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Effects of stripe rust on the evolution of genetically diverse wheat populations*

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Summary. Eighteen populations, composed of four wheat (*Triticum aestivum*) varieties that were originally mixed together at equal frequencies, were grown for one-to-three generations at two locations. In addition, pure stands of the four varieties were grown in each year. 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 variety's frequency versus generation number was used to calculate the relative fitness of each variety in each population. These analyses suggest that the relative fitnesses of the wheat varieties were affected by disease and geographic location and were constant over time. However, frequency-changes of varieties 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 variety 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 varieties that are more closely related and/or more uniformly adapted to the environment in which they are grown.

Key words: Evolution – Frequency-dependence – Pathogens – Host diversity – Equilibrium frequencies

Introduction

Plant host-pathogen systems have been studied with respect to several aspects that are all part of the coevolutionary process. It has been demonstrated that, in diverse host populations, epidemic development, and thus pathogen populatioon 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; Leonard 1969a; Chin and Wolfe 1984; 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. However, reports on frequency-dependence of disease severity have yielded contradictory results (Leonard 1969a; Augspurger and Kelly 1984; Jarosz and Levy 1988; Parker 1989; Alexander 1991; see Burdon and Chilvers 1982 for a review). We have recently shown that frequency-dependent effects can be obscured by plant–plant interactions in heterogeneous host populations (Finckh and Mundt 1992b).

Disease has also been shown to affect plant–plant interactions by altering competitive interactions among plant genotypes within a season (Burdon et al. 1984; Alexander et al. 1986; Paul and Ayres 1986a, 1987b; Paul 1989; Finckh and Mundt 1992a, b) and by affecting the survival and fitness of hosts differentially (Alexander 1984; Alexander and Burdon 1984; Augspurger 1984; Augspurger and Kelly 1984; Clay 1984; Paul and Ayres 1986b, c, 1987a; Jarosz et al.

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1989). In the intermediate or long term, the frequency of resistant host plants can be significantly increased by disease pressure (Wahl 1970; Burdon et al. 1981; Webster et al. 1986; Kilen and Keeling 1990). 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 modelling (e.g., Mode, 1958 1961; Chilvers and Brittain 1972; Leonard and Czochor 1980; May and Anderson 1983a, b; Gates et al. 1986). 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 Czochor 1980). The models of 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 species or 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., Spitters 1983a, b; Jolliffe et al. 1984; Firbank and Watkinson 1985).

Few data are available that differentiate 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, in addition to the already existing selective forces, on the population dynamics.

In this paper, we report on a study that was conducted over three seasons, involving mixtures of four wheat (*Triticum aestivum* L.) varieties that were grown in a variety of diseased and non-diseased environments. Cultivated wheat inbreeds almost exclusively. Thus, gene frequencies are practically identical with variety 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 varieties, locations, and experimental designs

We used four soft white, club-type winter wheat (*T. aestivum* L.) varieties with different stripe rust resistances, heights, chaff colors, and reactions to a phenol-based seed stain (Table 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 to or less than 1% (range = 22–64%). 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 (Finckh and Mundt 1992a, b). Experimental locations were Moro and Pendleton in north eastern Oregon, which receive approximately 300 and 450 mm annual precipitation respectively. In all years each experimental unit (plot) was 1.5 by 4.5 m. 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 and 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 triadimefon (as Bayleton 50 DF, Mobay Corp) at 284 g active ingredient 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 4.4 m experimental units. In the following, 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 to 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, b).

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

Variety	Chaff color	Relative height	Phenol stain[b]	Reaction[a] to *Puccinia striiformis* race	
				5	27
Faro	Brown	Tall	White	VAR	R
Jacmar	Brown	Short	Black	S	R
Tres	White	Tall	White	R	R
Tyee	White	Tall	Mixed	R	S

[a] VAR, reaction variable (approximately one-half of the plants were resistant and one-half susceptible); R, resistant; S, susceptible

[b] Reaction of seeds to exposure to 1% phenol solution

Populations

From 1986 to 1989 we created a total of 18 mixed populations that differed with respect to age (one-to-three generations), location of evolution, and exposure to stripe rust (Table 2). In 1986, a mixture of equal proportions of germinable seeds 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 seeds 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

