Production of Sori and Dispersal of Teliospores of *Ustilago scitaminea* in Louisiana

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Approved for publication by the director of the Louisiana Agricultural Experiment Station as manuscript no. 90-38-4355.

The authors gratefully acknowledge P. Bergeron, S. Bibbins, D. Bourg, L. B. Grelen, and C. Tolbert for technical assistance; and L. B. Grelen for preparation of figures.

Accepted for publication 17 January 1991 (submitted for electronic processing).

ABSTRACT

Hoy, J. W., Grisham, M. P., and Chao, C. P. 1991. Production of sori and dispersal of teliospores of *Ustilago scitaminea* in Louisiana. Phytopathology 81:574-579.

Production of sori by *Ustilago scitaminea* was monitored during two growing seasons in smut-inoculated sugarcane clones in Louisiana. The production of sori began during May, increased sharply during June, and continued at a lower rate through October. Smaller peaks in sorus production occurred in highly susceptible clones during August and October. Secondary infection cycles were detected in many highly and moderately susceptible clones and a few resistant clones. Sorus production began later and fewer sori were produced by resistant clones. Teliospore concentrations per cubic meter of air per day above the canopy increased with sorus production during June. Lower aerial spore concentrations during July and August were associated with increased precipitation. Aerial spore concentrations were reduced on average by 53 and 99% at distances of 15 and 135 m from the field. Mean spore concentrations increased during the afternoon and were highest from 5 to 7 p.m. Increasing spore concentrations were associated with increasing temperature and wind speed and decreasing relative humidity. The numbers of teliospores deposited on the soil within the crop were highest below and adjacent to sori, and then decreased rapidly with increasing distance.

Smut, caused by *Ustilago scitaminea* Syd., is an economically important disease in many regions where sugarcane, interspecific hybrids of *Saccharum* L., is grown (2). Sugarcane smut was first observed in Louisiana in 1981 (13), and the disease spread rapidly to all the sugarcane-growing areas of the state (12).

The characteristic symptom of this culmicolous smut is the production of a whip-like sorus at the apex of infected shoots (Fig. 1). Infected shoots are typically small in diameter and often extend above the surrounding canopy (2,21). Teliospores are produced and passively released from a hymenium that covers a core of parenchyma and fibrous tissues of plant origin (21).

The latent period (time between bud or young shoot infection and sorus emergence) differs between cultivars and is affected by environmental conditions, particularly temperature (3). Latent period lengths, ranging from 1.5 to 8.0 mo, have been reported (1,3,4,16,20,21). The production of sori also is affected by cultivar and environmental conditions (1,3,9,16,17,21,22). Individual sori may release as many as 8×10^6 spores per day over a period of 1–3 mo (21). In India, peaks in teliospore concentrations detected above the canopy coincided with the initial production of sori in July and August, and the expression of secondary infections later during October (20). Teliospores were detected as far as 40 m from an inoculum source.

Sugarcane is grown at the northern limit of its cultivation range in Louisiana. Freezing temperatures typically kill above-ground plant growth several times during the winter, and the growing season lasts only 8–9 mo (14). The severity of winter and the short length of the growing season are potential limiting factors for smut development. Smut infection levels in commercial fields of moderately susceptible cultivars generally continue to be lower than those observed in inoculation tests. However, infection levels sufficient to reduce yields by up to 40% (12) have been observed, and high infection levels are becoming more common. Adverse effects of severe winter conditions on disease spread and increase have been documented (9,10). Disease gradients are steep, and high rates of disease increase have not been observed (9). The extent to which secondary infections are expressed during the growing season is uncertain.

Fig. 1. Sori of *Ustilago scitaminea* produced at apex of infected sugarcane stalks.

Research to determine the epidemiology of smut in Louisiana, to assess the threat to the sugarcane industry, and to develop disease management strategies that can be used by farmers to minimize losses to smut was undertaken. In the studies reported here, seasonal patterns of smut sorus production in Louisiana and teliospore dispersal and deposition characteristics were determined. Preliminary results have been reported (11).

