Detection, Viability, and Possible Sources of Urediniospores of *Puccinia recondita* f. sp. *tritici* in Louisiana

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ABSTRACT

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Kramer-Collins 7-day spore samplers were operated continuously at two locations, Baton Rouge (BR) and Bossier City (BC) in Louisiana, and daily urediniospore counts were taken. The number and viability of spores trapped was maximum during the active epidemic period between February and May and was least during the summer. Viability of the urediniospores was significantly inversely correlated with ambient maximum temperature ($r = -0.81$ at BR and -0.59 at BC). The highest consecutive number of days that no urediniospores were trapped was 6 in 1986 and 7 in 1987 at BR, and 31 in 1986 and 14 in 1987 at BC. Cultivar McNair 1003, susceptible to the prevalent leaf rust population, was planted at BR from 1 May through 18 September in 1986 and 1987, at 14- to 20-day intervals. Leaf rust appeared in many plantings and survived temperatures up to 36 C for 82 days in 1986 and 74 days in 1987. McNair 1003 plants, in pots exposed at 14- to 15-day intervals during summer for 2 days in a field at BR and then incubated in an air-conditioned greenhouse, developed leaf rust with an incidence of 12.5–100%. Rusts from *Hordeum pusillum* and *Lolium multiflorum* failed to infect wheat and vice versa. Surveys during mid-December 1986 and 1987, at Alexandria and Baton Rouge, showed uniform distribution of leaf rust over a large area, indicating the possibility of a major exodemic origin of inoculum for winter wheat in Louisiana for these years.

Additional keyword: epidemiology

Soft red winter wheat (*Triticum aestivum* L.), harvested for grain in Louisiana, increased from approximately 27,000 hectares in 1980 to nearly 100,000 hectares in 1987 (2), owing to the popularity of wheat-soybean double-cropping. Leaf rust, caused by *Puccinia recondita* f. sp. *tritici* Rob. ex Desm., occurs more frequently in Louisiana than any other disease of wheat and causes yield losses of up to 50% (3). In Louisiana, winter wheat is normally planted in late October through late November and is harvested by mid-May.

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The time of onset of leaf rust varies from early December to early February. Disease progress generally slows with the onset of cooler temperatures in early January and then progresses faster with the onset of warmer temperatures in early March. Similar observations have been made in Texas (17). The critical period in the disease cycle for the survival of the fungus is the interval between the time of harvest in May and the emergence of new wheat in early November. How the fungus survives during this period has remained undetermined. *Thalictrum flavum* L. is an alternate host for *P. r.* f. sp. *tritici*, but is extremely rare in the United States (15,28). Other grasses such as *Aegilops* spp. (1), *Bromus* spp. (4,31), *Hordeum* spp. (1,13), and *Lolium* spp. (27) are occasionally infected by *P. r.* f. sp. *tritici*. The fungus also thrives on volunteer wheat plants, usually as dormant mycelium and occasionally as sporulating mycelium (5,29). Race determination studies have been used to demarcate distinct epidemiological zones, depending on the regularity and frequency of occurrence of certain races. Based on these results, oversummering and overwintering within each epidemiological zone was postulated (16), and circumstantial evidence obtained during an 8-yr leaf rust race survey in Pennsylvania supported this theory (23). Studies in the Great Plains in the United States have demonstrated the presence and local movement of viable inoculum throughout the year in locations where studies were conducted (10), and showed that one of the principle factors that determines the duration of urediniospore survival is temperature (8).

Sources of primary inoculum for leaf rust of wheat in Louisiana have not been determined. Conditions for the survival of *P. r.* f. sp. *tritici* (29) are marginal in Louisiana during the summer. Temperatures are usually in the range (33–37 C) that reduces the amount of sporulation (26) and longevity of spore viability (8). Longevity of spore viability at high temperatures is also known to be affected by the location of urediniospores on soil or on living tissue. Soilborne urediniospores survive a simulated temperature regime of 34 C day/22 C night for up to 22 days on moist soil, 13 days on dry soil, and 8 days on dry foliage (12). Urediniospores on dry wheat foliage are also known to survive for at least 9 days at near-optimal (20 ± 1 C) temperatures (30).

This study was undertaken to determine if any grasses in Louisiana support the growth and survival of the fungus, to determine the temporal availability of viable inoculum in the state and test its potential effectiveness, and finally to determine the possible sources of the inoculum for the state. Preliminary results of these studies have been published (24,25).

