Oospores of Sclerospora sorghi in Soils of South Texas and Their Relationships to the Incidence of Downy Mildew in Grain Sorghum

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ABSTRACT

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Oospores of *Sclerospora sorghi* from soil were concentrated among silt particles following removal of most sand and clay particles from aqueous suspensions of soil by washing and sedimentation. Oospores were counted in aliquots of silt suspensions at ×25-50 magnification. An average of 97% of oospores added to soils at three densities were recovered. In three naturally-infested soils, oospores also were counted in pieces of organic debris collected on sieves and cleared in potassium hydroxide. At least 97% of oospores were free in soil 5 mo after harvest. Soil samples from 18 sorghum fields were assayed to determine the relation between densities of oospores of *S. sorghi* and incidence of downy mildew. Population densities of oospores ranged from 8-95/g soil and incidence of downy mildew was 1-53% in the field and 0-47% in sorghum seedlings grown in the soils in pots. Oospore densities were not significantly correlated with incidence of downy mildew in plants in the field ($r = 0.33$, 16 df) or in pots ($r = 0.45$, 16 df) because little or no disease developed in some soils with high oospore densities. However, ratios of infected plants in the field to oospore densities were significantly correlated ($r = 0.72$, 16 df) with clay contents of soils; the highest ratios occurred in soils with the least clay. These results indicate that incidence of downy mildew in sorghum seedlings in the field is related to oospore densities and soil texture.

Sclerospora sorghi Weston & Uppal is the causal agent of downy mildew of sorghum and corn. This disease, which is endemic in Asia, first appeared in North America in south Texas in 1961 (16) and has since spread north to the Ohio River valley (5). *Sorghum* spp. and corn are the only known hosts of *S. sorghi* in North America.

In the 1960's, nearly all sorghum cultivars grown in Texas were highly susceptible to *S. sorghi* (6), and losses caused by downy mildew were estimated to exceed $2.5 million in 1969 alone (3). Resistance was found in several grain sorghum lines and cultivars (7, 11, 18); resistant commercial hybrids were first grown in 1972 (4) and their use has since become widespread. This resistance has been stable, and the severity of downy mildew has since decreased in Texas. However, the disease still causes economic losses owing to the continued preference of many growers for high-yielding yellow endosperm cultivars of grain sorghum and for the traditionally popular commercial hybrids, both of which are predominantly susceptible.

Systemic infection of sorghum and corn seedlings is believed to result from infection of roots by oospores in soil. Oospores cause infection when incorporated into soil (1, 21) or coated on seed (1, 17). Oospores are also produced in large numbers in the leaves of infected plants, and are incorporated into the soil during shredding and disking of stalks and leaves following combine harvesting of the grain.

Systemic infection in seedlings is first recognized when conidia appear uniformly over the undersides of the third or fourth leaves. On leaves which subsequently emerge, conidia are produced beneath white or yellow longitudinal stripes. Beginning in midseason, production of conidia ceases and oospores form in the discolored stripes (4).

Although soilborne oospores are believed to cause primary infection in the disease cycle of sorghum downy mildew (1, 4), techniques have not been developed for determining numbers of oospores in soil; thus, no information is available on oospore populations of naturally infested soils or their relation to disease incidence.

The purposes of this study were: (i) to develop a technique to quantify numbers of oospores of *S. sorghi* in soil, and (ii) to determine oospore population densities in naturally infested soils of south Texas and to relate these to incidence of downy mildew in grain sorghum. A preliminary report has been presented (14).