MATERIALS AND METHODS

Monitoring sorus production. Sorus production was monitored in smut inoculation tests conducted as part of the sugarcane breeding program during the 1985 and 1986 growing seasons. Experiments were planted in an area isolated from commercial sugarcane production at the Louisiana Agricultural Experiment Station, Citrus Experiment Station, in Port Sulphur, LA. Whole stalks, approximately 1.5 m in length, were dip-inoculated in a suspension containing 5×10^6 teliospores per milliliter for 10 min. An experiment replicate consisted of eight stalks planted in a single-row plot, 6.7 m in length. During September 1984, three replicates of four commercial cultivars and two replicates of 67 breeding lines were planted. During October 1984, three replicates of three cultivars and single replicates of 134 breeding lines were planted. In addition, three noninoculated replicates of 13 clones (three cultivars and 10 breeding lines) also were planted to study the occurrence of secondary infections.

During October 1985, three replicates of four commercial cultivars, two replicates of 76 breeding lines, and single replicates of 126 breeding lines were inoculated and planted as described previously at the Citrus Experiment Station. Three noninoculated replicates of 12 clones (four cultivars and eight breeding lines) also were planted.

Sori were counted and tagged at 1-wk intervals until September and at 2-wk intervals until November during the 1985 growing season. Sori were counted at 1-mo intervals during the 1986 growing season. Replicated clones were separated into resistant (R), moderately susceptible (MS), and highly susceptible (HS) categories on the basis of the number of sori produced by the end of July. Clones producing eight or fewer sori per replicate were rated as resistant. Clones producing nine to 50 sori and >50 sori were rated as moderately susceptible and highly susceptible, respectively.

Monitoring teliospore dispersal. Teliospores of *U. scitaminea* were collected in three Kramer-Collins, 7-day, drum-spore samplers (G. R. Manufacturing Co., Manhattan, KS) during the 1985 growing season. Two samplers were operated by 12-V batteries for 2 min every hour with PT-1-3 Programmable Timers (G. R. Manufacturing Co.). One sampler was placed near the center of the 96- × 36-m test field at a height of 2 m. Once the crop canopy height approached 2 m, the sampler height was increased to 4 m. The second battery-operated sampler was placed 15 m outside the field at a height of 4 m. A third sampler was operated by a 110-V power source continuously, 135 m outside the field at a height of 4 m. All three spore traps sampled air at a rate of 30 L/min.

Sampler tapes were cut into seven, 24-h segments and placed on microscope slides. Teliospores were counted in four lengthwise passes (10% of the total area) at ×40 with a compound microscope. Teliospore concentrations per cubic meter of air were calculated for 24-h periods and 2-h intervals during 24-h periods. Spore concentrations above the canopy were determined for 31 days in which no rainfall occurred. Spore concentrations at 15 and 135 m were calculated for 13 and 21 days, respectively, in which no rainfall occurred. Precipitation, relative humidity, temperature, and wind speed data were obtained from a weather station located at the Citrus Experiment Station.

Teliospore counts for 10 days from each of the three samplers were separated into groups of single spores and spore clusters of 2–5, 6–25, and >25 spores, and the frequencies at each distance were compared.

Monitoring teliospore disposition. Teliospore deposition was studied in commercial fields with low levels of natural infection. Silicone jelly-coated microscope slides were placed at ground level beneath a smut-infected plant with emerged sori and at the base of plants in adjacent rows at distances of 1.8, 3.6, 5.4, 7.2, 9.0, 10.8, 12.6, and 14.4 m across rows in two directions, perpendicular to the row containing the smut-infected plants. Additional slides were placed at 1.8 and 3.6 m in two directions in the same row as the spore source. Thirteen experiments were conducted during June, July, and August 1986. The number of distance intervals in different experiments ranged from three to eight.

Slides were left in the field for 1 wk and then were collected; teliospores were counted in four 0.09- or 0.20-cm^2 areas at ×40 with a compound microscope. Numbers of teliospores deposited per square centimeter per day were calculated from the counted area mean for each slide. In addition, the frequencies of occurrence of spore clusters of different sizes were determined for distance intervals to 7.2 m. The frequencies of occurrence of single spores and clusters of 2–5, 6–25, and >25 spores were averaged for eight gradients across the rows.

A spore deposition gradient for all experiments was determined. Spore counts on slides beneath sori were considered to be 100%, and counts from slides at various distances from the spore source were converted to a percentage of the number deposited beneath the sori. The percentage of depositions for each distance for all gradients across rows were averaged to determine the teliospore deposition gradient.

The relationship of actual numbers of teliospores deposited to distance from a spore source was examined for 18 gradients by using the power law ($Y = aD^{-b}$) (8) and exponential ($Y = ae^{-bD}$) (7) models, in which Y = spores deposited; D = distance; and a and b are parameters.

