Uredospore Dispersal from a Point Source within a Wheat Canopy

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ABSTRACT

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A small infection focus of *Puccinia graminis* f. sp. *tritici* was established on susceptible plants in two plots of otherwise resistant wheat. Stationary 5-mm-diameter rod impaction traps were placed in the foci and at 30.5 and 61.0 cm from the foci to detect spore dispersal. The number of uredospores impacted was determined for each 10-cm height within and just above the canopy. Daily numbers of spores trapped varied greatly depending on the environment and disease severity. Within the focus, the number of spores trapped decreased with height, and only 2% of the number trapped at 10 cm above the ground were trapped above the canopy. At 30.5 and 61.0 cm horizontally from the focus, spores trapped were 4 and 2%, respectively, of the numbers trapped at that same heights within the focus. The effect of wind direction was apparent in the numbers of spores trapped at the 30.5- and 61.0-cm locations, where 10 and 5%, respectively, of the amount at the source was normally the maximum.

Additional key words: aeriobiology, epidemiology, wheat stem rust.

Uredospore dispersal has been studied for more than 60 years (12). Most of these studies concentrated on the continental spread of spores. Long distance spore dispersal is important in introducing new virulence genes into an area (13) and in the development of continental epidemics in North America (6,12).

The development of the cereal rust disease in foci near an overwintering uredium stimulated our interest in uredospore dispersal near an inoculum source. Overwintering foci in the field often consist of severely diseased areas <1 m in diameter. surrounded by nearly disease-free plants (10). The soil beneath such foci is often covered with a visible layer of uredospores. These foci are observed in the United States in areas where the various small grain rust pathogens overwinter, but they seldom occur where spring-planted cereals are grown. In spring-planted cereals, initial infections are usually found on the flag or penultimate leaves and often appear nearly randomly dispersed. After secondary infections occur on spring-planted cereals, it is usually difficult to distinguish any concentration of uredia that could be recognized as a focus.

This study was undertaken to investigate the dispersal of uredospores in the immediate vicinity of a small inoculum source in the field and over a range of environmental conditions in both winter- and spring-wheat planted in the spring. The spring-planted spring wheat developed normally while the spring-planted winter wheat remained in a rosette-like condition throughout the spring and summer, duplicating the type of plant growth that occurs at sites where the pathogen overwinters.

MATERIALS AND METHODS

Ten culms of a wheat cultivar susceptible to stem rust were established in the centers of 3×3-m plots of a resistant spring wheat cultivar and of a resistant nonvernalized winter wheat cultivar in 1980 and 1981. The wheat was planted in rows 30.5 cm apart at a seeding rate of 100 seeds per meter of row. The rows were planted along a north-south axis. Approximately 60 culms developed per meter of row during the experiment. The susceptible wheat cultivars used were Baart (CI 1697, spring habit) and Cheyenne (CI 8885, winter habit). The resistant wheat cultivars were Chris (CI 13751, spring habit) and Blueboy II (CI 15281, winter habit).

The spring wheat and nonvernalized winter wheat plots were separated by 100 m of noncultivated land except for a 3×3-m plot of a resistant wheat midway between them and by an additional susceptible trap plot 100 m away in 1981. These plots were at least 14 km from the nearest known planting of small grain cereals. The land in the vicinity of the plots was occupied by numerous grass and forb species, among which *Agropyron repens* L. and *Poa pratensis* L. were common. Plants of these species, plus those in the additional susceptible plot were checked frequently for *Puccinia graminis*, which was not found.

The tillers of Baart and Cheyenne plants were inoculated when the first node was detectable by feeling the culm. Uredospores of race 56-MBC of *P. graminis* sp. *tritici* were suspended in water and injected into the leaf whorl. Race 56-MBC is well adapted to the northern Great Plains but now is rarely found; thus it was possible to distinguish it from exogenous inoculum.

Traps were placed in the center of the infection foci and at distances of 30.5 and 61.0 cm at the four cardinal points of the compass. The traps were 5-mm-diameter steel rods of varying lengths with 2-cm-wide bands of polyethylene coated with silicone grease (7,11) serving as trapping surfaces. The trapping surfaces were centered at 10-cm intervals from ground level to ~10 cm above the top of the crop canopy. The traps were changed each morning from the time of initial sporulation in the inoculated foci until those plants matured and no more uredospores were being produced.