MATERIALS AND METHODS

Experiments reported in this paper were conducted during 1986 and 1987 at three Louisiana agricultural experiment stations: the Ben Hur Research Station, the Red River Research Station, and the Dean Lee Research Station, located at Baton Rouge (BR), Bossier City (BC), and Alexandria (Alex), respectively (Fig. 1). Leaf rust surveys were conducted at BR and Alex.

Monitoring urediniospores. Kramer-Collins 7-day spore samplers (GR Manufacturing Co., Manhattan, KS) were operated continuously at BR and BC. Silicone grease-coated tape on drums was changed weekly at all locations. Daily urediniospore counts were made, and the number of urediniospores per cubic meter of air per day was calculated following the procedures of Eversmeyer et al (10). Tapes showing more than two trapped spores per day were incubated in moist chambers for 12 hr at 23 ± 1 C.

A spore was considered germinated if a germ tube of at least 3 μm was observed. Germinated urediniospores were counted after 14 hr of incubation, and the percentage of the number of germinated divided by the total number trapped was used as a measure of the viability of the inoculum (10). Daily ambient air temperature data were collected from automated weather stations at both locations, and weekly mean maximum temperatures were computed for each location in both years. The relationship between the weekly urediniospore viability and the weekly mean maximum temperature was determined by correlation and regression analysis with SAS procedure CORR (22) and PLOTIT procedure NONL (7).

Field experiments at BR. To confirm the potential effectiveness of the airborne inoculum, cultivar McNair 1003, susceptible to the prevalent pathogen populations, was planted in 1-m^2 plots during the 1986 and 1987 summer seasons at BR at 14- to 20-day intervals beginning 3 May and continuing until 18 October. Successive plantings were separated by 50 m to reduce the chances of contamination from one plot to another. The percentage (incidence) of infected plants observed and area percentage (severity) of the individual leaves on each infected plant were determined using modified Cobb's scale (18). The number of days that leaf rust persisted was recorded for each planting. Leaf rust isolates from each of these plantings, along with an isolate from the previous season maintained on the susceptible cultivar McNair 1003 in an air-conditioned greenhouse, were sent to the Cereal Rust Laboratory,

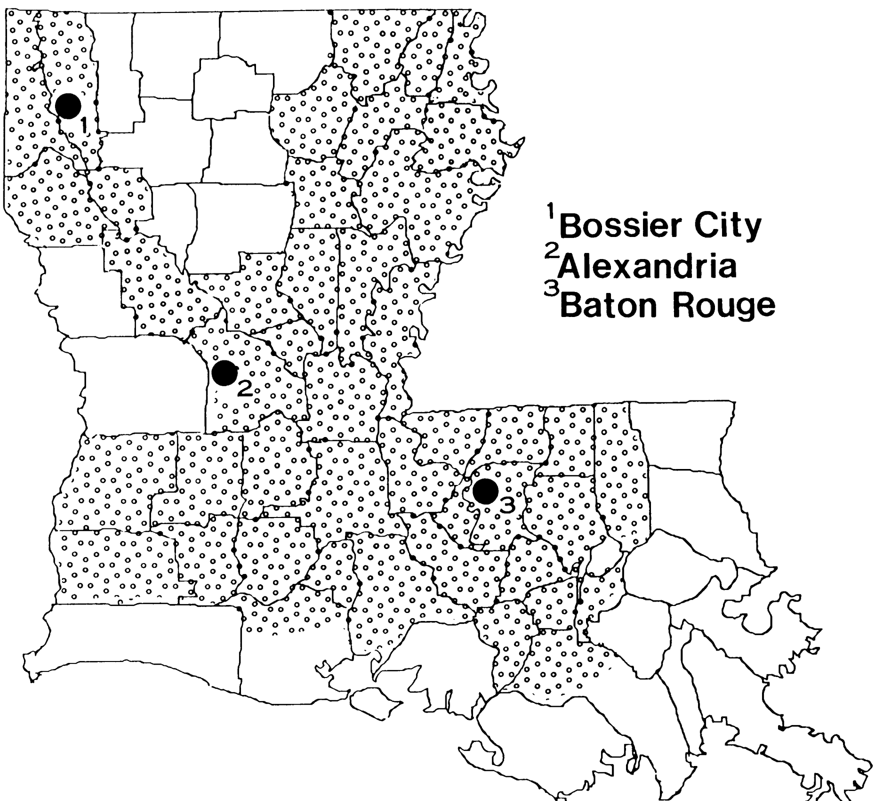

Fig. 1. Locations in which studies were conducted in Louisiana. The shaded area represents areas where wheat is commercially grown in Louisiana.

