Wheat Leaf Rust Severity as Affected by Plant Density and Species Proportion in Simple Communities of Wheat and Wild Oats

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Accepted for publication 31 March 1998.

ABSTRACT

Pfleegeer, T. G., and Mundt, C. C. 1998. Wheat leaf rust severity as affected by plant density and species proportion in simple communities of wheat and wild oats. *Phytopathology* 88:708-714.

While it is generally accepted that dense stands of plants exacerbate epidemics caused by foliar pathogens, there is little experimental evidence to support this view. We grew model plant communities consisting of wheat and wild oats at different densities and proportions and exposed these communities to *Puccinia recondita* to induce wheat leaf rust. Wild oats was included because it is a common competitor of wheat and may act as a barrier to the dispersal of *P. recondita* spores among wheat plants. Disease severity was estimated as percentage of wheat flag leaves cov-

ered by rust lesions. Seeding density rarely had a significant influence on rust severity, probably because of compensation due to increased tillering at low seeding densities. In contrast, increasing the proportion of wheat in mixtures with wild oats consistently increased wheat leaf rust severity. Regression parameters describing wheat leaf rust severity as a function of wheat seeding density did not differ significantly between pure wheat stands and wheat-wild oat mixtures and, thus, failed to support an effect of wild oats on wheat leaf rust other than through its competitive impact on wheat tiller density.

Additional keywords: *Avena fatua*, *Triticum aestivum*.

According to Burdon and Chilvers (10), the concept that growing plants in dense stands contribute to severe epidemics is an accepted axiom with few experimental data to support it. They further questioned the contribution of density of resistant plants in mixed stands on disease control, as opposed to changes in density of susceptible plants. Since then, some progress has been made in determining the effects of plant density on disease severity (3,5). The difficulty in determining the effects of plant density on disease severity is due, in part, to the diversity of life strategies that plants and their pathogens exhibit, making it difficult to make generalizations concerning plant disease and host-nonhost densities. For example, the severity of rosette disease in groundnut (*Arachis hypogea*) is negatively correlated with plant density (1,16). The causal agent of groundnut rosette disease is an aphid (*Aphis craccivora*)-transmitted virus. The flying aphids preferentially land on plants associated with surrounding bare ground (16). In contrast, the spread of white rot in onions (*Allium cepa*) by the fungal pathogen *Sclerotium cepivorum* is positively correlated with plant density and can be controlled by spacing the host to eliminate root contact between adjacent plants (27).

In an attempt to clarify the effect of plant density on disease, Burdon and Chilvers (10) classified plant-pathogen interactions into categories based on a temporal scale. They further subdivided each of these three defined time scales (short, medium, and long) by type of pathogen (virus or fungus) and type of dispersal (soil-

borne, airborne, or splash-dispersed). Even with this detailed analysis, they were able to conclude nothing more specific than the suggestion that host density plays an important role in the host-pathogen-environment triangle (10). Others (3,5) have suggested, based on these and more recent data, that there is a tendency for viral-mediated diseases to decrease with increasing host density and for fungal-mediated diseases to increase with increasing host density. However, it is also becoming clearer that host-nonhost density effects may be disease specific, and even temporally and spatially specific. For example, steep spore-deposition gradients will intensify disease locally, but slow the spread of disease, whereas pathogens with shallow gradients will intensify more slowly, but spread more rapidly (18). In addition, the effects of plant density have not yet been evaluated for many diseases (5).

Planting mixtures of plant genotypes, species, or both for control of herbivores and pathogens have been and continue to be practiced by aboriginal peoples (25,32). Mixtures are also becoming an increasing part of modern agriculture, because in some cases, they reduce both the incidence and rate of increase of disease (35). Several workers have suggested that mixtures will be most effective against pathogens with shallow spore-dispersal gradients and for hosts with small plants (18,24). However, intercropping can increase, decrease, or have no effect on disease severity (5). For example, Van Rheenen et al. (34), working with a bean-maize intercrop at seven sites over 5 years in Kenya, found that, while 8 of 10 bean diseases were likely to be more severe in a monocrop than in the intercrop, there was always the exception in which a given disease was worse or not affected in the intercrop. The success of intercropping systems for disease control is dependent to a large degree on the interactions between the amount and location of each crop's tissues, pathogen dispersal properties, microclimatic conditions, and interspecific competition (5).