MATERIALS AND METHODS

Addition of oospores to soil.—Oospores were added to soils at known concentrations to evaluate the efficiency of the assay technique. Two grams of dried and shredded leaf pieces from infected mature sorghum plants were comminuted in 100 ml distilled water in a Waring Blendor for 60 sec. The solution was filtered through a double

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layer of cheesecloth to remove leaf fragments. Aliquots of the oospore suspension, collected during rapid stirring, were serially diluted with distilled water to concentrations of 1/10 and 1/100 of the original. Diluted portions were stirred and 0.1-ml aliquots were pipetted onto glass slides. Oospores in each aliquot were counted with a dissecting microscope at ×25-50. Concentrations of oospores in the original suspension were determined from the means of five counts of each of five replicate dilutions. Then portions of the oospore suspension, collected during stirring, were evenly pipetted onto air-dried and sieved (7.40-mesh/cm screen, 0.84 mm pore size) soils to provide initial concentrations of 1,000 oospores/g soil (oven-dried weight equivalent). Infested soil was mixed thoroughly by hand and portions were diluted with additional soil to provide concentrations of 100 and 10 oospores/g soil.

Recovery of oospores from soil.—The assay technique was based upon the progressive separation of coarse sand, clay, and fine sand particles from soil suspensions by washing and sedimentation, and upon the retention of oospores with the silt particles. Five grams (oven-dried weight equivalent) of infested soil was dispersed in distilled water (50 ml total suspension) by rapid mixing with a stirring bar for 10 min. During mixing, 20 ml were pipetted into a test tube.

To separate the coarse sand particles, the tube was shaken vigorously, allowed to settle for 40 sec and the supernatant poured into a second tube. This process was repeated four more times with the same 20-ml suspension. To wash the coarse sand, particles from the five sedimentations were rinsed into a single tube, adjusted to 20 ml with distilled water, shaken, settled 40 sec, and the supernatant was decanted and retained. Additional distilled water was added and the process was repeated nine more times.

To remove clay particles, the single test tube containing the original soil suspension (minus coarse sand) and the 10 test tubes of solution from the washes of coarse sand, each were adjusted to 20 ml with distilled water, shaken, and allowed to settle 30 min. The upper 16 ml were drawn off with a pipette and filler and discarded. The lower 4 ml of liquid and sediment in the eleven tubes were partially combined by rinsing into five tubes, which were each adjusted to 20 ml, shaken, and allowed to settle 30 min for the second clay wash. This process was repeated three more times, with most clay particles discarded and with remaining fine sand and silt particles eventually combined into a single test tube containing 4 ml.

To separate fine sand and silt particles, the 4 ml of suspension were shaken, allowed to settle 40 sec, and the upper 2 ml were rapidly drawn off with a suction-bulb pipette with adjustable plunger and transferred to a second test tube. The original tube was readjusted to 4 ml with additional distilled water and the process was repeated nine more times, with each upper 2-ml fraction transferred to the same test tube to give 20 ml. This was shaken, allowed to settle 30 min to sediment the oospores, and the upper 16 ml was drawn off and discarded. The remaining 4 ml consisted primarily of silt particles and oospores from 2 g of the initial 5 g of soil.

To observe and count oospores, the 4 ml of silt in suspension were dispersed by stirring and a 0.5-ml aliquot was drawn off and deposited in droplets in a plastic grid petri dish (9-cm diameter) containing a shallow layer of distilled water. Oospores were observed by scanning along the lines at ×25 or ×50 with a dissecting microscope. The total oospores counted in each aliquot were multiplied by four to give the number detected per gram of soil.

Detection of oospores in plant debris from soil.—Samples of field soils were sieved through 1.36, 3.45, and 7.40 mesh/cm screens (pore sizes 5.66, 2.00, and 0.84 mm, respectively), and any organic debris retained, other than obvious root and stalk tissue, was recombined with soil. Distilled water was added to 20 g (oven-dried weight equivalent) of sieved soil to bring the mixture to 200 ml. Coarse sand particles were removed from stirred solutions by sedimentation and washed five times, and the remaining soil solution and wash water were poured through a 46.3 mesh/cm (0.125 mm pore size) screen. Particles of organic matter retained on the screen were immersed in 5.0% potassium hydroxide at 90 C for clearing. After 20 min, clearing solutions were cooled, poured into petri dishes, and examined at ×25-50 for oospores embedded in particles or free in solution.