The polyethylene bands were removed from the rod and placed on a microscope slide for counting. Uredospores were counted at ×100 , and counts were converted from spores per trapping band (1.57 × 2.0 cm) to spores per square centimeter. For various analyses of the data, spore counts were accumulated for specific heights or locations for varying time periods. In studying environmental factors, each day with similar conditions served as a replicate.

Temperature and relative humidity were recorded in a standard weather shelter 50 cm above the ground. Cloud cover, wind direction, and wind speed were recorded at 0800 and 1700 hours daily. Precipitation and dew periods were recorded daily.

RESULTS

Numbers of uredospores trapped increased rapidly during the season, reaching a maximum as the host plants matured or, in the

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TABLE 1. Season cumulative totals of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci consisting of a few susceptible plants infected with *Puccinia graminis* f. sp. *tritici* in a spring-planted plot of resistant spring wheat in 1980 and 1981

Year, sampler direction, and distance from foci	Height above the ground (cm)								Total
	10	20	30	40	50	60	70	80	
1980									
Foci	31,984	38,813	46,940	44,354	59,069	25,802	6,234	4,701	257,899
East 30.5 em	2,421	2,202	2,506	4,014	3,189	1,023	523	288	16,108
61.0	368	608	703	480	477	319	109	76	3,141
South 30.5 cm	1,477	831	1,057	996	1,305	1,365	669	510	8,211
61.0	299	366	601	582	265	481	159	108	2,862
West 30.5 cm	1,650	2,727	2,211	3,962	2,702	1,013	476	178	14,920
61.0	635	922	852	686	562	382	233	118	4,388
North 30.5 cm	638	556	1,329	896	1,692	813	334	187	8,937
61.0	752	1,067	1,474	1,090	735	417	198	72	6,179
Total, 1980	40,226	48,091	57,673	57,061	68,996	31,617	8,937	6,179	319,780
1981									
Foci	33,298	28,305	17,265	13,703	12,502	2,300	1,099	70	108,543
East 30.5 cm	801	711	532	353	414	445	36	29	3,323
61.0	52	28	116	69	58	79	48	48	497
South 30.5 cm	178	327	514	304	238	88	98	44	1,791
61.0	125	281	180	118	108	67	76	70	1,025
West 30.5 cm	338	334	716	288	156	392	44	53	2,322
61.0	57	77	95	88	47	51	53	28	497
North 30.5 cm	2,306	2,870	3,188	2,072	873	1,156	92	44	12,602
61.0	195	259	432	322	158	187	49	58	1,655
Total, 1981	37,350	33,191	23,039	17,317	14,553	4,766	1,596	444	132,256

case of the nonvernalized winter wheat, when the disease killed the plants. After reaching a maximum, numbers of spores trapped remained high for about 2 wk when a significant rainfall occurred. Thereafter few spores were trapped.

Numbers of uredospores trapped daily varied greatly depending on the disease severity in the foci and on the environmental conditions of that and preceding days. Only a total of 266 and 112 spores per square centimeter in 1980 and 1981, respectively, were trapped in either year in the resistant check plot. Uredospores collected at various times during the experiment were found to be race 56-MBC, including those from five off-type plants (without *Sr*24) found in the Blueboy II plot. These plants were detected by abnormally high daily numbers of spores at a trapping location outside the foci. The off-type plants so detected had <10 uredia each and were within 15 cm of the trapping sites. These plants were removed the day after detection. In 1981, no stem rust was found in the susceptible check plot of Baart throughout the season.

Cumulative numbers of uredospores trapped outside the foci generally decreased with height (Table 1 and 2) above the ground. However on individual days (especially later in the growing season) large numbers of uredospores were impacted at midplant height (30–40 cm). Only about 2% as many uredospores were trapped 10 cm above the canopy as were trapped 10 cm above the ground. After the flag leaves of plants in the foci had senesced, the number of spores trapped above the canopy increased and often nearly as many were trapped above the canopy at the 30.5 and 61.0 cm annuli as directly above the foci. This was especially true in 1981.

