.
- Johnson, T. 1961. Man-guided evolution in plant rusts. *Science* 133:357-362.
- Johnson, T., Green, G. J., and Samborski, D. J. 1967. The world situation of the cereal rusts. *Annu. Rev. Phytopathol.* 5:183-200.
- Jolliffe, P. A., Minjas, A. N., and Runeckles, V. C. 1984. A reinterpretation of yield relationships in replacement series experiments. *J. Appl. Ecology* 21:227-243.
- Kilen, T. C., and Keeling, B. L. 1990. Gene frequency changes in soybean bulk populations exposed to *Phytophthora* rot. *Crop Sci.* 30:575-578.
- Klages, K. H. W. 1936. Changes in the proportions of the components of seeded and harvested cereal mixtures in abnormal seasons. *J. Am. Soc. Agron.* 28, 935-940.
- Knott, E. A., and Mundt, C. C. 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and non-diseased conditions. *Theor. Appl. Gen.* 80:313-320.

- Knott, R. D. 1972. Using race-specific resistance to manage the evolution of plant pathogens. *J. Environ. Quality*, 1:227-231.
- Leonard, K. J. 1969a. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. *Phytopathology* 59:1845-1850.
- Leonard, K. J. 1969b. Selection in heterogeneous populations of Puccinia graminis f. sp. avenae. *Phytopathology* 59:1851-1857.
- Leonard, K. J. 1969c. Genetic equilibria in host-pathogen systems. *Phytopathology* 59:1858-1863.
- Leonard, K. J. 1977a. Selection pressures and plant pathogens. *Ann. N. Y. Acad. Sci.* 287:207-222.
- Leonard, K. J. 1977b. Virulence, temperature optima, and competitive abilities of isolines of races T and O of Bipolaris maydis. *Phytopathology* 67:1273-1279.
- Leonard, K. J., and Czocho, R. J. 1980. Theory of genetic interactions among populations of plants and their pathogens. *Annu. Rev. Phytopathol.* 18:337-358.
- Leonard, K. J., and Mundt, C. C. 1984. Methods for estimating epidemiological effects of quantitative resistance to plant diseases. *Theor. Appl. Gen.* 67:219-230.
- Mahmood, T., Marshall, D., and McDaniel, M. E. 1991. Effect of winter wheat cultivar mixtures on leaf rust severity and grain yield. *Phytopathology* 81:470-474.
- Marshall, D. R. 1977. The advantages and hazards of genetic homogeneity. *Ann. N. Y. Acad. Sci.* 287:1-20.
- May, R. M. 1985. Host-parasite associations: Their population biology and population genetics. In: *Ecology and Genetics of Host-Parasite Interactions*, pp. 243-262.
- May, R. M., and Anderson, R. M. 1979. Population biology of infectious diseases: Part II. *Nature* 280:455-461.
- May, R. M., and Anderson, R. M. 1983a. Epidemiology and genetics in the coevolution of parasites and hosts. *Royal Soc. London, Proc. Ser. B* 219:281-313.

- May, R. M., and Anderson, R. M. 1983b. Parasite-host coevolution. In: Coevolution. D. J. Futuyma and M. Slatkin, eds. Sinauer, pp.186-206.
- McDonald, B. A., Allard, R. W., and Webster, R. K. 1988. Responses of two-, three-, and four-component barley mixtures to a variable pathogen population. *Crop Sci.* 28:447-452.
- McDonald, B. A., McDermott, J. M., Allard, R. W., and Webster, R. K. 1989. Coevolution of host and pathogen populations in the Hordeum vulgare - Rhynchosporium secalis pathosystem. *Proc. Nat. Acad. Sci.* 86:3924-3927.
- Mode, C. J. 1958. A mathematical model for the coevolution of obligate parasites and their hosts. *Evolution* 12:158-165.
- Mode, C. J. 1961. A generalized model of a host-pathogen system. *Biometrics*, 17:386-404.
- Montgomery, E. G. 1912. Competition in cereals. *Bull. Neb. Agric. Exp. Stn.* No. 127:3-22.
- Mooney, P. R. 1979. Seeds of the Earth. A Private or Public Resource. Published by Inter Pares (Ottawa) for the Canadian Council for Intern. Co-operation and the Intern. Coalition for Development Action (London). Mutual Press Limited, Ottawa.
- Mundt, C. C. 1989 Modeling disease increase in host mixtures. In: Plant Disease Epidemiology Vol II. K. J. Leonard and W. Fry, eds. McGraw-Hill, New York, pp. 150-181.
- Mundt, C. C., and Browning, J. A. 1985a. Genetic diversity and cereal rust management. In: The Cereal Rusts Vol. II. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando. pp. 527-559.
- Mundt, C. C., and Browning, J. A. 1985b. Development of crown rust epidemics in genetically diverse oat populations: effect of genotype unit area. *Phytopathology* 75:607-610.
- Mundt, C. C., and Leonard, K. J. 1985. Effect of host genotype unit area on epidemic development of crown rust following focal and general inoculations of mixtures of immune and susceptible oat plants. *Phytopathology* 75:1141-1145.