Table 2. Mixed populations composed of the winter wheat varieties Faro, Jacmar, Tres, and Tyee that were grown for one-to-three generations[a] in Pendleton and Moro. Populations were either protected from stripe rust with fungicide (f) or inoculated with two stripe rust races (i)

Population	Season		
	1986/87	1987/88	1988/89
I	f	f	f
II	i	i	i
III	f	i	f
IV	i	f	i
V		f	f
VI		i	i
VII		f	i[b]
VIII		i	f[b]
IX			f
X			i

[a] E.g., population III treated with fungicide in 1986/87; seeds harvested, replanted, and inoculated in 1987/88; and harvested, replanted, and treated with fungicide in 1988/89

[b] Populations not included in Moro

in Pendleton. Due to spatial constraints, the alternating carry-over of the first-generation populations had to be omitted in Moro 1989 (Table 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. 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 variety 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 41 cm (Pendleton) and 56 cm (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 was also 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 3 years and allowed for a qualitative comparison of the two assessment methods in all 3 seasons.

Harvest and laboratory procedures

Single plants could not be distinguished because of tillering. Therefore, no estimate of the number of plants per plot is available.

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 variety frequencies. Miniplots ranged from 30 to 66 cm 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 seeds 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 seeds 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 1). Tyee plants from the pure stands served as controls to assure that inoculations had been effective, and Tres plants were used as controls for contamination by rust race(s) virulent on Tres. A seed-staining procedure was used to determine the frequencies of Faro and Jacmar. Seeds were soaked in hot water for at least 10 min and then placed embryo-up on filter paper soaked with a 1% phenol solution. Within 60–90 min, Jacmar seeds turned uniformly black whereas Faro seeds remained uniformly white for at least 4 h. Seeds 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 seeds, 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 variety 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 seeds counted and weighed. Differential tests with race 27 and the phenol assays were performed as described above on five seedlings or seeds 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 Institute 1986). Fisher's nonprotected 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 resistance 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 – % disease severity)] (Finckh and Mundt 1992b) 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 varieties were calculated using the following equation:

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

where p_n is the frequency at which the variety occurred after n generations, p_0 is the initial frequency, and s is the selection coefficient (Leonard 1969b, 1977). Taking logarithms of equation

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:

$$s = 1 - e^b \tag{2}$$

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 variety on its initially planted frequencies. If the slope is negative, the intercept with the x-axis is the equilibrium point at which a variety 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 3 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 2).

Results

Disease severity in pure stands and in mixtures

Natural stipe rust infestations in the regions where we conducted the experiments were relatively low in 1987 to 1989. Therefore, external inoculum could be neglected as a source of variation.

Disease severity on the pure stands ranged from 2.5% on Tres to 84.0% on Jacmar in the whole plots (Table 3). Although the single-tiller assessments differed from the whole-plot data (Table 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 3). In Pendleton 1989, there appeared to be an effect of population age on disease severity. Disease severity on the 1st generation population was significantly higher than on the 2nd and 3rd generation populations ($P < 0.05$, linear contrast). However, 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 2nd and 3rd 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 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 did the whole-plot assessments (Tables 3 and 4). Disease severity was lower in the 3rd generation than in the 1st

Table 3. Percent leaf area covered with stripe rust in whole plots[a] and percent of the F_1 leaf covered with stripe rust on single tillers[b] in pure stands and in mixed populations of four wheat varieties in two locations and 3 years

Location/ year	Assessment	Pure stands					Mixtures[c]				
		Faro	Jacmar	Tres	Tyee	Mean	i	ii	iii	fi	ifi
Moro 1987	Plot	16.8	69.3	3.3	38.3	31.9	16.3				
	Tiller	15.3	80.5	0.3	27.2		(49)[d]				
Penleton 1987	Plot	27.0	65.5	12.8	63.0	42.1	22.3				
	Tiller	24.2	68.9	2.4	45.2		(47)				
Moro 1988	Plot	10.5	42.5	4.5	47.3	26.2	14.7	12.8	14.5		
	Tiller	22.4	57.8	4.9	54.6		(44)	(35)	(29)		
Pendleton 1988	Plot	11.0	53.8	2.5	60.7	32.0	11.0	8.2	11.3		
	Tiller	8.2	40.5	1.0	39.9		(66)	(63)	(53)		
Moro 1989	Plot	–[e]	–	–	–	–	–	–	–	–	–
	Tiller	29.2	83.3	2.7	66.0						
Pendleton 1989	Plot	6.7	84.0	2.1	65.0	39.5	12.7	6.0	4.3	2.3	5.3
	Tiller	18.6	87.8	1.6	49.5		(68)	(74)	(82)	(82)	(72)