At a given height, the number of uredospores trapped decreased rapidly with distance from the source (Tables 1 and 2). Spore traps at 30.5 and 61.0 cm trapped about 4 and 2%, respectively, as many spores as were trapped at the same height at the foci. These percentages did not hold for 1981 data above the canopy (Table 3). There was generally a directional dispersal of spores daily. When the spore count values for the downwind axes were cumulated for

TABLE 2. Season cumulative totals of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci consisting of a few susceptible plants infected with *Puccinia graminis* f. sp. *tritici* in a spring-planted plot of nonvernalized winter wheat in 1980 and 1981

Year, sampler direction, and distance from foci	Height above the ground (cm)				Total
	10	20	30	40	
1980					
Foci	27,552	24,049	14,569		66,170
East 30.5 cm	1,220	1,312	674		3,207
61.0	329	213	265		808
South 30.5 cm	1,274	1,134	668		3,076
61.0	340	635	365		1,340
West 30.5 cm	1,421	1,397	906		3,723
61.0	1,475	920	486		2,880
North 30.5 cm	2,372	2,676	1,039		6,087
61.0	283	467	288		1,039
Total, 1980	36,266	32,802	19,262		88,330
1981					
Foci	30,657	22,743	8,398	342	62,142
East 30.5 cm	1,255	962	394	199	2,811
61.0	1,110	84	208	155	517
South 30.5 cm	2,069	1,323	471	139	4,002
61.0	399	168	131	114	688
West 30.5 cm	1,194	789	708	232	2,922
61.0	136	116	212	224	688
North 30.5 cm	1,829	1,039	439	182	3,489
61.0	299	217	230	146	892
Total, 1981	37,947	27,440	11,193	1,692	78,272

TABLE 3. Percent of uredospores of *Puccinia graminis* f. sp. *tritici* impacted on 5-mm-diameter spore trap rods at various heights at 30.5 and 61.0 cm from infection foci (a few susceptible plants) in spring-planted plots of otherwise resistant spring and nonvernalized winter wheat in 1980 and 1981 as a percent of those impacted within the foci

Year, wheat type, and sampling height (cm)	Percent of uredospores impacted at various directions and distances (cm) from foci								Check plot
	East		South		West		North		
	30.5	61.0	30.5	61.0	30.5	61.0	30.5	61.0	
1980									
Spring wheat									
10	7.57	1.15	4.62	0.94	5.16	1.98	2.00	0.23	0.01
20	5.67	1.56	2.14	0.94	7.02	2.38	1.43	2.75	0.18
30	5.34	1.50	2.25	1.28	4.71	1.81	2.83	3.14	0.06
40	9.05	1.08	2.24	1.31	8.91	1.55	2.02	2.46	0.04
50	5.40	0.81	2.21	0.45	4.58	0.95	2.86	1.24	0.04
60	3.97	1.23	5.29	1.87	3.93	1.48	3.15	1.62	0.10
70	8.40	1.76	10.73	2.56	7.63	3.73	5.32	3.17	0.04
80	4.86	1.61	10.86	2.29	3.78	2.50	3.98	1.53	0.04
Nonvernalized winter wheat									
10	4.43	1.20	4.62	1.23	5.16	5.35	8.61	1.03	0.13
20	5.46	0.89	4.72	2.64	5.81	3.82	11.12	1.94	0.30
30	4.63	1.82	4.58	2.50	6.22	3.34	7.13	1.98	0.22
1981									
Spring wheat									
10	2.41	0.16	0.54	0.37	1.01	0.17	6.92	0.58	0.07
20	2.51	0.10	1.15	1.00	1.18	0.27	10.14	0.91	0.03
30	3.08	0.67	2.98	1.04	4.15	0.55	18.47	2.50	0.04
40	2.58	0.50	2.22	0.86	2.10	0.64	15.12	2.35	0.02
50	3.31	0.46	1.90	0.86	1.25	0.38	6.98	1.25	0.04
60	19.35	3.45	3.84	2.92	17.03	2.23	50.26	8.14	0.05
70	3.26	4.34	8.91	6.93	4.04	4.86	8.38	4.42	0.25
80	41.48	68.35	62.84	1.09	76.26	40.82	63.76	82.57	0.19
Nonvernalized winter wheat									
10	4.09	0.35	6.75	1.30	3.90	0.44	5.97	0.97	0.07
20	4.23	0.37	5.82	0.74	3.47	5.12	4.57	0.96	0.07
30	4.70	2.48	5.61	1.56	8.42	2.52	5.23	2.74	0.20
40	58.33	33.71	40.64	33.24	67.79	65.54	53.28	42.70	3.65