Table 1. Mean number of urediniospores of *Puccinia recondita* trapped during 1986 and 1987 by Kramer-Collins 7-day volumetric spore samplers at Baton Rouge and Bossier City in Louisiana

	Mean no. of urediniospores trapped per cubic meter of air per day				Viability[a] (%)				Consecutive days on which no spores were trapped			
	Baton Rouge		Bossier City		Baton Rouge		Bossier City		Baton Rouge		Bossier City	
Month	**1986**	**1987**	**1986**	**1987**	**1986**	**1987**	**1986**	**1987**	**1986**	**1987**	**1986**	**1987**
January	···[b]	0.6	···	0.1	···	77.5	···	70.9	···	5	···	3
February	···	1.2	0.1	0.1	···	80.2	···	70.9	···	1	6	5
March	0.9	6.0	0.0	0.2	···	72.7	···	78.0	1	1	31	5
April	0.4	74.9	···	2.1	···	76.8	···	69.5	0	0	···	3
May	2.6	···	···	0.9	32.4	···	···	70.4	0	···	···	4
June	0.5	0.2	0.1	0.2	27.5	37.5	···	42.5	0	1	2	3
July	0.2	0.2	0.1	0.1	28.9	35.0	11.5	33.8	5	4	7	3
August	0.1	0.1	0.1	0.1	30.0	28.0	···	30.0	6	3	8	4
September	···	0.1	0.1	0.1	···	35.5	50.0	···	···	7	9	11
October	0.1	0.1	0.1	0.1	50.0	49.9	66.7	33.3	3	7	11	12
November	0.1	0.1	0.1	0.1	72.2	75.0	···	···	2	5	10	14
December	0.2	0.2	0.1	0.1	70.3	80.0	83.3	···	5	2	9	12

[a] Viability test conducted only when more than two urediniospores were trapped on a day. Figures are the mean of 4 wk. Spores with germ tube at least 3 μm long were considered germinated and viable.
[b] Spore sampler not operational.

University of Minnesota, St. Paul, for race identification. In another experiment, McNair 1003 was planted in 8-cm-diameter pots in an air-conditioned greenhouse. At growth stage (GS) 4 of Feeke's scale (14), 50 plants were exposed for 2 days in a field at the Ben Hur Research Station. The plants were then transferred to the greenhouse and incubated initially in a dew chamber for 16 hr at 18 C and, subsequently, on greenhouse benches at 21 C for 10 days. Unexposed plants were incubated in a similar manner to serve as controls. The number of rusted plants and the number of uredinia on rusted plants were counted.

Collateral hosts. Rust was observed on *Hordeum pusillum* Nutt. and *Lolium multiflorum* Lam. at BR during the 1986 and 1987 wheat growing seasons. Infected plants were uprooted, transplanted into pots, and maintained in the greenhouse. The size and color of 100 randomly selected urediniospores of the rust on grasses and leaf rust of wheat were determined. To test the pathogenicity of rusts from the two grasses on wheat and vice versa, leaf blades of all plants to be inoculated were gently rubbed with a cotton swab to remove wax coating. An aqueous suspension of urediniospores (about 10^6/ml) from the grasses was inoculated to 10 McNair 1003 seedlings at GS 4, and wheat leaf rust urediniospores were inoculated to 10 plants of each grass. The inoculated plants were incubated in a dew chamber at 18 C for 16–18 hr, followed by 10 days in the greenhouse at 21 C. Observations on the presence or absence of leaf rust on inoculated plants were made 15 days after inoculation. This experiment was repeated three times.

Field survey during December 1986 and 1987. Field surveys were conducted in two fields of leaf rust susceptible McNair 1003 at Alex and BR during mid-December of 1986 and 1987. The surveyed fields measured 500 × 200 m at Alex and 150 × 60 m at BR. Seedlings were at GS 4 and GS 3 at Alex and BR, respectively. The field at BR was observed at 4-day intervals from seedling emergence for the onset of leaf rust. A diagonal method of field sampling was employed with 20 1-m^2 plots in 1986 and row plots 1 m long in 1987, observed to determine the leaf rust incidence in each plot, the number of leaves infected on each seedling, and secondary pustule occurrence. Lesions on five randomly selected seedlings from each plot were measured using a microscope with an ocular micrometer at ×160.

The time of infection was determined using the method of Eversmeyer et al (9), which takes into consideration the effective accumulated temperature and the corresponding length of the incubation period. An alternative method of deduction, using the initial date the disease was observed on the uppermost leaf and the date of emergence of the first uninfected leaf, was used to confirm the time of infection. The number of spores sampled by the Kramer-Collins 7-day sampler was also consulted for dramatic changes in the number of spores trapped per day.