[a] Assessments were done on whole plots (see Materials and methods for details)

[b] Assessments were done on single tillers within miniplots (see Materials and methods for details)

[c] i, inoculated with stripe rust; f, fungicide treated; more than one letter indicates the sequence of treatments over generations; see Table 2 for description of populations

[d] Numbers in brackets indicate the percent reduction in mixtures relative to the mean of the pure stands weighted by the planted variety frequencies

[e] No whole-plot data were collected in Moro 1989

Table 4. Percent of F – 1 leaf covered with stripe rust of four wheat varieties when grown in pure stands and when grown in mixtures based on single-tiller assessments in two locations in 1989

Pop.[a]	Variety				Weighted mean[b]	Disease reduction[c]
	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

[a] i, inoculated with stripe rust; f, fungicide treated; more than one letter indicates the sequence of treatments over generations; see also Table 2 for explanation of population names

[b] The weighted mean disease severity is based on the actual tiller frequencies of the varieties in the populations

[c] $$\text{Disease reduction} = 1 - \frac{\text{observed disease severity}}{\text{mean of pure stands weighted by harvested tiller frequencies}}$$

*, **, *** 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)

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

In the absence of disease, there were no statistically significant differences in seed production per plot among the four varieties in pure stands except for Pendleton 1988 where Faro and Tyee outyielded Jacmar and Tres (Table 5). In the presence of disease, Faro and Tres often produced a significantly greater number of seeds than did Jacmar and Tyee. Variation in seed 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 5) and, therefore, in the total yield per plot (Finckh and Mundt 1992a, b).

Despite similar performance in pure stands, the performance of the varieties differed greatly in mixtures. In mixtures, Faro and Tres increased in frequency while Jacmar and Tyee decreased (Fig. 1, Table 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. 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. 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 varieties were affected by location and disease. Jacmar was more fit in Moro than in Pendleton (Fig. 2).

Table 5. Yield per miniplot[x] and 1000 seed weight of four wheat varieties in pure stands in two locations and three years

Year	Variety	Location			
		Moro		Pendleton	
		Fungicide[y]	Inoculated	Fungicide	Inoculated
Number of seed per miniplot					
1987	Faro	5944 a	5484 a	3894 a	4175 ab[z]
	Jacmar	5320 a	4155 a	4452 a	3373 c
	Tres	4853 a	4256 a	3412 a	4036 a
	Tyee	4689 a	3765 a	4329 a	3549 bc
1988	Faro	6188 a	6482 a	5072 a	4787 a
	Jacmar	7001 a	4706 b	4518 b	2740 c
	Tres	5913 a	6235 a	3987 b	4189 a
	Tyee	5442 a	5177 b	4960 ab	3787 b
1989	Faro	5761 a	5204 ab	5652 a	5089 ab
	Jacmar	4689 a	3076 c	5101 a	3463 d
	Tres	4785 a	5771 a	5474 a	5017 a
	Tyee	4912 a	3399 bc	6081 a	4251 bc
1000 seed weight (g)					
1987	Faro	23.3 a	20.9 a	30.2 bc	28.0 ab
	Jacmar	29.2 a	21.7 a	28.5 c	25.5 ab
	Tres	28.5 a	21.5 a	33.7 a	29.6 a
	Tyee	28.7 a	21.6 a	30.8 b	26.8 b
1988	Faro	29.2 ab	28.0 a	31.1 b	25.5 b
	Jacmar	25.1 c	21.9 b	30.1 bc	21.5 c
	Tres	31.5 a	28.3 a	33.7 a	33.9 a
	Tyee	27.8 bc	23.5 b	29.4 c	24.3 b
1989	Faro	29.7 a	29.2 a	37.1 ab	32.2 b
	Jacmar	31.0 a	28.4 a	33.8 c	27.3 c
	Tres	32.8 a	31.4 a	38.4 a	38.2 a
	Tyee	32.0 a	29.6 a	35.6 bc	31.1 b

[x] Plot size varied from year to year; see Materials and methods for details

[y] Inoculated, plots were inoculated with stripe rust; fungicide, plots were not inoculated and protected from stripe rust

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

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 varieties 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 7, Fig. 3) and the sums of the predicted equilibrium frequencies for the varieties ranged from 0.97 to 1.08 (Table 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 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 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 varieties 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 performance among the cultivars when grown in mixtures were consistent with competitive interactions observed in two-component mixtures (Finckh and Mundt 1992a, b).