TABLE 4. Number of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci of *Puccinia graminis* f. sp. *tritici* in spring-planted plots of spring and nonvernalized winter wheat on 1 July 1980[a]

Wheat type, sampler direction, and distance from foci	Height above the ground (cm)								Total
	10	20	30	40	50	60	70	80	
Spring wheat									
Foci	564	768	960	3,200	480	35	58	28	6,094
East 30.5 cm	26	90	73	236	45	6	20	4	497
61.0	2	9	4	1	1	3	2	1	26
South 30.5 cm	86	31	334	293	448	520	76	370	2,157
61.0	40	32	52	82	18	35	5	4	268
West 30.5 cm	11	5	26	41	10	8	7	8	119
61.0	5	4	7	5	23	23	10	11	87
North 30.5 cm	5	4	21	7	21	7	5	1	75
61.0	1	7	14	10	8	1	4	†[b]	42
Nonvernalized winter wheat									
Foci	544	371	809						1,724
East 30.5 cm	24	162	36						221
61.0	1	17	7						25
South 30.5 cm	108	185	146						439
61.0	10	28	44						82
West 30.5 cm	22	33	25						79
61.0	12	2	3						17
North 30.5 cm	25	111	111						246
61.0	9	3	7						19
Rust-free check	1	1	2	2	1	0	2	0	9

[a]Weather factors: 24–5 C, partly cloudly, northwest wind 4.5–8.5 m/sec. The wind was measured at about 0800 and 1630 hours daily.
[b]Dagger (†) = fewer than 0.6 spores per square centimeter were trapped.

TABLE 5. Numbers of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci of *Puccinia graminis* f. sp. *tritici* in spring-planted plots of spring and nonvernalized winter wheat on 10 July 1980[a]

Wheat type, sampler direction, and distance from foci	Height above the ground (cm)								
	10	20	30	40	50	60	70	80	Total
Spring wheat									
Foci	186	207	332	264	143	71	666	56	1,924
East 30.5 cm	5	52	102	156	181	141	136	45	820
61.0	4	2	42	97	37	79	28	10	301
South 30.5 cm	9	53	45	42	68	4	4	5	230
61.0	4	48	23	5	4	2	2	2	90
West 30.5 cm	12	144	41	431	240	23	18	1	910
61.0	6	31	25	10	16	6	6	1	101
North 30.5 cm	70	72	111	87	152	33	15	19	562
61.0	12	10	50	58	40	13	10	5	199
Nonvernalized winter wheat									
Foci	633	530	104						1,267
East 30.5 cm	14	20	7						41
61.0	5	†[b]	4						9
South 30.5 cm	9	1	0						10
61.0	1	†	0						1
West 30.5 cm	12	7	7						26
61.0	1	1	†						2
North 30.5 cm	22	18	4						44
61.0	2	23	0						24
Rust-free check	0	0	0	1	0	0	0	0	1

[a]Weather factors: 29–15 C, clear, north wind 2.2 m/sec. The wind was measured at about 0800 and 1630 hours daily.
[b]Dagger (†) = <0.6 spores per square centimeter.