In an attempt to clarify the importance of plant density and species proportion on cereal rust severity, we grew artificial communities consisting of spring wheat (*Triticum aestivum* L.) and wild

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Publication no. P-1998-0511-01R

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oats (*Avena fatua* L.) at different densities and proportions and exposed these communities to the wheat leaf rust pathogen *Puccinia recondita* Rob. ex. Desm. This system was chosen because wheat is a valuable agricultural crop, the interaction between wheat and *P. recondita* is fairly well understood, and wild oats is a commonly occurring competitor of wheat. We hypothesized that increased host (wheat) density in monocultures and increased host proportion in mixtures would result in increased wheat leaf rust.

MATERIALS AND METHODS

Experimental plots were located at the Oregon State University (OSU) Botany and Plant Pathology Field Laboratory immediately east of Corvallis, OR. Different fields (approximately 0.2 ha) were used for each year (1995 and 1996). No grain crops had been grown in the fields for several years prior to this experiment. The Chehalis silty clay loam soil was prepared using standard agricul-

Fig. 1. Plot of wheat culm number (flag leaf number) on seeding density of two cultivars (Twin and Penawawa) in monocultures and wheat-wild oats mixtures. Each bar is the mean of four replicate plots planted at one of four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75) for each of three seeding densities (81, 162, and 324 seeds per m^2). A, 'Twin' wheat 1995; B, 'Twin' wheat 1996; C, 'Penawawa' wheat 1995; and D, 'Penawawa' wheat 1996.

tural practices in the fall prior to spring planting. Several days prior to planting (28 March 1995 and 16 March 1996), the field was sprayed with the herbicide glyphosate. A standard soil nutrient test (OSU Central Analytical Laboratory) indicated that nitrogen levels were below recommended concentrations for growing wheat. Nitrogen (46-0-0) as urea was added twice over the 1995 growing season at a rate of 56 kg/ha for a total of 112 kg/ha, and three times in 1996, once at 56 kg/ha and twice at 45 kg/ha, for a total of 146 kg/ha. Bromoxynil (Buctril) was sprayed postemergence to control broadleaf plants. The fields were irrigated with overhead sprinklers three times each year in June and early July.

The experiment was arranged in a randomized complete block design with four replicates consisting of 30 1.2 × 3-m plots. Two commercial, economically important cultivars of spring wheat (Twin and Penawawa) and wild oats (*A. fatua* L.) were planted with a small plot grain drill at three densities of 81, 162, and 324 germinable seeds per m² and at five proportions (100:0, 75:25, 50:50, 25:75, and 0:100) of wheat/wild oats. A total of 24 cultivar

× density × proportion combinations were used for disease analysis; the 100% wild oats plots were excluded. No plot contained both wheat varieties. Between rows of plots, a 1.2-m-wide buffer strip of barley (*Hordeum vulgare* L. cv. Steptoe in 1995) or triticale (× *Triticosecale* Wittmack cv. Celia in 1996) was planted to reduce the spread of spores between plots.

The wheat cultivar Twin is susceptible to wheat leaf rust, whereas 'Penawawa' is moderately resistant and wild oats is immune. Wild oats was chosen because it is a competitor of cultivated wheat in western Oregon and many other wheat-growing areas and may act as a barrier to the dispersal of *P. recondita* spores among wheat plants. Several sources of wild oats seed were tested for germination. Seed collected as screenings from a grain elevator in Alberta, Canada, was used, as it had the highest germination rate. Wheat also was tested for germination prior to planting, and seeding rates for both species were adjusted to produce densities of 81, 162, and 324 germinable seeds per m².