Collection and assay of samples of naturally infested soil.—Ten portions (approximately 500 ml each) were collected from the upper 15-cm of an area (0.1-0.2 ha) of similar soil type in a field and composited for each soil sample. Each sample was mixed thoroughly by hand, sieved through 3.45 and 7.40 mesh/cm screens, and stored in paper bags at 4 C for 1-6 wk prior to assays for oospores and for 8 wk prior to planting to sorghum. Samples were collected from current-season fields when plants were in the four-leaf stage. In each area sampled, numbers of plants with symptoms of downy mildew were recorded among 100 plants in each of three randomly-chosen rows.

Textures of soils were determined by the Bouyoucos hydrometer method of mechanical analysis (10).

A downy-mildew-susceptible commercial sorghum hybrid (TE-Y-101) was planted in portions of soil samples. Styrofoam cups (178 ml and 9 cm tall), with cheesecloth pads overlaying bottom drainage holes, were filled with soil to a depth of 7.5 cm after settling and each planted with 10 seeds covered 1 cm deep with additional soil. Seedlings were thinned to six or seven per cup after emergence and grown out-of-doors in sunlight for 5 wk. Cups were watered as required to prevent surface drying of soil and were observed twice daily. Seedlings with downy mildew were recorded and removed at the first appearance of symptoms to prevent spread of the pathogen to adjacent plants by conidia.

RESULTS

Assays of oospores from artificially infested soils.—Oospores of *S. sorghi* were added to two soils of different textures (Table 1) from areas not previously planted to sorghum or corn. The amounts added gave estimated initial densities of 1,000, 100, and 10 oospores/g. Coarse sand, fine sand + silt, and silt fractions were separated by the washing and sedimentation technique in three assays of each soil at each inoculum level. In evaluations of the technique using artificially infested soils, oospores were counted in 0.5-ml aliquots of 4.0-ml suspensions of each particle-size fraction. In subsequent assays of naturally infested soils,

oospores were counted only in the silt fractions. Estimates of percentages of initial oospores recovered in silt fractions of artificially infested soils were adjusted to compensate for the numbers of oospores removed from tubes in the preceding counts with fine sand + silt fractions (Table 1). Oospores present in clay fractions of the two soils were not estimated; however, in preliminary experiments it was determined that all oospores settled out of the upper 16 ml of 20-ml suspensions of water or clay within 30 min.

In both soils, virtually all oospores were recovered among fine sand + silt particles (average of 101.2% for all assays) and few were recovered among the coarse sand particles (Table 1). Following the subsequent separation of silt from fine sand particles, an average of 97% of estimated initial oospores were recovered among the silt particles. Therefore, this percentage was considered to represent, on the average, numbers of oospores recovered in assays of naturally infested soils.

Although particles within each fraction were not uniform in size or shape, particles in the coarse sand fraction always averaged greater than 200 μm in maximum diameter, particles in the fine sand fractions from the two soils averaged 36.8 and 40.9 μm, and particles from the silt fractions averaged 17.3 and 16.5 μm. These sizes are within ranges designated for coarse sand, fine sand, and silt particles by the International Soil Science Society (10).

Oospores of *S. sorghi* were recognized by their nearly uniform size and by the characteristic orange-red to purple pigmentation and ridges and fluted surfaces of oogonial walls. These features were discernible when aqueous suspensions of soil particles containing oospores were observed with a dissecting microscope at ×25-50

TABLE 1. Oospores of *Sclerospora sorghi* from artificially infested soils recovered in three soil particle-size fractions obtained from aqueous suspensions by a washing and sedimentation technique

Soil	Estimated oospores added per gram (no.)	Estimated percentages of added oospores recovered in soil particle-size fractions[a]		
		Coarse sand (%)	Fine sand + silt (%)	Silt[b] (%)
Clay loam	1,000	1.7	106.3	88.4
	100	0.3	91.8	83.4
	10	0.0	125.1	131.7
Sandy clay loam	1,000	3.5	102.1	100.5
	100	0.1	78.1	81.0
	10	0.0	98.1	94.4

[a]Determined from numbers of spores observed with a dissecting microscope at ×25-50 in 0.5-ml aliquots of 4.0-ml suspensions of particles in water. Each value is a mean of three single values obtained from three replicated assays of each soil at each inoculum level.