TABLE 6. Numbers of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci of *Puccinia graminis* f. sp. *tritici* in spring-planted plots of spring and nonvernalized winter wheat on 7 July 1981[a]

Wheat type, sampler direction, and distance from foci	Height above the ground (cm)								
	10	20	30	40	50	60	70	80	Total
Spring wheat									
Foci	2,111	5,735	2,153	487	1,801	504	348	44	13,183
East 30.5 cm	22	28	42	4	90	78	5	4	95
61.0	1	2	9	4	6	7	10	7	26
South 30.5 cm	2	5	8	4	46	7	15	7	274
61.0	2	1	1	1	6	4	5	6	47
West 30.5 cm	98	4	111	116	4	12	4	3	351
61.0	1	1	2	5	9	7	3	2	31
North 30.5 cm	149	778	1,573	712	229	515	22	16	3,995
61.0	30	76	214	143	4	52	4	33	556
Nonvernalized winter wheat									
Foci	2,380	1,006	1,464	28					4,878
East 30.5 cm	136	221	87	15					458
61.0	31	18	36	14					98
South 30.5 cm	88	78	7	3					177
61.0	2	12	2	8					23
West 30.5 cm	72	44	35	17					167
61.0	4	4	5	10					23
North 30.5 cm	265	58	61	16					400
61.0	32	32	31	48					143
Rust-free check	3	4	4	3	1	1	3	†[b]	20

[a]Weather factors: 33–24 C, hazy, south wind 3.6–4.5 m/sec. The wind was measured at about 0800 and 1630 hours daily.
[b]Dagger (†) = <0.6 spores per square centimeter.

the season, about 10 and 5% as many spores as were trapped at the foci were trapped at 30.5 and 61.0 cm, respectively. Tables 4 to 7 show examples of individual days of spore distribution.

We found no strong correlation between any of the measured environmental factors and numbers of uredospores trapped at the various heights and locations. An exception was for wind direction and number of spores for days when the wind blew from a constant direction.

No major difference existed in the extent of uredospore dispersal in the plots having spring or winter growth habits (Tables 1 and 2). Furthermore, the total numbers of uredospores trapped at a given height within the canopy were generally similar.

DISCUSSION

Recently, studies of fungal spore dispersal near disease foci were done to show the effect of spore dispersal on disease spread in pure stands and multilines (1–3,5,9). These studies showed a rapid decrease in spore concentrations within a few meters of the source. Differences in mechanisms of spore release and transport, differences in spore shape and weight, as well as differences in the density and structure of the crop canopies all probably influenced spore dispersal near disease foci.

No measurement of spore production per day was attempted in this study. However, the range of values from other studies leads us to believe that during peak disease development (after 1 July) 50 to 100×10^6 uredospores were produced daily in the 10-tiller focus. This calculation is based on $5–10^3$ uredospores being produced daily per uredium from 10^3 uredia per tiller. During this period, seldom were more than 10^3 spores per centimeter trapped at stations 30.5 cm from the focus even on the downwind axis. The traps that were used are not 100% efficient (Gregory [4] estimated an efficiency of ~45% for particles 32 μm in diameter with a wind speed of 3.3 to 5.75 m/sec and a trap diameter of 5 mm). Data from 7 July 1981 (Table 6) showed that an estimated 2.2×10^6 spores reached the 30.5-cm annulus within the crop canopy. The estimate was made as follows: total number of spores trapped at the 30.5-cm annulus for seven heights and four stations was 4,682/cm^2. Mean number of spores per square centimeter around the annulus was $4{,}682 \div (4 \times 7) = 167$. An annulus with a height of 70 cm would have an area of 13,414 cm^2, and an estimated 2.2×10^6 spores impacted ($13{,}414 \times 167$). Thus, only 2.5–4.5% of the estimated number of spores produced were impacted above an annulus 30.5 cm from the focus within the canopy. Even with correction for the trapping efficiency, the calculations indicate a major loss of spores within 30.5 cm of the focus. The mean number of uredospores trapped at the 61.0-cm annulus was $\sim 586 \times 10^3$ or 1.17–2.34% of those trapped at the focus. The circumference doubles when increasing from the 30.5- to 61.0-cm annulus and interestingly, the number of spores impacted is about one-half. Thus, the difference in numbers of urediospores impacted can be accounted for by the horizontal diffusion of spores alone. Although large numbers of spores are impacted 15 cm above the crop canopy (8,10) with larger areas of diseased crop, in this study of small foci the proportion of spores trapped 10 cm above the canopy remained small in comparison to the numbers trapped within the canopy throughout the study. The loss of spores in the first 30.5 cm must have been due to deposition on the ground, vertical transport from the canopy (although estimated by impaction trapping to be small), and from impaction on host tissue within the infected foci.