Uredospores of *P. recondita* were collected from greenhouse-inoculated wheat and mixed with talc powder prior to field application. Plots were inoculated with uredospores using a hand-held duster in the early morning or late evening during periods of low wind to minimize drifting. Generalized inoculation was used to diminish sampling difficulties associated with focal point inoculation and because generalized inoculation more closely simulates the natural inoculation of wheat with wheat leaf rust in western Oregon. In 1995, a total of 11.2 g of uredospores was applied on 3 and 4 June. In 1996, a total of 15 g was applied over 7 days from 5 May to 13 June. More spores and days of application were required in 1996 because cold temperatures during May prevented disease establishment. Inoculation was started earlier in 1996 to assure the disease was established during flag leaf emergence.

Disease severity readings were taken on 18 to 19 July 1995 and on 27 to 28 June and 10 to 11 July 1996 by estimating the percentage of leaf area covered by pustules and associated chlorosis for 10 randomly chosen wheat flag leaves in each plot. One hundred percent disease was defined as a leaf blade covered completely with pustules and associated chlorosis. All disease readings were performed prior to each assessment by T. Pfleger, following training using the DISTRAIN computer program (33). The final proportions of wheat and wild oats in the mixtures were determined by counting the number of culms of each species from a 0.25-m² subplot in the center of each plot at harvest.

Data were initially compiled in a computer spreadsheet for preliminary statistical measures. Final statistical analyses were performed using the statistical analysis system (SAS Institute Inc., Cary, NC). Four plots were lost to planting and seed mixing errors in 1995.

Analysis of variance (ANOVA) for disease severity was performed using the SAS general linear models procedure (PROC GLM) to test for cultivar, seeding density, species proportion main effects, and all possible interactions among these main effects. The percent disease readings were transformed using the arcsin of the square root transformation to better meet the homogeneity of variance and normality assumptions. One outlier was removed from the analysis for the June 1996 data, although the ANOVA with and without the outlier indicated little difference in results. Post-ANOVA polynomial contrasts were used to describe the effects of density, proportion, and their interaction on rust severity.

Regression of wheat leaf rust severity on measured wheat density was performed on two subsets of the data that consisted of (i) plots containing 100% wheat, but planted at different densities, and (ii) mixed wheat-wild oats plots planted at one seeding density (324 seeds per m²). These regressions were used to differentiate between the effects of density of susceptible plants versus the barrier effects of resistant plants (interception of spores by nonhost species). Tests for equality of regression lines and y intercepts were performed on the two subsets by using *F* tests.

Fig. 2. Regression of combined wheat and wild oats culm number on combined seeding density of wheat (cultivar Twin or Penawawa) in monocultures and wheat-wild oats mixtures. Regressions were performed on transformed number of culms per m² (square root) and the data were back-transformed for plotting. Each point is the mean of 16 data points: four replicate plots planted at four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75) for each of three seeding densities (81, 162, and 324 seeds per m²). *R*² values were calculated from the entire data set for each cultivar by year. *P* values are from *F* tests to determine if the model had a significant linear component, a significant nonlinear component, or both.

RESULTS

Generally, there was an increase in the number of wheat culms or flag leaves with increasing wheat seeding density in plots containing 100% wheat, indicating that density of resources for pathogen multiplication increased with seeding density (Fig. 1). Increasing the proportion of wild oats in mixed stands with wheat decreased the number of culms per wheat plant, indicating a negative competitive effect of wild oats on wheat (Fig. 1). Regressions of wheat and wild oat culm number on total seeding density showed that, while overall culm density was greater at higher seeding densities, there was not a 1-to-1 ratio or even a linear relation between planting density and the resulting number of culms (Fig. 2).

Wheat leaf rust severity was not significantly affected by seeding density. However, disease severity was significantly impacted by the proportion of wheat in wheat-wild oats mixtures for both July data sets (Table 1). The wheat cultivar Twin was significantly more susceptible than 'Penawawa' for both years and at all samplings (Table 1, Fig. 3). Generally, there was a lack of interactions between experimental treatments. Only 2 of the 12

interactions including density, proportion, or both were significant (Table 1).