RESULTS

Production of sori. Smut incidence was higher in the cultivars and those breeding lines included in both experiments in 1985 than in the experiment in 1986. However, the temporal patterns of production of sori were similar in both years. The data for the 1985 experiments are presented.

The first smut sorus was observed on 9 May 1985. Total sorus production by all clones increased sharply during June, decreased during July, continued at a lower level during August and September, increased again during October, and ceased during November (Fig. 2).

Mean dates on which sori were first observed for HS, MS, and R clones were 23 May, 30 May, and 13 June, respectively. HS and MS clones showed sharp increases in sorus production

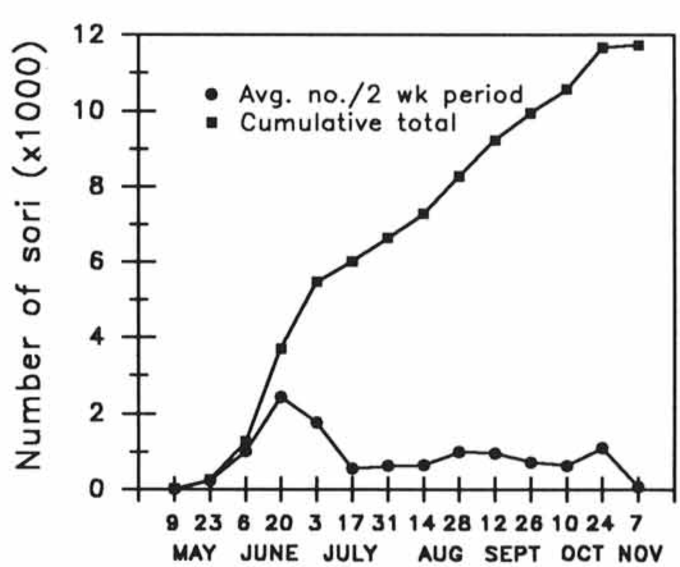

Fig. 2. Cumulative total and 2-wk average numbers of sori caused by *Ustilago scitaminea* that were produced by infected sugarcane plants during the 1985 growing season.

during June (Fig. 3). Smaller peaks in production occurred in HS clones during August and October. Low numbers of sori were produced by R clones, and most sori were produced during June and early July (Fig. 3). Total sorus production for the season and the percentage of sori produced by 24 July for clones in each resistance category are presented in Table 1.

Disease progress curves based on the mean number of sori produced per plot were plotted for each clone. Sori continued to be produced by all HS clones after the initial sharp increase, and 54% of the clones showed strong bimodal disease progress curves. Some MS clones (24%) showed little or no disease increase after the initial sori were produced. Strongly bimodal disease progress curves were detected in 53% of the MS clones. Bimodal disease progress curves were detected in only 14% of the R clones.

Evidence for secondary infections was indicated by the production of sori in noninoculated plots of five of six HS clones (83%), three of five MS clones (60%), and none of two R clones. The percentages of sori produced in all noninoculated plots each month were 0, 2, 1, 5, 36, and 56% for May, June, July, August, September, and October, respectively.

Teliospore aerial concentrations. Concentrations of teliospores per cubic meter of air per day determined from spore-trap counts were variable (Fig. 4). Spore concentrations increased as sorus production increased during June (Fig. 2). The maximum number of teliospores per cubic meter of air per day, 34,938, was detected on 26 June. Lower spore concentrations were detected from July to September. Precipitation increased during July and August compared with levels in May and June (Fig. 4).

At a distance of 15 m from the field, the mean teliospore concentration per cubic meter of air per day was 1,792 ± 266 (standard error) and ranged from 625 to 3,172. The percentage of reduction in spore concentration compared with the concentration above the canopy on the same days ranged from 12 to 93% with a mean of 53 ± 7%. At a distance of 135 m, the mean spore concentration per cubic meter of air per day was 25 ± 7 and ranged from 1 to 107. The percentage of reduction in spore concentration compared with spore numbers above the canopy ranged from 94.72 to 99.99% with a mean of 98.99 ± 0.33%.

The frequencies of dispersal units of *U. scitaminea*, consisting of teliospore clusters of increasing size, decreased with distance from a spore source (Table 2). The frequencies of occurrence for spore clusters of all sizes were 17.0, 5.8, and 8.8%, respectively, above, 15, and 135 m from the spore source.