[b]The percentages determined from numbers of spores observed in silt fractions were adjusted to compensate for numbers of spores removed in preceding counts of fine sand + silt fractions.

TABLE 2. Oospores of *Sclerospora sorghi* detected in organic matter and free in soil in samples of three naturally infested soils

Soil	Previous crop and disease	Sample[a] no.	Oospores per gram soil[b]		Percentage oospores free in soil (%)
			Embedded in organic matter (no.)	Free in soil (no.)	
1	Grain sorghum	1	1.4	99.1	98.5
	Very severe	2	3.3	122.9	97.3
	downy mildew	3	3.2	176.4	98.2
2	Grain sorghum	1	0.1	25.9	99.6
	Moderately severe	2	0.4	30.5	98.7
	downy mildew	3	0.1	13.8	99.3
3	Sorghum-sudan	1	0.0	8.5	100.0
	Slight	2	0.1	13.0	99.2
	downy mildew	3	0.0	12.7	100.0

[a]Each sample from a different area (approximately 0.1 hectare) and comprised of a composite of 10 portions (approximately 500 ml each) of soil scooped from the upper 15 cm at random points.

[b]Oospores in organic matter determined from observations with a dissecting microscope at ×25-50 of all particles of plant debris collected from 20.0 g soil on a 46.3 mesh/cm (0.125-mm pore size) screen and cleared in potassium hydroxide. Oospores free in soil determined from observations of 0.5 ml of a 4.0-ml aqueous suspension of silt particles from 2.0 g soil, obtained by a washing and sedimentation technique and presumed to contain 97% of oospores from soil.

(Fig. 1). Oospores were very difficult to observe among particles of fine sand, which were similar in size to the spores, and also among the larger particles of coarse sand. However, oospores were observed much more readily in silt fractions because their diameters (with oogonial walls) were two to three times greater than diameters of most silt particles (Fig. 1).

Presence of oospores of Sclerospora sorghi in plant debris from soil.—Oospores embedded in pieces of plant debris (screened from samples of three naturally infested soils collected 5 mo after harvest) were counted and compared with the numbers estimated to be free in soil. After immersion of organic debris in potassium hydroxide for 20 min, much pigment was removed while oospores retained their color and could be detected within the debris. Suspensions were examined thoroughly to detect oospores liberated by disintegration of some pieces of debris during clearing.

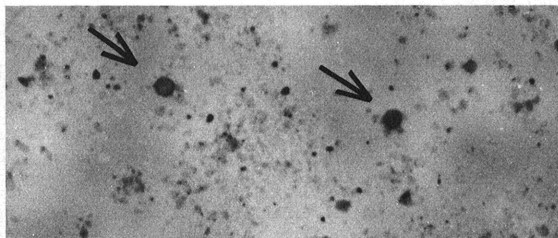

Fig. 1. Oospores of *Sclerospora sorghi* (arrows) and silt particles from soil in water suspension as observed and counted through a dissecting microscope at ×25. Diameters of the spores are two to three times the diameters of the particles of silt.

Numbers of oospores present in organic matter and free in soil varied greatly among the three soils and were correlated with severity of disease in the previous season's crop (Table 2). Less than 3% of the oospores were detected in organic matter in all soils; 97% or more were free in soil. In subsequent assays of samples of naturally infested soils, collected 9 mo after harvest of the preceding crop, numbers of oospores present in organic matter were considred negligible and estimates of oospore densities were based only on spores free in soil.

Oospore population densities in field soils and relationships to disease incidence in grain sorghum.—Samples of soil were collected from 18 fields of grain sorghum in which plants with downy mildew were observed in Nueces County, Texas, in 1977. Incidence of downy mildew was estimated from counts in each field. Five grams of soil was obtained from approximately 5 liters of mixed and sieved soil. Oospore densities were estimated from single counts of oospores in a silt suspension separated from soil equivalent to 2.0 g of 5.0 g in suspension for each sample. Portions of each 5-liter sample also were planted to sorghum in pots and numbers of plants with downy mildew were recorded.