- Mundt, C. C., and Leonard, K. J. 1986a. Analysis of factors affecting disease increase and spread in mixtures of immune and susceptible plants in computer simulated epidemics. *Pytopathology* 76:832-840.
- Mundt, C. C., and Leonard, K. J. 1986b. Effect of host genotype unit area on development of focal epidemics of bean rust and common maize rust in mixtures of resistant and susceptible plants. *Phytopathology* 76:895-900.
- Muona, O., and Allard, R. W. 1982. Evolution of resistance to Rhynchosporium secalis (Oud.) Davis in Barley Composite Cross II. *Theor. Appl. Genet.* 61:209-214.
- Murphy, J. P., Hebsel, D. B., Elliott, A., Thro, A. M., and Frey, K. J. 1982. Compositional stability of an oat multiline. *Euphytica* 31:33-40.
- Nitzsche, W., and Hesselbach, J. 1983. Sortenmischungen statt Vielliniensorten. *Z. Pflanzenz.* 90:68-74.
- Norrington-Davies, J., and Hutto, J. M. 1972. Diallel analysis of competition between diploid and tetraploid genotypes of Secale cereale grown at two densities. *J. Agric. Sci. Camb.* 78:251-256.
- Oates, J. D., Burdon, J. J., and Brower, J. B. 1983. Interactions between Avena and Puccinia species II. The pathogens: Puccinia coronata CDA and P. graminis Pers. F. Sp. Avenae Eriks. & Henn. *J. Appl. Ecology* 20:585-596.
- Ouchi, S. 1983. Induction of resistance and susceptibility. *Annu. Rev. Phytopathol.* 21:289-315.
- Parker, M. A. 1989. Disease impact and local genetic diversity in the clonal plant Podophyllum peltatum. *Evolution* 43:540-547.
- Parker, M. A. 1991. Nonadaptive evolution of disease resistance in an annual legume. *Evolution* 45:1209-1217.
- Paul, N. D. 1989. The effects of Puccinia lagenophorae on Senecio vulgaris in competition with Euphorbia peplus. *J. Ecol.* 77:552-564.

- Paul, N. D., and Ayres, P. G. 1986a. Interference between healthy and rusted groundsel within mixed populations of different densities and proportions. *New Phytol.* 104:257-269.
- Paul, N. D., and Ayres, P. G. 1986b. The impact of a pathogen (*Puccinia lagenophorae*) on populations of groundsel (*Senecio vulgaris*) overwintering in the field; I. Mortality, vegetative growth and the development of size hierarchies. *J. Ecol.* 74:1069-1084.
- Paul, N. D., and Ayres, P. G. 1986c. The impact of a pathogen (*Puccinia lagenophorae*) on populations of groundsel (*Senecio vulgaris*) overwintering in the field; II. Reproduction. *J. Ecol.* 74:1085-1094.
- Paul, N. D., and Ayres, P. G. 1987a. Survival, growth and reproduction of groundsel (*Senecio vulgaris*) infected by rust (*Puccinia lagenophorae*) in the field during summer. *J. Ecol.* 75:61-71.
- Paul, N. D., and Ayres, P. G. 1987b. Effects of rust infection of *Senecio vulgaris* on competition with lettuce. *Weed Res.* 27:431-441.
- Person, C. 1966. Genetic polymorphism in parasitic systems. *Nature (London)* 212:266-267.
- Prakash, C. S., and Heather, W. A. 1988. Antagonisms between races of *Melampsora medusae* on poplar, resulting in reduced disease expression. *Plant Pathology*
- Richards, F. J. 1969. The quantitative analysis of growth. In: *Plant Physiology*, Vol 5A. F. C. Steward, ed. Academic Press New York, pp. 3-76.
- SAS Institute Inc. 1988. SAS/STAT User's Guide Ed. 6.03. SAS Institute, Cary, NC. 1029 pp.
- Spitters, C. J. T. 1983a. An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. *Neth. J. Agric. Sci.* 31, 1-11.
- Spitters, C. J. T. 1983b. An alternative approach to the analysis of mixed cropping experiments. 2. Marketable yield. *Neth. J. Agric. Sci.* 31:143-153.
- Stakman, E. C. 1947. Plant diseases are shifting enemies. *Am. Scientist* 35:321-350.