RESULTS

Spore trapping. At BR, the highest number of urediniospores trapped per cubic meter of air per day was 2.6 in May 1986, and 74.9 in April 1987. The least number of urediniospores trapped at BR was 0.1/m^3 of air per day during August–November in both years (Table 1). At BC, the highest number of spores trapped in 1986 was 0.1, and no spores were trapped during March 1986. In 1987, the highest number of spores trapped was in April and the least was during January–February and July–December (Table 1). Spore numbers were low in BC during February–April 1987 compared with the spore numbers in BR (Table 1).

The percent viability of the trapped urediniospores was highest during November 1986 and February 1987 at BR, and December 1986 and March 1987 at BC. Viability ranged between 27 and 32% during May–August 1986, and 28 and 37% during June–September 1987 at BR. Viability was least in BC in July 1986 and August 1987 (Table 1).

Viability of urediniospores was significantly correlated inversely with ambient temperature at both locations ($r = -0.81$, $P = 0.0001$ at BR and

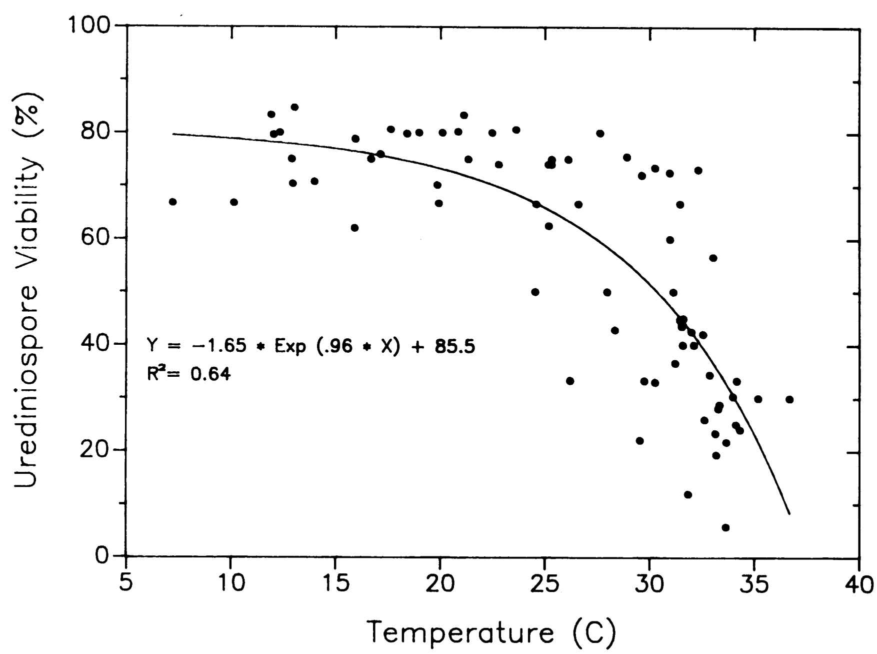

Fig. 2. Relationship between the percentage of urediniospore viability and mean weekly maximum temperature for Baton Rouge and Bossier City during the years 1986 and 1987.

Table 2. Development of *Puccinia recondita* f. sp. *tritici* on susceptible cultivar McNair 1003, planted at 14- to 20-day intervals during 1986 and 1987 summer seasons in a field at Baton Rouge, LA

	Leaf rust appeared[a]		No. of days rust persisted[b]		Incidence[c] (%)		Severity[d] (%)	
Planted	1986	1987	1986	1987	1986	1987	1986	1987
1 May	15 May	···	82	0	100	0	60	0
18 May	6 July	···	15	0	40	0	10	0
3 June	···[e]	18 June	0	74	0	90	0	35
18 June	···	15 July	0	68	0	64	0	15
3 July	···	29 July	0	20	0	34	0	2
18 July	···	···	0	0	0	0	0	0
3 Aug.	4 Oct.	···	>130	0	100	0	60	0
18 Aug.	17 Nov.	···	>85	0	100	0	30	0
3 Sept.	24 Nov.	26 Oct.	>75	>86	55	27	20	1
18 Sept.	24 Nov.	26 Oct.	>75	>86	10	25	2	1

[a] Plots observed at 4-day intervals for the presence of leaf rust.
[b] Number of days leaf rust persisted in the plots on living plants.
[c] Incidence scored on the date leaf rust appeared. Based on one plot for each date of planting.
[d] Leaf rust severity scored 10 days after it appeared, using the modified Cobb's scale.
[e] Leaf rust did not appear in these plantings.