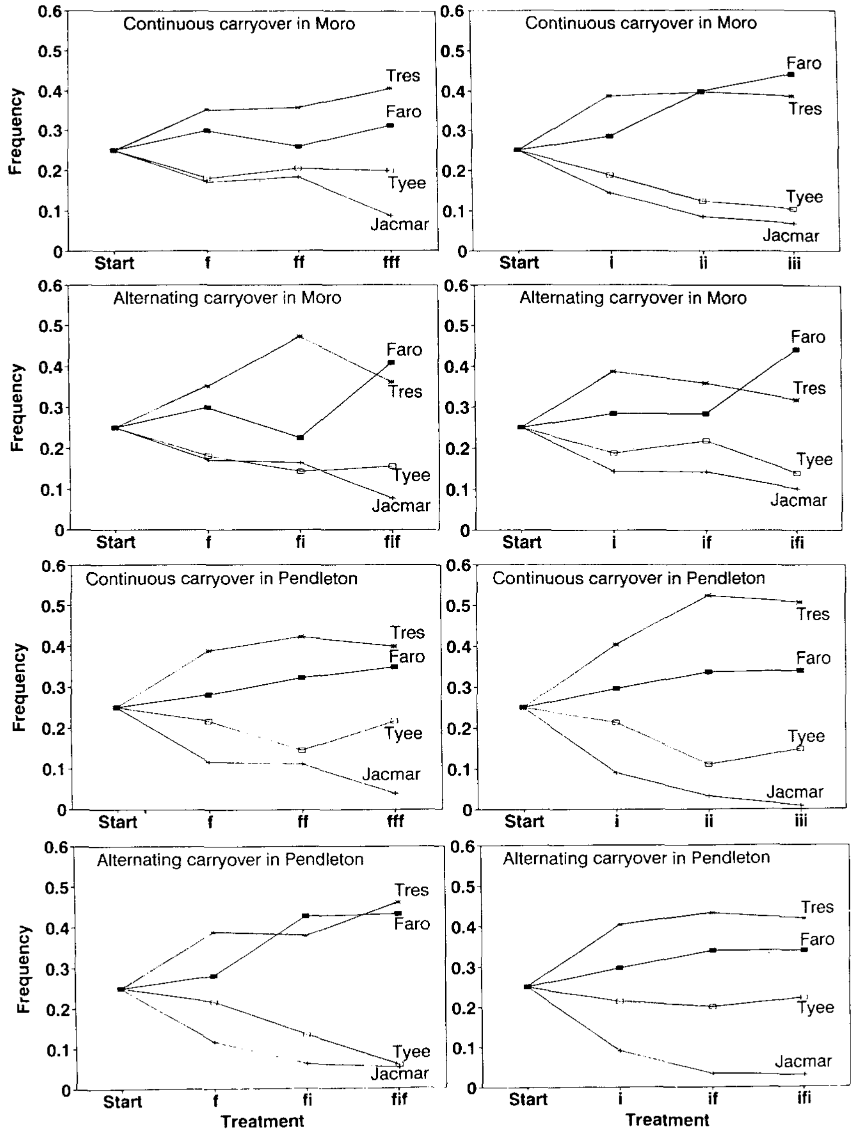

Fig. 1. Seed production (presented as frequencies) of four wheat varieties when grown in mixed populations over three generations in two locations, Moro and Pendleton. Populations were either continuously protected from stripe rust by fungicide applications (designated by *f*) or inoculated with stripe rust (designated by *i*) or exposed to stripe rust in alternating years. Populations were all started at equal proportions of the varieties 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

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 3 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. 1, Table 6) the vulnerability of the mixtures to stripe rust race 41 would also have increased.

Our failure to detect frequency-dependence of disease severity on Tyee may be due to at least two factors. First, interactions among the varieties in the mixtures might have affected disease severity on the different varieties. In experiments with two-way mixtures, we found that the companion variety can have a profound effect on the disease severity of a variety in mixtures if the competitive abilities of the varieties are very different (Finckh and Mundt 1992b). 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 1992a).