The significant interaction between proportion and cultivar in June 1996, along with the known differential sensitivity of each cultivar to wheat leaf rust, indicated the need for separate ANOVAs by cultivar (Table 2). At the cultivar level, density of wheat was again not a significant factor in determining rust severity, whereas proportion of wheat in mixture with wild oats was always a significant factor in the July data sets (Table 2). The exception was the cultivar Twin in July 1996, when density had a significant effect (Table 2). The June 1996 data indicated a difference based on cultivar (Table 1), in which seeding density and proportion were significant factors influencing disease severity for 'Twin', but not for 'Penawawa' (Table 2, Fig. 3).

There was often a positive and linear relationship between percent rust severity and wheat proportion (Table 2). In some cases, there was also a significant nonlinear component, but in all of these cases, the nonlinear component was less significant than the linear component (Table 2). The proportion $\times$ density interaction reported for combined cultivars (Table 1) in 1995 was not present when

TABLE 1. Analyses of variance for percent leaf rust severity of two spring wheat cultivars (Twin and Panawawa) grown at three planting densities (81, 162, and 324 seeds per m²) in both pure stands and in mixture with wild oats at four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75)^a

Source of variation	July 1995			June 1996 ^b			July 1996		
	df	MS ^c	P > F	df	MS	P > F	df	MS	P > F
Block	3	0.0288	0.0172	3	0.0629	0.0009	3	0.1259	0.0001
Cultivar	1	4.194	0.0001	1	0.0681	0.012	1	0.8789	0.0001
Density	2	0.0145	0.1689	2	0.0177	0.184	2	0.0147	0.3901
Cultivar $\times$ density	2	0.0128	0.2074	2	0.015	0.2372	2	0.0263	0.188
Proportion	3	0.1018	0.0001	3	0.0172	0.1791	3	0.2149	0.0001
Cultivar $\times$ proportion	3	0.0055	0.5577	3	0.0318	0.0316	3	0.0059	0.7643
Density $\times$ proportion	6	0.0218	0.019	6	0.0085	0.5458	6	0.0102	0.6768
Cultivar $\times$ density $\times$ proportion	6	0.0089	0.3592	6	0.0085	0.551	6	0.0112	0.6285
Error	65	0.0079		68	0.0102		69	0.0514	
Total	91			94			95		
R ²	0.90			0.45			0.68		

^a Analyses were conducted on the arcsin of square root-transformed values.

^b One outlier was removed from the June 1996 data.

^c Mean square.

TABLE 2. Analyses of variance by cultivar (Penawawa or Twin) for percent leaf rust severity of two spring wheat cultivars grown at three planting densities (81, 162, and 324 seeds per m²) in both pure stands and in mixture with wild oats at four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75)^a

Cultivar, source of variation	July 1995			June 1996 ^b			July 1996		
	df	MS ^c	P > F	df	MS	P > F	df	MS	P > F
Penawawa ^d									
Block	3	0.0164	0.0144	3	0.0345	0.0756	3	0.0949	0.0231
Density	2	0.0045	0.3393	2	0.0002	0.9869	2	0.0215	0.4467
Proportion	3	0.0373	0.0001	3	0.0087	0.5988	3	0.1088	0.0133
Linear	1	0.0613	0.0005	1	0.0004	0.8566	1	0.2986	0.0019
Nonlinear	2	0.0231	0.0073	2	0.0128	0.4027	2	0.0138	0.5949
Density $\times$ proportion	6	0.0055	0.2577	6	0.0064	0.8266	6	0.0101	0.8831
Error	31	0.004		32	0.0137		33	0.0262	
Total	45			46			47		
R ²	0.63			0.28			0.45		
Twin ^e									
Block	3	0.0156	0.303	3	0.0472	0.0004	3	0.051	0.0001
Density	2	0.023	0.1708	2	0.033	0.0089	2	0.0193	0.0159
Proportion	3	0.0714	0.0029	3	0.0407	0.0011	3	0.112	0.0001
Linear	1	0.1984	0.0003	1	0.097	0.0003	1	0.3028	0.0001
Nonlinear	2	0.0062	0.6065	2	0.0125	0.1425	2	0.0165	0.0274
Density $\times$ proportion	6	0.0349	0.0922	6	0.0101	0.1576	6	0.0113	0.0277
Error	33	0.0041		33	0.006		33		0.004
Total	47			47			47		
R ²	0.81			0.66			0.81		

^a Analyses were conducted on the arcsin of square root-transformed values.