$r = -0.59$, $P = 0.0003$ at BC). The data fit the exponential decay regression model with a significant $R^2 = 0.64$, $P = 0.01$ (Fig. 2). The optimum range of temperature for high viability was from 12 to 27 C (Fig. 2).

The number of consecutive days that no urediniospores were trapped varied from 0 to 7 in both years at BR, and from 2 to 31 in 1986 and 3 to 14 in 1987 at BC. The number of consecutive days that no urediniospores were trapped was least from February to May at BR in both years.

Field experiments at BR. Leaf rust appeared in microplots of McNair 1003 seedlings planted in May, August, and September 1986. Leaf rust also appeared in McNair 1003 seedlings planted in June, on 3 July, and in September 1987 (Table 2).

Leaf rust that appeared on 15 May 1986 and 18 June 1987 (Table 2) survived summer temperatures in the range of 33–37 C for 82 and 74 days, respectively. Leaf rust on McNair 1003 planted in August 1986 and September 1987 persisted for more than 130 and 86 days, respectively (Table 2), and continued well into the early stages of the wheat growing season. The incidence and severity in 1986 varied from 0 to 100% and 0 to 60%, respectively, and in 1987, incidence ranged from 0 to 90% and severity from 0 to 35% (Table 2). Leaf rust isolates sent to the Cereal Rust Laboratory were identified as race UN 2 with a phenotype of *p* 3,11 in 1986 and *p* 3,10 in 1987. The former (*p* 3,11) is a race frequently observed wherever soft red winter wheat is grown.

Leaf rust appeared on McNair 1003 in all the treatments exposed in the field from May to October 1986 and June to September 1987 (Table 3). Rust incidence was low in plants exposed in July 1987. The incidence varied from 25 to 100% in 1986 and 12 to 100% in 1987 (Table 3). The percentage of infected leaves (within-plant incidence) was 3–20% in 1986 and 5–14% in 1987 (Table 3). The number of uredinia tended to be least during August 1986 and July 1987. Severity was low in all treatments (Table 3). Urediniospores were trapped on many days when seedlings were exposed. None of the unexposed seedlings maintained as checks developed leaf rust (Table 3).

Collateral hosts. The urediniospores from all three sampled hosts were brown and round. Spores from *H. pusillum* and *L. multiflorum* measured 20.7–29.9 μm and 18.0–30.0 μm, respectively, whereas urediniospores from *P. r.* f. sp. *tritici* on wheat were 20.7–29.9 μm. In inoculation experiments, urediniospores from the two grasses failed to infect wheat, and vice versa.

Field survey during mid-December 1986 and 1987. No leaf rust was observed on McNair 1003 wheat seeded in mid-October until mid-December 1986 and 1987 at BR. Growth stage of the surveyed wheat was GS 3 in BR and GS 4 at Alex both years (Table 4). The plot rust incidence ranged from 60 to 100% in 1986 and from 2.4 to 15.4% in 1987 at Alex, and varied between 50–100% in 1986 and 2.1–12.5% in 1987 at BR (Table 4). The percent infected leaves in the seedlings in 1986 was 17.2–57.1% at Alex and 17.2–60% at BR. In 1987, the percentage of infected leaves at Alex and BR was 14.3–50% and 42.8–57.5%, respectively (Table 4). The initial infections were similar in age and position on the wheat seedlings. The position of the uppermost infected leaves in plants was uniform throughout the plots at each location in both years, and secondary pustules were absent on all plants.

Both deduction methods determined the date of inoculum arrival and possible period of infection as 23–25 November 1986 and 16–18 November 1987. Rainfall occurred during the indicated infection periods at both locations each year (Fig. 3). Low numbers of urediniospores were trapped during 21–25 November 1986 and 16–18 November 1987 (Table 1).

DISCUSSION

The presence of viable leaf rust urediniospores in Louisiana was confirmed by spore sampling. The degree of the viability of urediniospores of *P. recondita* was associated with the ambient maximum temperature prevalent in Louisiana.

The germination of urediniospores trapped in summer months (Table 1), the initiation of leaf rust on wheat sown in summer (Table 2), and the development of leaf rust on wheat seedlings exposed during summer and incubated in the greenhouse (Table 3) indicate that the urediniospores of *P. recondita* trapped during summer months were viable. However, rust severity was low on the exposed seedlings and did not increase on summer-sown wheat plants during summer. It is interesting to note that viable inoculum was present during the summer months when the temperatures were usually more than 32 C. In a similar study, Eversmeyer et al (11) also reported the occurrence of *P. recondita* uredinia on both early planted and late-planted (August–October) wheat in Kansas.