Table 6. Seed production of varieties 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 1–3 generations in two locations

Location			Harvested seed frequencies			
Pop[a]	Year of harvest	Trt[b]	Faro	Jacmar	Tres	Tyee
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
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

[a] Pop, population; see Table 2 for descriptions

[b] Trt, treatment; i, inoculated with stripe rust; f, fungicide-treated

Table 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 1–3 generations at two locations

Location treatment[a]	Cultivar	Slope	*P*	r^2	Pred. frequencies at equilibrium (sum)[b]	
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	

[a] 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 2). Corresponding data were included in the inoculated sets

[b] 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 varieties in the mixed populations

In Pendleton, the plants grew taller and denser because of the higher precipitation, and competition for light was probably more important in Pendleton than in Moro.

The fit of Leonard's (1969b, 1977) model for relative fitnesses on the one hand and the negative slopes for the regression of frequency changes on planted frequencies on the other hand would not be expected to be consistent with the same data set.

Problems are associated with both models: if frequency-dependent selection occurs, selection coefficients change over time and straight lines should not result when transforming frequency data following Leonard's model. Due to the limited number of generations studied it is not possible to judge if there are specific trends or non-linearities in our data (Fig. 2).

The regressions of untransformed frequency changes on planted frequencies (Fig. 3, Table 7) are independent from the number of generations. However, when evaluating frequency changes, it is important to bear in mind that a variety that was planted at a low frequency, e.g., 5%, cannot change as much in one generation as when planted at an intermediate frequency, e.g., 25%. At high frequencies, the changes will again be small as the companion varieties must be present at low frequencies. Therefore, frequency changes should follow a sine-shaped curve. The frequencies of the different varieties in the populations did not range over more than 30% (Fig. 3). The limited range in frequencies and the small number of data points