Teliospore concentrations for 2-h intervals during individual days were variable; however, the 2-h interval means indicated that spore concentrations in the air increase during the afternoon and are highest during the evening from 5 to 7 p.m. (Fig. 5). Comparisons with weather data suggested that increases in spore concentrations per cubic meter of air were associated with increasing temperature and wind speed and decreasing relative humidity (Fig. 5).

Teliospore deposition. The average numbers of teliospores deposited per square centimeter per day after 1 wk at soil level were highest directly below and at the bases of plants in rows adjacent to plants containing smut sori. Deposited spore numbers decreased rapidly with increasing distance from a spore point source (Fig. 6). Numbers of deposited spores determined in experiments conducted at different times during the growing season were variable. The mean spore number per square centimeter per day in 13 experiments under smut sori and at distances of 1.8, 3.6, 5.4, 7.2, 9.0, 10.8, and 12.6 m across rows were 678 ± 248, 1,031 ± 749, 293 ± 159, 132 ± 57, 108 ± 46, 52 ± 11, 53 ± 17, and 24 ± 2, respectively. The average number of spores deposited per square centimeter per day was higher at distances of 1.8 and 3.6 m than directly beneath smut sori in three of 22 (14%) gradients. The occurrence of strong coastal winds during

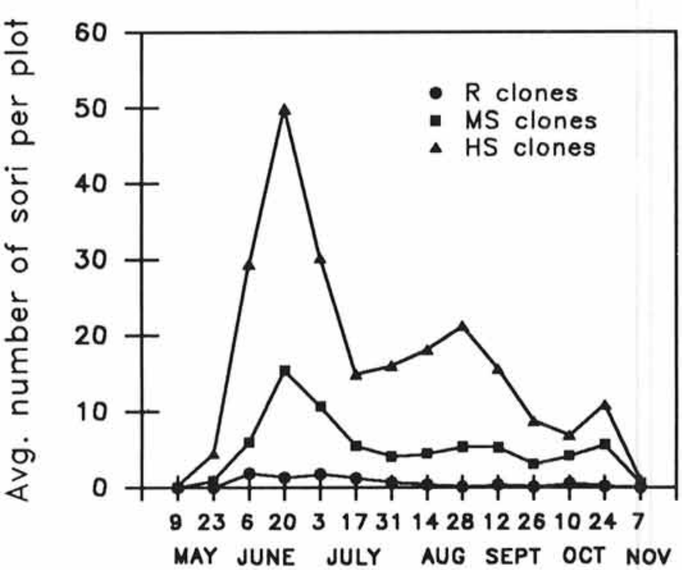

Fig. 3. Average numbers of sori of *Ustilago scitaminea* produced every 2 wk in a single-row plot, 6.7 m in length, of sugarcane clones rated as resistant (R), moderately susceptible (MS), or highly susceptible (HS) to smut.

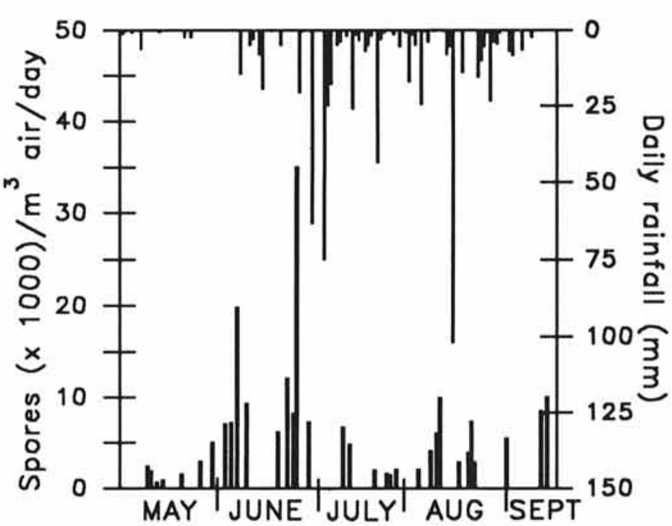

Fig. 4. Smut teliospore concentrations per cubic meter of air above the canopy of a sugarcane crop (0.4 ha) compared with daily rainfall data.