- Stevens, N. E. 1942. How plant breeding programs complicate plant disease problems. *Science* 95,:313-316.
- Suneson, C. A. 1949. Survival of four barley varieties in mixture. *Agron. J.* 41:459-461.
- Suneson, C. A. 1956. An evolutionary plant breeding method. *Agron. J.* 48:188-191.
- Suneson, C. A., and Wiebe, G. A. 1942. Survival of barley and wheat varieties in mixtures. *J. Am. Soc. Agron.* 34:1052-1056.
- Thomas, S. C., and Weiner, J. 1989. Including competitive asymmetry in measures of local interference in plant populations. *Oecologia* 80:349-355.
- Trenbath, B. R. 1977. Interactions among diverse hosts and diverse parasites. *Ann. N. Y. Acad. Sci.* 287:124-150.
- Ullstrup, J. A. 1972. the impact of the southern corn leaf blight epidemics of 1979-1971. *Annu REV. Phytopathol.* 10:37-50.
- van Leur, J. A. G., Ceccarelli, S., and Grando, S. 1989. Diversity for disease resistance in barley landraces from Syria and Jordan. *Plant Breeding* 103:324-335.
- Vanderplank, J. E. 1963. *Plant Diseases: Epidemics and Control.* Academic Press, New York.
- Vanderplank J. E. 1968. *Disease Resistance in Plants.* Academic Press, New York.
- Wahl, I. 1970. Prevalence and geographic distribution of resistance to crown rust in Avena sterilis. *Phytopathology* 60:746-749.
- Wahl, I., Anikster, Y., Manisterski, J., and Segal, A. 1984. Evolution at the center of origin. In: *The Cereal Rusts Vol. I.* W. R. Bushnell and A. P. Roelfs, eds. Academic Press, Orlando, pp. 39-77.
- Webster, R. K., Saghai-Maroo, M. A., and Allard, R. W. 1986. Evolutionary response of Barley Composite Cross II to Rhynchosporium secalis analyzed by pathogenic complexity and by gene-by-race relationships. *Phytopathology* 76:661-668.

- Wolfe, M. S. 1973. Changes and diversity in populations of fungal pathogens. *Ann. Appl. Biol.* 75:132-136.
- Wolfe, M. S. 1978. Some practical implications of the use of cereal variety mixtures. *In: Plant Disease Epidemiology.* P. R. Scott and A. Bainbridge, eds. Blackwell, Oxford. pp. 201-207.
- Wolfe, M. S. 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annu. Rev. Phytopathol.* 23:251-273.
- Wolfe, M. S., and Barrett, J. A. 1977. Population genetics of powdery mildew epidemics. *Ann. N. Y. Acad. Sci.* 287:151-163.
- Wolfe, M. S., and Barrett, J. A. 1980. Can we lead the pathogen astray? *Plant Dis.* 64:148-155.
- Wolfe, M. S., Barrett, J. A., and Jenkins, J. E. E. 1981. The use of cultivar mixtures for disease control. *In: Strategies for the Control of Cereal Diseases.* J. F. Jenkyn and R. T. Plumb, eds. Blackwell, Oxford. pp. 73-80.
- Young, L. D., and Hartwig, E. E. 1988. Selection pressure in soybean cyst nematode from soybean cropping sequences. *Crop Science* 28:845-847.
- Zwer, P. K. 1989. History of club wheat cultivars in the Pacific Northwest. Special report 840. *Agric. Exp. Stn. Oregon State University*, pp. 35-39.