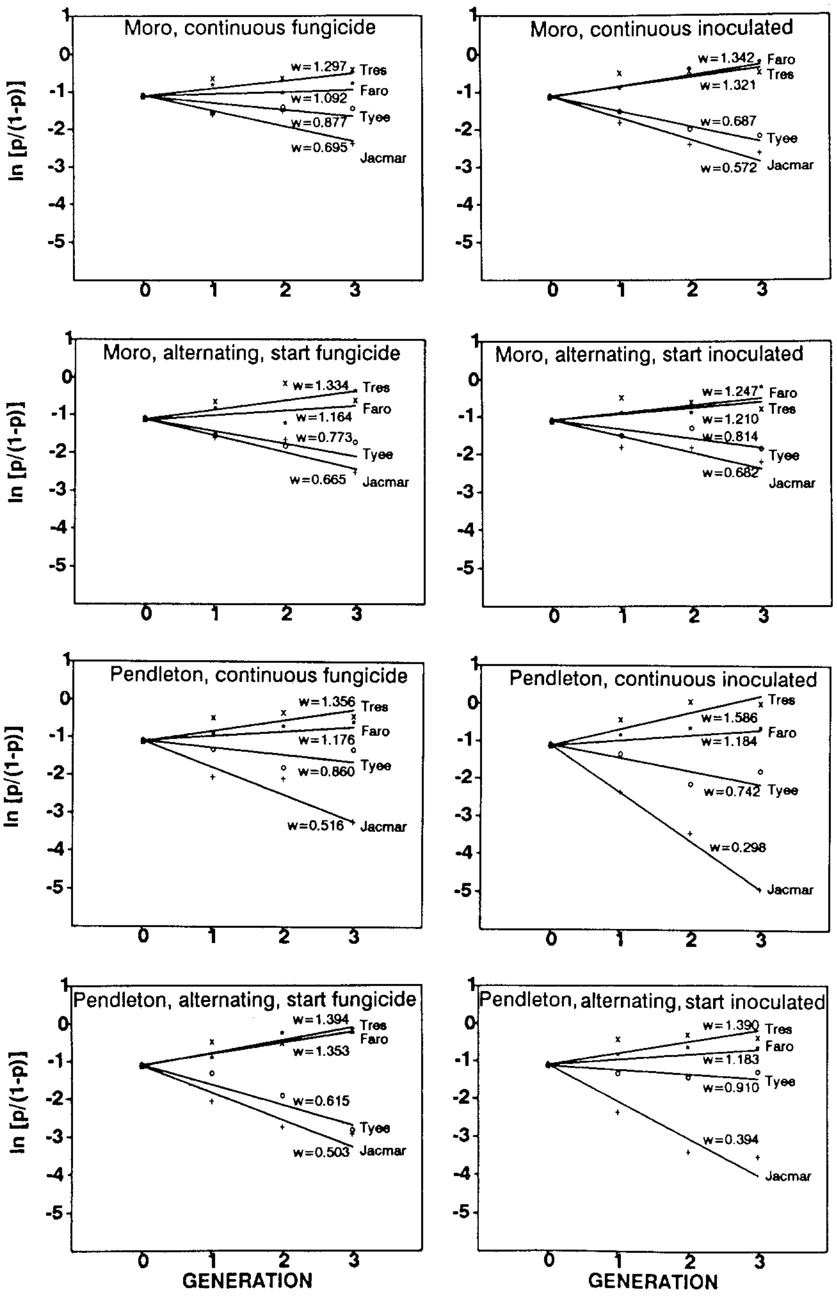

Fig. 2. Rates of change in frequency of four wheat varieties grown in mixed populations at two locations for three generations. Populations were either carried over from season to season inoculated with stripe rust each year, or fungicide-treated each year, or inoculated and fungicide-treated in alternating years (see Table 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 variety 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)

(eight in Moro and nine in Pendleton) are probably responsible for the lack of pattern in the deviations from the straight lines in Fig. 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 ten locations over 2–12 generations. Blijenburg and Sneep (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 (1969a, b, 1977) model (Table 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. 4). Straight lines (1 in Fig. 4), with positive or negative slopes indicating positive or negative selection