TABLE 1. Comparison of average numbers of sori of *Ustilago scitaminea* produced during the season and the percentage of sori produced by 24 July 1985 for sugarcane clones resistant (R), moderately susceptible (MS), or highly susceptible (HS) to smut

Resistance category	Number of clones	Number of sori produced per plot		Percentage of sori by 24 July	
		Mean	Range	Mean	Range
R	14	5	2–10	78	50–100
MS	38	38	10–79	66	29–98
HS	11	134	84–201	63	51–76

TABLE 2. Frequencies of dispersal units of *Ustilago scitaminea* containing different numbers of teliospores detected in spore samplers operated within a sugarcane field and at distances of 15 and 135 m from the field

Number of spores per dispersal unit	Dispersal unit means (%)		
	In field	15 m	135 m
1	83.1	94.2	91.2
2–5	14.5	4.8	6.5
6–25	2.1	0.8	2.3
26+	0.4	0.2	0.0

one experiment resulted in the deposition of high numbers of spores beneath the sori (3,413/cm^2/day) and at 1.8 m (16,720/cm^2/day) and 3.6 m (3,598/cm^2/day) downwind of the sori. The numbers of spores deposited at 1.8 and 3.6 m within the same row as sori were lower than at the same distances in gradients measured across rows. The mean numbers of spores deposited per square centimeter per day at 1.8 and 3.6 m within rows were 123 ± 19 and 74 ± 15, respectively. The frequencies of deposited dispersal units consisting of spore clusters decreased with increasing distance from a spore source (Table 3).

The power law model significantly fit the spore deposition data for 13 of 18 (72%) gradients, and the exponential model significantly fit the deposition data for 12 of 18 (67%) gradients (Table 4). The power law model explained slightly more experimental variation than the exponential model for 13 of 18 gradients (Table 4). Slopes for the deposition gradients determined by the models showed some variation and ranged from −0.67 to −2.31 and from −0.15 to −0.65 m for the power law and exponential models, respectively. Prevailing coastal winds occurred during the weeks of 21–28 May, 3–10 July, and 10–17 July. Downwind gradients were shallow in experiments 1 and 7 (Table 4), and spore numbers deposited 1.8 and 3.6 m downwind were higher than beneath sori in experiments 1, 6, and 7. Model fits to downwind gradients were nonsignificant.

DISCUSSION

In Louisiana, the increase of smut is limited when sugarcane growth and smut development are interrupted and then synchronized by the occurrence of winter. During the growing season, all fields are similar; plants in late-planted fields are in the same stage of growth as those planted early. Sugarcane tillering increases until July, then the number of shoots begins to decline. In one study (18), the average percentages of tillers produced by the end of April (before sorus emergence) were 32 and 72% for plant cane and ratoon crops, respectively. The average percentages for tillers produced by the end of June were 87 and 94%, respectively. In the studies reported here, high numbers of smut sori were not produced until June. As a result, many potential infection sites (germinating buds) escaped exposure to spores. The period of active growth is also short in Louisiana compared to tropical areas. The short growing season limits the number of infection cycles per season and the number of secondary infections expressed (sori produced).

Cooler temperatures have been shown to increase the length of the latent period and decrease the number of sori produced (3). In addition, increases in latent period for resistant compared with susceptible clones have been reported (1,3,16). In Louisiana, smut latent period and disease development were affected by an interaction between cool spring and fall temperatures and the level of cultivar resistance. The first emergence of sori occurred, on average, 2–3 wk later for R compared with MS and HS clones; however, differences in latent periods were most important in determining whether sori developed from secondary infections before the onset of cooler temperatures in the fall.

Differences in the maximum number of sori produced were evident between R, MS, and HS clones. These differences were due to increasingly greater numbers of infections and sori resulting from primary infections in R, MS, and HS clones; from continuing production of sori by infected plants at progressively higher rates by MS and HS clones; and from increasing levels of secondary infections occurring in MS and HS clones. Disease progress curves were not consistent for clones in any of the three resistance

Fig. 5. Means and standard errors of **A,** wind speed (m/sec); **B,** temperature; **C,** relative humidity; and **D,** smut teliospore concentrations per cubic meter of air during 2-h intervals for 33 days.