Temperatures above 32 C have been reported to be suboptimal for urediniospore production (26) and viability (8). We observed the lowest levels of urediniospore viability during months when the maximum temperatures were above 32 C. The urediniospores of *P. recondita* have a wide range on either side

Table 3. Wheat leaf rust incidence on cultivar McNair 1003 plants at Feeke's growth stage 4 exposed for 2 days during May–October 1986, and incubated in a dew chamber for 16 hr followed by incubation on benches in an air-conditioned greenouse at Baton Rouge, LA

	Leaf rust incidence (%)		Leaves per plant infected[a] (%)		Mean no. of uredinia per plant[a]		Mean severity[a] (%)		Mean no. of spores per cubic meter of air on days of exposure	
Exposed	1986	1987	1986	1987	1986	1987	1986	1987	1986	1987
3 May	75.0	…[b]	15.5	…	21.2	…	<5	…	0.0	…
18 May	100.0	…	15.8	…	27.9	…	<5	…	0.4	…
3 June	62.5	100.0	4.3	13.9	1.6	4.5	<1	<1	1.0	…
18 June	85.7	25.0	11.0	11.2	20.8	2.0	<2	<1	1.3	0.2
3 July	37.5	25.0	10.7	7.9	6.3	3.5	<2	<1	0.0	0.1
18 July	75.0	12.5	3.3	5.0	1.5	1.0	<1	<1	1.1	0.0
3 Aug.	50.0	50.0	3.1	7.0	1.0	1.7	<1	<1	0.1	0.1
18 Aug.	50.0	37.5	5.1	8.9	1.0	4.0	<1	<1	0.0	0.1
3 Sept.	…	37.5	…	10.2	…	2.7	…	<1	…	0.0
18 Sept.	25.0	50.0	8.6	12.2	2.5	3.7	<1	<1	0.0	1.1
4 Oct.	50.0	…	7.9	…	2.5	…	<1	…	0.0	…
18 Oct.	100.0	…	19.8	…	13.4	…	<2	…	0.2	…
Check	0.0	0.0	0.0	0.0	0.0	0.0	0			

[a] Mean of 50 plants.
[b] Sampler nonfunctional; treatments not included.

of the optimum temperature (20 C) for maximum viability, with a rapid reduction in the viability at temperatures above 32 C (Fig. 2). This is similar to the relationship between the leaf rust fungal growth and temperature (19). The deviation from the predicted value (Fig. 2) could possibly be due to the delayed viability tests in some weeks. Eversmeyer et al (10) reported that the viability of urediniospores trapped during the summer months in the Great Plains varied from 33 to 81%. Viability of the trapped urediniospores during summer in Louisiana was in the range from 11.5 to 42.5%. Therefore, conditions in Louisiana may not prevent leaf rust from surviving during summer months.

Greatest urediniospore concentration and highest viability in the Great Plains was observed during the active epidemic development (10). Our results also indicate that the highest spore concentration and viability occur during the active epidemic phase. In 1986, the spore trap at BR was located in an area used for fungicidal screening trials. Therefore, the lowest numbers of urediniospores were probably due to low disease incidence in sprayed plots.

Leaf rust is reported to survive on dry wheat foliage (30), residual wheat, and volunteer wheat plants (5,6), which can act as green bridges between seasons (20). Numerous field surveys during summer months showed that volunteer wheat plants in Louisiana are rare and, as a result, volunteer plants would probably not be a significant source of inoculum. However, in Mexico, oversummering of leaf rust on volunteer wheat plants in 1976 provided abundant inoculum to cause severe leaf rust epidemics in large areas planted with the susceptible wheat cultivar, Jupateco 73 (6). Volunteer wheat plants may, therefore, become a significant source of leaf rust inoculum when they survive in large numbers. In Louisiana, rarely do the areas planted with wheat remain untilled. Soybean crop usually follows wheat crop, thereby reducing the chances of volunteer wheat growth and survival. The number of urediniospores detected in air is low in summer and further studies are needed to elucidate the source(s) of the urediniospores trapped during this period and to explore the movement of inoculum from the neighboring states.