Little difference was detected between the distribution or numbers of uredospores impacted near foci in plots of spring wheat or nonvernalized winter wheat (Tables 1 and 2). The existing differences could relate as much to differences in amounts of diseased tissue as to differences in density and structure of the canopies.

Numbers of uredospores impacted were much less 10 cm above the canopy than at the top of the canopy (Tables 1 and 2). This difference existed regardless of environmental conditions or crop growth habit. A major exception occurred late in the 1981 season after crop maturity and prior to the first rain when for several days about equal numbers of spores were trapped 10 cm above the canopy at the focus and at stations on the downwind axis. This is reflected in the high percentage of spores impacted over the canopy

TABLE 7. Numbers of uredospores impacted on 5-mm-diameter spore trap rods in and around infection foci of *Puccinia graminis* f. sp. *tritici* in plots of spring-planted plots of spring and nonvernalized winter wheat on 4 July 1981[a]

Wheat type, sampler direction, and distance from foci	Height above the ground (cm)								Total
	10	20	30	40	50	60	70	80	
Spring wheat									
Foci	1,257	764	897	18	346	54	1	0	3,335
East 30.5 cm	0	0	6	0	7	0	0	†	12
61.0	1	0	†	0	0	0	0	0	2
South 30.5 cm	2	5	3	11	29	1	4	0	56
61.0	1	9	†	18	4	0	0	0	32
West 30.5 cm	0	6	0	8	0	0	0	0	14
61.0	†	0	†	0	0	1	†	0	1
North 30.5 cm	7	16	85	75	29	2	0	0	215
61.0	0	0	†	1	0	0	0	0	1
Nonvernalized winter wheat									
Foci	912	3,458	801	2					5,173
East 30.5 cm	83	17	3	5					108
61.0	0	0	7	0					7
South 30.5 cm	56	108	64	5					234
61.0	0	14	7	12					33
West 30.5 cm	27	1	5	0					33
61.0	0	6	0	0					6
North 30.5 cm	52	1	2	2					57
61.0	†	1	3	0					5
Rust-free check	0	0	0	0	0	†	3	0	3

[a] Weather factors: 31–15 C, clear, calm. The wind was measured at about 0800 and 1630 hours daily.
[b] Dagger (†) = <0.6 spores per square centimeter.

at stations on the annuli compared to directly above the foci (Table 3). These were not spores from an exogenous inoculum source as practically no spores were trapped on those days above plants in the resistant check plot.

On most of the 92 days of sampling, the wind shifted direction or greatly changed speeds over the 24-hr sampling period. Spore movement was light and erratic on calm days (Table 7, 4 July 1981 example) and greater and more directional on days with greater wind velocity (Table 4, 1 July 1980 example).

Spore release in *P. graminis* f. sp. *tritici* may occur throughout the day but often has very sharp peaks that last for <1 hr (8). Thus, wind direction is important during that brief period. An example of this problem is shown in Table 5. On 10 July 1980, wind speed and direction at 0800 and 1700 hours CDT was 2.2 m/sec and from the north. In the plot of spring wheat, most of the spores were trapped on the east and west axes. On 7 July 1981 (Table 6), in the plot of spring growth habit wheat, the assumed northward movement of spores occurred with an 12.9–16.1.1 km/hr (8–10 mph) south wind. However, in the plot of nonvernalized winter wheat the data show a northeastward dispersal of spores.

Daily values for cloud cover, relative humidity, temperature, and precipitation seemed to have little correlation with spore dispersal under field conditions.

The results of this study indicate that foci develop due to the steep inoculum gradient near the source. This would be most visible when conditions for infection were marginal, as is often the case in the southern United States where the stem rust pathogen overwinters.

Additional studies are needed to clarify spore dispersal within the canopy near a focus. The physical and biological factors that determine the duration and quantity of spores liberated from a uredium need to be studied through a range of field conditions. The effect of sedimentation on spore concentrations near the source is essentially unknown under field conditions. Under some environmental conditions, sedimentation near the spore source may remove many spores from the air. A determination is needed of the vertical dispersal of spores above a known spore source over a range of conditions.

LITERATURE CITED

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