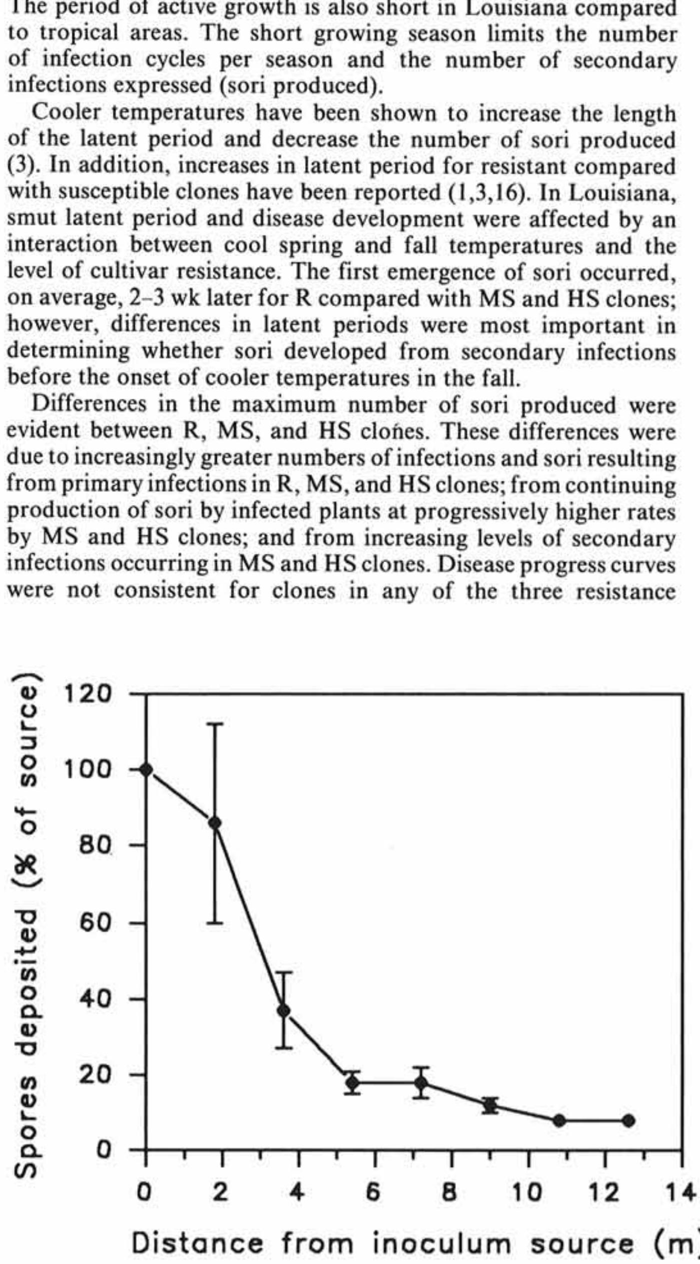

Fig. 6. Average smut teliospore deposition gradient at the soil surface within a sugarcane crop determined from 22 gradients. Data points are means, with standard error bars, for percentages of the number of spores deposited per square centimeter per day below smut sori that were detected at increasing distances from a spore point source.

TABLE 3. Frequencies of dispersal units of *Ustilago scitaminea* containing different numbers of teliospores deposited at ground level five distances from an inoculum source

Distance from sori (m)	Frequency means of size categories of dispersal units (%)				Frequency ranges for single-spore dispersal units (%)
	Single	2–5	6–25	>25	
0.0	76.0	20.2	2.6	0.8	63–87
1.8	78.6	16.0	3.7	1.5	65–92
3.6	84.8	12.7	1.7	0.7	70–95
5.4	85.9	11.2	1.9	6.3	77–97
7.2	91.0	8.0	0.3	0.8	88–93

TABLE 4. Description of deposition gradients for teliospores of *Ustilago scitaminea* at ground level in sugarcane fields with the power law and exponential models