Both grasses used in the study are annuals and did not develop leaf rust in repeated controlled inoculations with *P. r.* f. sp. *tritici*. Thus, it appears that they do not function in the disease cycle. Leaf rust has also been observed on *Aegilops cylindrica* Host. in many states in the United States (D. L. Long, *unpublished data*). In Louisiana, however, *A. cylindrica* does not occur, and is not, therefore, a source for urediniospore survival.

In Louisiana, appearance of leaf rust during the wheat growing season varies from early December to early February. In December of 1986 and 1987, leaf rust suddenly appeared over a large area. This suggests the possibility of an exogenous source of initial inoculum. Occurrence of rainfall during the indicated infection period (Fig. 3) and the characteristics of the disease resulting from exogenous inoculum (19), such as uniformity of the position of infections on wheat seedlings, uniformity in the size of pustules (Table 4), and the absence of secondary pustules at both locations each year, are circumstantial evidence suggesting that rain-washed urediniospores were probably responsible for infection. Further, the similarity of events at both locations seems to indicate that infection at the locations occurred at or about the same time. Similar observations on stem rust were made by Rowell and Roelfs (21). The spore traps failed to detect an increase in the urediniospores in air probably because of scrubbing of urediniospores by rain from air during the deposition process.

Eversmeyer et al (11) compared the pathogenicity of overwintering leaf rust inoculum and airborne inoculum deposited on plots in Kansas and concluded that the overwintering inoculum may cause higher yield losses than the airborne inoculum.

It is possible, therefore, that in years when exodemic inoculum is present the disease appears early in the wheat growing season. In the absence of the exodemic inoculum the local viable inoculum may build up on susceptible wheat sown in September for forage purposes. This may provide the initial inoculum for the winter wheat cultivars and perhaps explains why there is a delay in leaf rust appearance in some years in Louisiana.

Table 4. Wheat leaf rust incidence on cultivar McNair 1003 at Feeke's growth stage 3–4 during December at Alexandria and Baton Rouge in Louisiana

		Incidence (%)				Pustule diameter (mm)[b]	
		Plot[a]		Leaves per plant infected (%)			
Plot	Location	1986	1987	1986	1987	1986	1987
1	Alexandria	87.0	6.1	46.7	42.8	0.03	0.03
	Baton Rouge	100.0	7.7	50.0	42.8	0.09	0.10
2	Alexandria	90.0	12.5	45.0	28.6	0.13	0.10
	Baton Rouge	100.0	7.3	50.0	42.8	0.13	0.12
3	Alexandria	100.0	6.2	36.0	42.8	0.03	0.06
	Baton Rouge	100.0	7.1	50.0	42.8	0.10	0.08
4	Alexandria	86.0	3.5	33.0	28.6	0.14	0.03
	Baton Rouge	92.0	3.8	40.0	42.8	0.10	0.10
5	Alexandria	100.0	8.7	42.0	33.3	0.09	0.12
	Baton Rouge	80.0	7.3	43.3	57.1	0.11	0.11
6	Alexandria	60.0	6.6	17.2	50.0	0.13	0.12
	Baton Rouge	100.0	5.9	60.0	57.5	0.10	0.11
7	Alexandria	100.0	3.4	40.0	28.5	0.23	0.15
	Baton Rouge	65.0	7.9	17.2	42.8	0.12	0.10
8	Alexandria	100.0	6.1	40.0	42.8	0.18	0.05
	Baton Rouge	75.0	4.8	46.7	42.8	0.21	0.09
9	Alexandria	100.0	5.6	40.0	42.8	0.12	0.12
	Baton Rouge	80.0	6.5	30.0	49.9	0.13	0.08
10	Alexandria	100.0	2.4	40.0	42.8	0.19	0.04
	Baton Rouge	55.0	12.5	26.7	49.9	0.25	0.09
11	Alexandria	100.0	7.1	39.9	42.8	0.19	0.11
	Baton Rouge	85.0	7.7	20.0	49.9	0.28	0.08
12	Alexandria	100.0	6.1	57.1	14.3	0.18	0.09
	Baton Rouge	55.0	2.1	26.7	49.9	0.34	0.06
13	Alexandria	100.0	6.2	48.5	14.3	0.24	0.11
	Baton Rouge	50.0	6.8	50.0	49.9	0.33	0.08
14	Alexandria	100.0	6.4	48.5	50.0	0.20	0.13
	Baton Rouge	50.0	4.9	33.3	42.8	0.18	0.11
15	Alexandria	100.0	10.9	39.9	28.6	0.23	0.07
	Baton Rouge	50.0	6.5	60.0	42.8	0.34	0.10
16	Alexandria	100.0	9.7	57.1	28.6	0.03	0.14
	Baton Rouge	78.0	4.0	24.0	57.5	0.22	0.09
17	Alexandria	100.0	7.6	48.5	31.4	0.13	0.12
	Baton Rouge	82.0	3.8	28.5	57.5	0.18	0.11
18	Alexandria	92.1	15.4	45.2	42.8	0.10	0.10
	Baton Rouge	75.0	7.3	46.1	57.5	0.22	0.08
19	Alexandria	95.0	12.5	47.8	40.4	0.12	0.21
	Baton Rouge	68.0	4.3	26.4	57.5	0.21	0.08
20	Alexandria	90.0	9.7	48.5	35.5	0.13	0.08
	Baton Rouge	76.8	2.5	33.2	42.8	0.19	0.12