^b One outlier was removed from the June 1996 'Penawawa' data.

^c Mean square.

^d 'Penawawa' is moderately resistant to wheat leaf rust.

^e 'Twin' is susceptible to wheat leaf rust.

cultivars where analyzed separately, except for 'Twin' in July 1996 (Table 2).

Leaf rust severity increased with the proportion of wheat in all cases, except the June 1996 data for 'Penawawa' (Fig. 3). The proportion of wheat in mixtures with wild oats was pooled across different seeding densities for regression analysis (Fig. 3), because density was rarely significant and there was an absence of significant density by proportion interactions in the 1996 data, and because the proportion mean square was much larger than the density by proportion interaction mean square in the 1995 data set (Table 1). As expected, the slopes and y intercepts for the susceptible cultivar Twin were greater than for the more resistant cultivar

Penawawa (Fig. 3). Slopes increased from June to July 1996 for both cultivars.

There was no evidence to suggest that the barrier effect of wild oats in mixtures was significant in decreasing disease severity. This was tested using regression analysis to determine if the effects of differing culm density in pure stands were significantly different from the effects of differing culm density (changes in proportion) of wheat in wheat-wild oats mixtures (Table 3). In no case was there statistical evidence to suggest that the slopes for rust severity on culm number per unit area were different for density versus proportion treatments (Table 3), and in only one case ('Penawawa', July 1996) was there evidence that the regression lines were not equivalent (Table 3).

DISCUSSION

Host density. Planting density did not affect rust severity significantly, even though the highest seeding density was 4× the lowest. This lack of significance probably can be explained by the plastic response of plants in response to space (20) and, in particular, the ability of wheat to make compensatory growth in response to variable growing conditions (19). The plastic growth of plants, particularly annuals, is a confounding factor with density treatments, as density remains fixed while individual plants change by growing in response to their environment. For example, the range in density of harvested culms among treatments was much smaller (1.1 to 1.9×) than the fourfold range in initial seeding rates (Figs. 1 and 2). This response held regardless of the proportion of wheat in a mixture (Fig. 1). However, wheat culm density changed the least with increasing seeding density in the mixed plots having the lowest percentages of wheat, probably due to the competitive effect of wild oats on wheat.

A wider range in seeding densities than we used might help clarify the effects of density on rust severity, but at high densities self-thinning may occur (14,36). Darwinkel (14,15) planted winter wheat at densities varying up to 160-fold, but only a 4.3- to 5.7-fold increase in culm number at harvest was found due to an increased number of culms per plant with decreased planting density. Shah et al. (28) planted winter wheat at two moderate densities (84 and 168 kg/ha) and found no significant difference in grain yield when seeded early. Yields differed with later-planted wheat, and they attributed this difference to the greater tillering ability of early-planted wheat.

Gassner (cited by Chester [12]) sowed wheat from 30 to 160 kg/ha and found no difference in the amount of wheat leaf rust, because the wheat had a tendency to regulate its stand to a uniform density. When artificial density gradients were maintained, he still found no correlation between plant density and disease severity. In contrast, Russian scientists (Smitikova-Rusakova; cited by Chester [12]) did similar controlled-density studies with wheat and found that rust intensity increased with density. Gassner (cited by Chester [12]) conducted his studies in Uruguay, where he suggested that microclimatic conditions were conducive to rust infection at all wheat densities, whereas optimal conditions for rust development were met only in the higher densities of wheat in Russia (12).