Experiment[a]	Dates	Distance (m)	Power law model[b] *b*	*a*	R^2	Exponential model *b*	*a*	R^2
1 x	21–28 May	7.2	−2.31	3.57	0.98**	−0.65	8.01	0.98**
y			−1.64	3.76	0.44	−0.30	9.06	0.53
2 x	18–25 June	7.2	−0.97	2.38	0.86**	−0.18	5.11	0.77**
3 x	18–25 June	10.8	−0.89	2.84	0.85**	−0.18	6.24	0.67*
y			−1.01	2.85	0.85**	−0.21	6.24	0.72*
4 x	25 June–2 July	7.2	−1.07	2.26	0.86*	−0.29	5.06	0.81*
y			−1.25	2.42	0.98**	−0.35	5.43	0.94**
5 x	26 June–3 July	9.0	−1.20	2.68	0.79*	−0.29	5.95	0.74*
6 x	3–10 July	7.2	−0.86	2.67	0.61	−0.27	6.18	0.74
7 x	3–10 July	9.0	−0.67	2.09	0.61	−0.16	4.65	0.52
y			−1.03	1.99	0.88**	−0.25	4.39	0.81*
8 x	10–17 July	9.0	−0.78	2.70	0.41	−0.23	6.24	0.56
9 x	10–17 July	9.0	−0.76	2.39	0.52	−0.15	5.20	0.34
y			−0.73	2.61	0.58*	−0.17	5.84	0.52
10 x	22–29 August	9.0	−0.97	2.68	0.76*	−0.26	5.70	0.98**
y			−1.13	2.51	0.94**	−0.28	5.60	0.92**
11 x	22–29 August	9.0	−1.14	2.75	0.94**	−0.29	6.15	0.92**
y			−1.21	2.74	0.94**	−0.30	6.03	0.88**

[a] Deposition gradients were determined after 7 days over various distances from an inoculum source in one direction only (x) or two directions (x and y) measured perpendicularly across rows.
[b] Parameters *a* and *b* represent deposition at the source and the change in deposition with distance, respectively, in each model. Coefficients of determination followed by one or two asterisks were significant at $P = 0.05$ or $P = 0.01$, respectively.

categories. Patterns of disease progress were highly variable for MS and HS clones. Secondary infection cycles were sometimes obscured by the continuous production of sori by infected plants. The continuous production of sori was observed in inoculated single plants of susceptible clones (G. T. A. Benda, *unpublished*), and secondary infection cycles were evident in single plants monitored in Florida (16,17). Variability in disease progress patterns among clones also has been noted in Barbados (22) and Florida (16,17). Of four models compared, the Von Bertalanffy-Richards model (19) gave the best fit to the smut increase data recorded for four clones in Florida (16,17).

Aerial teliospore concentrations increased as sorus production increased during June. Individual sori emerge continuously and release spores over a period of 1–3 mo (20,21), so the high numbers of spores would be anticipated to last several months. Instead, reduced spore concentrations were detected during July and August compared with June. The lower concentrations of teliospores were associated with increased levels of rainfall during these months. An inverse relationship between rainfall and aerial spore concentrations of *U. scitaminea* was detected previously in India (20).

A diurnal teliospore-release pattern, with peak spore release occurring from 10 to 12 a.m., was reported in India (20). The daily pattern of spore release in Louisiana was different. In this study, the highest concentrations of spores were detected during the late afternoon. One possible difference between conditions affecting teliospore release in India and Louisiana could be that overnight dew formation occurs regularly during the summer in Louisiana. Aerial spore numbers increased as temperatures and wind speed increased and relative humidity decreased during the day. These observed patterns would result in drying of smut sori and a pattern of spore release like the one observed.

Comparisons of aerial spore concentrations above the canopy with concentrations 15 and 135 m outside the source field indicate a steep spore dispersal gradient for *U. scitaminea*. The mean reduction in aerial spore concentration of 53% at 15 m was similar to reductions of 66 and 76% reported for distances of 10 and 20 m, respectively, in India (20).

A high proportion (83%) of the *U. scitaminea* dispersal units detected in the air and at the soil surface consisted of single spores. In comparison, spore clusters accounted for over 50% of the dispersal units of *Uromyces phaseoli* (5) and 60–80% of the dispersal units of *Erysiphe graminis* (15).

Both the power law and exponential models described teliospore deposition gradients of *U. scitaminea*. The goodness of fit was generally slightly better with the power law model. These results are similar to the findings of previous research of deposition gradients for fungi with small airborne spores (6). Determining the average number of spores deposited per day after 1 wk minimized the short-term effect of wind on the deposition gradients. However, gradients showed some variation between experiments and between directions in the same experiment. Downwind gradients during times of prevailing coastal winds were more shallow than upwind gradients, and model fits to downwind gradients were nonsignificant. A seasonal pattern of change in gradient slopes as the canopy developed was not detected.