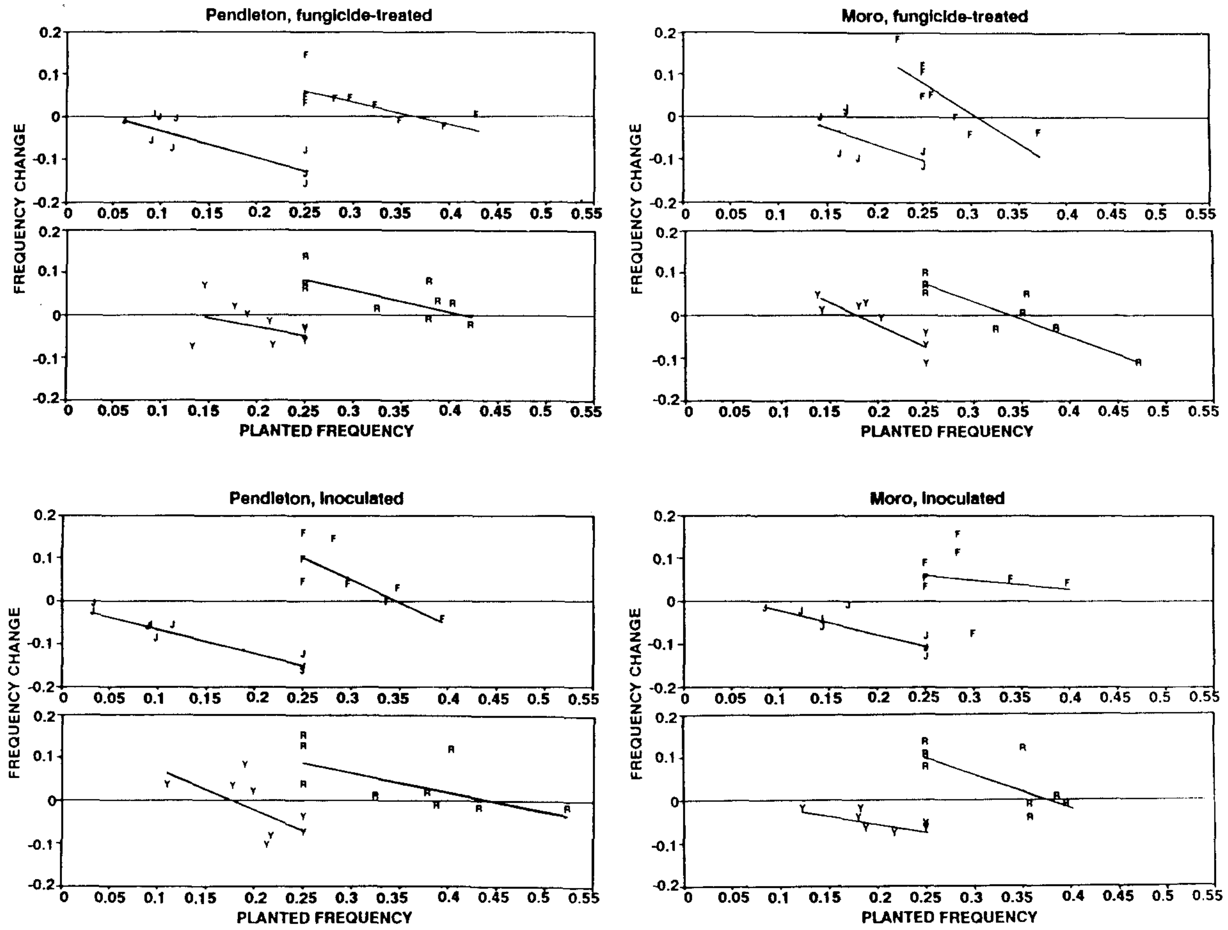

Fig. 3. Frequency changes of four wheat varieties grown in mixed populations in two locations versus their planted frequencies. Data from all populations that were protected from stripe rust in each of three years are included in the graphs titled 'fungicide-treated', and all populations that were inoculated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

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, variety *a* might produce many more seeds than variety *b* in pure stands. However, variety *b* may be a strong competitor with respect to *a* and therefore, in mixtures *a* may produce only few more seeds 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 (Suneson and Wiebe 1942; Suneson 1949; Jennings and de Jesus 1968; Hamblin 1975) 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 asymptotic plateaus, i.e., $s=0$. If genotypes are identical in their reproductive and competitive abilities they may also coexist, however, this would not be a stable equilibrium.

Table 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[a]	Regressions with $P<0.05$[b]	Number of non-linear regressions[c]
Harlan and Martini (1938), 11 barley varieties[d]			
Aberdeen	12	10/10	3
Arlington	3	8/9[e]	–[f]
Davis	4	7/10	–[f]
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	–[f]
St. Paul	9	8/10	6
Blijenburg and Sneep (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

[a] Number of generations that a population was evaluated

[b] Number of significant regressions ($P<0.05$)/total number of regressions performed

[c] Number of curves that clearly showed non-linear trends by visual examination

[d] Harlan and Martini (1938) used 11 barley varieties. However, two varieties were indistinguishable and were treated as one composite variety. Therefore, only ten regressions were performed in each location

[e] One variety disappeared from the mixture in Arlington within one generation. Therefore, fitnesses were calculated for only nine

[f] Too few generations for appropriate evaluation of non-linear trends

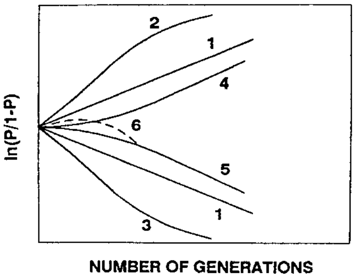

Fig. 4. Types of curves resulting from plotting logits of the frequencies p $\{\ln[p/(1-p)]\}$ versus the number of generations for the data of Blijenburg and Sneep (1975), Harlan and Martini (1938) and Murphy et al. (1982). All populations were started at equal proportions of all varieties and the starting point on the y-axis is $\ln[p_0/(1-p_0)]$. See text for explanations

The results from the analysis of the data from the literature (Table 8, Fig. 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 12 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 to all the other varieties in the mixtures 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. 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 Sneep (1975) also contained one variety that was highly superior to all others. 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 Harlan and Martini (1938) and Blijenburg and Sneep (1975), frequency changes in the mixture of near-isogenic lines (NILs) of oats 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. Harlan and Martini (1938) and Blijenburg and Sneep (1975) 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, though not as close as NILs (Zwer 1989), and were all bred for the semi-arid wheat growing environments of 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. However, only continuation of our experiments over more generations and the addition of populations starting at different variety frequencies could provide more definite answers to whether there is frequency-dependence, whether equilibrium frequencies exist, and how equilibrium frequencies will be affected by disease.

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