Since the early work described above, others (4,7,11,31) have suggested that microclimatic changes resulting from higher plant densities has lead to improved conditions for disease development. This, in part, may explain the year-to-year differences seen in epidemic length and severity (Fig. 3), because the 1995 crop was less productive and probably had microclimatic differences less conducive to disease development than the 1996 field environment. Thus, proximity of plants may not be the only cause of positive correlations between plant density and disease severity. However, dense stands also produce higher levels of competition and the subsequent loss of leaf tissue lower in the canopy, which could otherwise become infected (7,12,29). In addition, plant nutritional status

Fig. 3. Regression of wheat leaf rust severity on proportion of wheat culms of two cultivars (Twin and Penawawa) in wheat monocultures and wheat-wild oats mixtures at harvest. Regressions were performed on transformed percent disease severity measurements (arcsin of the square root) and the data were back-transformed for plotting. Each point is the mean of 12 data points: four replicate plots planted at three seeding densities (81, 162, and 324 seeds per m²) for each of four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75). R^2 values were calculated from the entire data set for each cultivar by date. P values are from F tests to determine if slopes were significantly different from zero.

probably differed with density, and host nutritional levels can have a significant impact on disease susceptibility and progression (12).

Species proportion. The relation between disease severity and wheat proportion was linear and positively correlated for both transformed and back-transformed scales. A similar result was found for stripe rust, caused by *P. striiformis*, in wheat cultivar mixtures (2). Leonard (21) developed an analytical model, based on the biology of rust pathogens, to predict the impact on disease of the proportion of susceptible plants in mixtures of resistant and susceptible plants. This model predicts a logarithmic relationship between the proportion of susceptible plants in mixture and the rate of epidemic development, a relationship that is supported by experimental studies (9,21,22). As the relationship between epidemic rate and disease severity is not linear for a polycyclic epidemic, it is not surprising that the proportion of susceptible to non-susceptible plants in a population has a different impact on these two parameters. Regardless, treatments with the lowest proportion of susceptible plants had the least disease in our study, as is usually the case for rusts and mildews of small grains (6,23,35).

Mechanisms of nonhost influence. The question remains as to the role wild oats played in reducing wheat leaf rust severity. Did the oats act as a physical barrier to the movement of inoculum, or did it merely occupy space and effectively change the density of wheat? As the proportion of wheat increases in a series of mixed-species plots planted at the same combined total density, the density of wheat increases, while the barrier effect provided by the nonhost species decreases. If the regression lines from the two subsets of data (Table 3) are the same, then the density component of proportion would be the most important factor. In contrast, if the slope from the changing proportion data is steeper, then there could be a significant barrier effect from the wild oats. We found no significant difference between the regression lines, suggesting that non-host tissue was not an effective barrier to inoculum movement. However, the variability associated with our measurements was quite high, and larger sample sizes are needed to clarify the issue. In addition, it is possible that competitive interactions between wheat and wild oats altered the susceptibility of wheat to rust, as was suggested for wheat cultivar mixtures infected by stripe rust (17).

While at the end of the growing season wild oats is much taller than wheat, wild oats height extension does not occur until wheat has already set seed. Therefore, the effect of height differences between wild oats and wheat are probably limited to later epidemic stages that would impact wheat seed size (as other yield compo-

nents will already have been established), and to potential dispersal to other, later-maturing fields.

Burdon and Chilvers (8,9) have suggested that a decrease in disease caused by fungal pathogens in mixed-species assemblages is not a response to the nonhost interception of airborne inoculum, but rather to a reduction in density of the host. Chin and Wolfe (13), in an elegant experiment to separate effects of density, proportion, and induced resistance in cultivar mixtures, were never able to quantify the difference between density and proportion. They concluded that the effect of cultivar mixtures could be partitioned into three categories: (i) when plants were small, changes in plant density controlled disease levels; (ii) as plants grew, the presence of resistant cultivars increased in importance by acting as barriers to inoculum movement; and (iii) later in the season, differentially susceptible cultivars helped control disease by allowing induced resistance to occur. In addition, changes in plant competition and microclimate are also likely to change with host density. For example, a species that is competitively superior might have more resources available for obligate pathogen infection when grown in mixture than in monoculture at the same density.