Disease gradients determined previously for sugarcane smut in Louisiana (9) were affected by winter conditions and growing-season rainfall and were generally steeper than the teliospore deposition gradients reported here. Disease gradient slope means were -1.68 ± -0.16 and -0.36 ± -0.05 m for the power law and exponential models, respectively; whereas, deposition gradient slope means were -1.09 ± -0.09 and -0.27 ± -0.03 m, respectively.

LITERATURE CITED

1. Amorim, L., Cardoso, C. O. N., Ricci, A., and Barreto, J. N. 1986. Epidemiologia do carvao da cana-de-acucar. Semin. Technol. Agron., Centro Technol. Copersucar 3:208-214.
2. Antoine, R. 1961. Smut. Pages 327-354 in: Sugarcane Diseases of the World. Vol. 1. J. P. Martin, E. V. Abbott, and C. G. Hughes, eds. Elsevier Publishing Co., Amsterdam. 542 pp.
3. Bock, K. R. 1964. Studies on sugar-cane smut (*Ustilago scitaminea*) in Kenya. Trans. Br. Mycol. Soc. 47:403-407.
4. Dean, J. L. 1982. The effect of wounding and high-pressure spray inoculation on the smut reactions of sugarcane clones. Phytopathology 72:1023-1025.
5. Ferradino, F. J., and Aylor, D. E. 1987. Relative abundance and deposition gradients of clusters of urediniospores of *Uromyces phaseoli*. Phytopathology 77:107-111.
6. Fitt, B. D. L., Gregory, P. H., Todd, A. D., McCartney, H. A., and MacDonald, O. C. 1987. Spore dispersal and plant disease gradients: A comparison between two empirical models. J. Phytopathol. 118:227-242.
7. Frampton, V. L., Linn, M. B., and Hansing, E. D. 1942. The spread of virus diseases of the yellows type under field conditions. Phytopathology 32:799-808.

8. Gregory, P. H. 1968. Interpreting plant disease dispersal gradients. Annu. Rev. Phytopathol. 6:189-212.
9. Hoy, J. W., and Grisham, M. P. 1988. Spread and increase of sugarcane smut in Louisiana. Phytopathology 78:1371-1376.
10. Hoy, J. W., Grisham, M. P., and Benda, G. T. A. 1987. Effect of Louisiana growing conditions on the overwintering of smut-infected sugarcane. Sugar Cane 1987 (3):11-15.
11. Hoy, J. W., Grisham, M. P., and Chao, C. P. 1989. *Ustilago scitaminea* sorus production and teliospore dissemination and deposition in Louisiana. (Abstr.) Phytopathology 79:1218.
12. Hoy, J. W., Hollier, C. A., Fontenot, D. B., and Grelen, L. B. 1986. Incidence of sugarcane smut in Louisiana and its effect on yield. Plant Dis. 70:59-60.
13. Koike, H., Fontenot, D., Damann, K., and Schlub, R. 1981. Smut of sugarcane in Louisiana. Plant Dis. 65:1018.
14. Matherne, R. J., Breaux, R. D., and Millhollon, R. W. 1977. Culture of sugarcane for sugar production in the Mississippi delta. U.S. Dep. Agric., Agric. Handb. 417. 42 pp.
15. McCartney, H. A., and Bainbridge, A. 1987. Deposition of *Erysiphe graminis* conidia on a barley crop. I. Sedimentation and impaction. J. Phytopathol. 118:243-257.
16. Momol, M. T. 1986. Epidemiological studies of sugarcane smut. Ph.D. thesis. University of Florida, Gainesville. 71 pp.
17. Momol, M. T., Purdy, L. H., and Schmidt, R. A. 1990. Analysis of disease progress curves of sugar cane smut in Florida. Sugar Cane 1990 (1):8-9.
18. Ricaud, R., and Landry, G., Jr. 1976. Effects of rate of planting on yield and some yield components of sugarcane. La State Univ. Agric. Exp. Stn. Bull. 694. 28 pp.
19. Richards, J. J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.
20. Sreeramulu, T., and Vittal, B. P. R. 1972. Spore dispersal of the sugarcane smut (*Ustilago scitaminea*). Trans. Br. Mycol. Soc. 58:301-312.
21. Waller, J. M. 1969. Sugarcane smut (*Ustilago scitaminea*) in Kenya. I. Epidemiology. Trans. Br. Mycol. Soc. 52:139-151.
22. Whittle, A. M., and Walker, D. I. T. 1982. Interpretation of sugarcane smut susceptibility trials. Trop. Pest Manage. 28:228-237.