[a] Each plot contained >180 seedlings in 1986 and >80 seedlings in 1987.
[b] Mean of 20 pustules.

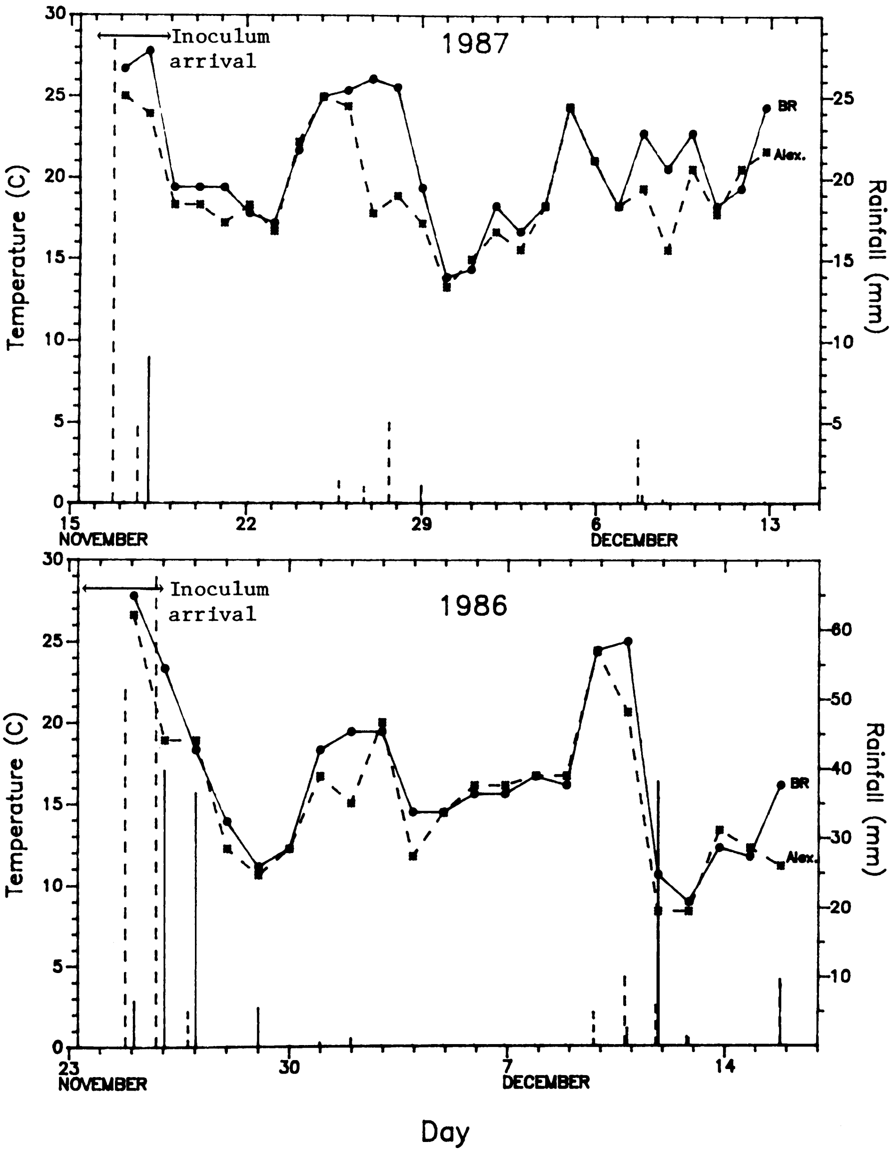

Fig. 3. Daily rainfall (vertical lines) and temperature (horizontal curves) for the period of 24 November–15 December 1986, and 16 November–12 December 1987, and the possible dates of inoculum arrival for Alexandria (broken lines) and Baton Rouge (solid lines).

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