As suggested by Power (26), the general difference attributed to insect-vectored pathogens versus wind-dispersed fungal pathogens in relation to host density may be due to active selection of host plants by a limited number of insects. In contrast, fungal pathogens passively disperse spores and spores may be transported to plant genotypes on which they cannot reproduce. When nonhost species acquire significant space, they reduce host species densities, act as traps for inoculum, or both. In doing so, they may have an important role in natural communities by decreasing the severity of some diseases. Thus, plant diversity may help to sustain rare but susceptible species in plant communities, in contrast to some herbivore-plant interactions, in which a plant's susceptibility to herbivory can increase if surrounded by diverse, acceptable host plants when attacked by polyphagous insects (30). Therefore, rarity could be a more successful strategy for plants to escape fungal pathogens than to escape herbivores.

The conceptual problem of trying to attribute part of wheat leaf rust progression to host density, proportion, or both is that neither term is adequately inclusive to explain the dynamic nature of the process. Wheat leaf rust progression might be better considered as space acquisition by the host. Initially, plant hosts functionally exist in two-dimensional space, in which the number of seedlings is a meaningful way to interpret the potential for infection. Later, as

TABLE 3. y Intercepts and slopes for regression of percent left rust severity on density of wheat culms (culms per m²) in pure stands^a and in wheat-wild oats mixtures^b grown at Corvallis, OR, during 1995 and 1996^c

Date	Cultivar	Plot type	y Intercept	SE ^d	Slope	SE ^e	P > F ^f	P > F ^g
July 1995	Penawawa	Mixed stand	0.249	0.038	0.0008	0.0009	0.89	0.73
		Pure stand	0.266	0.044	0.0009	0.0005		
	Twin	Mixed stand	0.740	0.088	-0.0012	0.0015	0.24	0.17
		Pure stand	0.692	0.135	0.0009	0.0010		
June 1996	Penawawa	Mixed stand	0.508	0.083	0.0002	0.0012	0.77	0.84
		Pure stand	0.608	0.190	-0.0003	0.0013		
	Twin	Mixed stand	0.529	0.049	0.0008	0.0006	0.43	0.58
		Pure stand	0.396	0.127	0.0015	0.0008		
July 1996	Penawawa	Mixed stand	0.849	0.093	0.0006	0.0013	0.23	0.03
		Pure stand	1.363	0.211	-0.0019	0.0015		
	Twin	Mixed stand	1.025	0.048	0.0017	0.0005	0.43	0.70
		Pure stand	1.108	0.125	0.0009	0.0008		

^a Wheat seeded at densities of 81, 162, and 324 seeds per m².

^b Wheat-wild oats mixtures seeded at a combined density of 324 seeds per m² at four proportions (wheat/wild oats = 100:0, 75:25, 50:50, and 25:75).

^c Analyses were conducted on the arcsin of square root-transformed values.

^d Standard error of the estimates for the y intercept.

^e Standard error of the estimates for slope.

^f Testing the hypothesis H₀: regression slopes for pure and mixed stands are equal, using an F test.

^g Testing the hypothesis H₀: regression lines (i.e., joint test for equal intercepts and equal slopes) for pure and mixed stands are equal, using an F test.

plants grow and occupy three-dimensional space, inoculum is not limited to landing on bare ground or seedlings, but can also be intercepted by nonhost tissue. However, locally, inoculum may be so plentiful that nonhost interception is insignificant. At a larger spatial scale, wheat leaf rust progression across the landscape is additionally influenced by such factors as the distribution of infected tissue, its relation to prevailing winds, and changes in wind speed at the source and potential infection sites.

ACKNOWLEDGMENTS

The information in this article has been funded by the United States Environmental Protection Agency (EPA). It has been subjected to the Agency's peer and administrative review, and it has been approved for publication as an EPA document. We thank M. da Luz and R. Hayes for technical assistance; H. Lee for statistical support; and L. Tate for field management.

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