Oospores of *S. sorghi* were found in samples of soil from all fields. The estimated densities ranged from 8-95 oospores/g soil (Table 3). Incidence of downy mildew in the same fields ranged from 1-53%. Oospore densities were not significantly correlated ($r = 0.33$, 16 df) with

TABLE 3. Densities of oospores of *Sclerospora sorghi,* frequencies of plants with downy mildew, and clay contents of soils from 18 fields of grain sorghum in Nueces County, Texas

Field[a]	Oospores/g soil[b]	Seedling-systemic downy mildew (%)[c]		Clay content of soil (%)[d]
		Field	Pots	
1	8	1	5	31.0
2	12	7	10	16.3
3	12	10	0	27.0
4	21	3	10	30.0
5	21	10	0	20.0
6	25	43	5	15.3
7	25	45	5	15.3
8	25	24	0	22.0
9	41	37	0	23.3
10	41	11	0	26.0
11	54	12	15	26.0
12	58	48	10	22.0
13	62	2	10	21.3
14	62	14	5	24.3
15	66	32	35	22.0
16	70	9	20	28.3
17	74	53	47	17.3
18	95	31	0	21.3

[a]Ten portions (approximately 500 ml each) of soil from the upper 15 cm at random points within an area of 0.1-0.2 hectare in each field were composited and mixed prior to determinations of oospore densities, incidence of downy mildew in pots, and clay contents.

[b]Determined from observations with a dissecting microscope at ×25-50 of 0.5 ml of a 4.0-ml aqueous suspension of silt particles from 2.0 g of soil, obtained by a washing and sedimentation technique and presumed to contain 97% of oospores from soil.

[c]Frequency of plants with downy mildew in each field determined at the four-leaf stage from counts in 100 adjacent plants in each of three randomly-chosen rows. Frequencies in pots determined from numbers of infected plants of 20 seedlings (TE-Y-101) grown in soil for 5 wk.

[d]Clay contents of the soils were determined by the Bouyoucos hydrometer method of mechanical analysis.

disease incidence. However, ratios of percentages of infected plants to oospore densities (percent downy mildew per oospores per gram soil) were significantly correlated (r = 0.72, 16 df) with clay contents of soils (Table 3). These ratios were usually low in soils with the highest clay contents and highest in soils with the least clay (Fig. 2).

Downy mildew developed in seedlings of the susceptible sorghum hybrid grown in samples of 12 of the 18 soils, but oospore densities were not significantly correlated (r = 0.45, 16 df) with disease incidence.

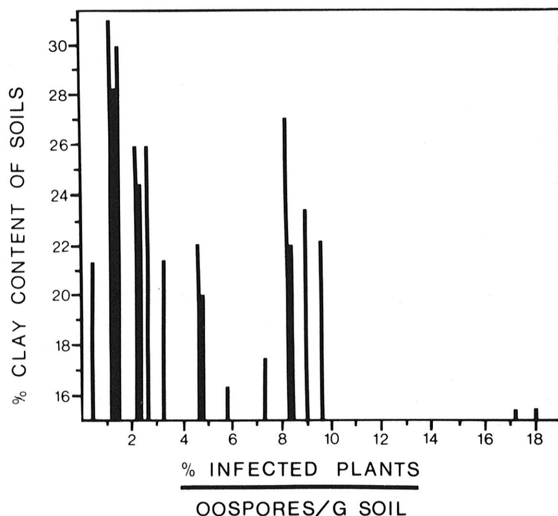

Fig. 2. Ratios of field-grown grain sorghum plants with downy mildew to estimated oospore population densities of *Sclerospora sorghi* and clay contents of the soils of 18 sorghum fields in Nueces County, Texas. Each bar represents data from one field. The correlation between clay contents of soils and ratios of disease frequency to inoculum density was highly significant ($P=0.01$).

DISCUSSION

This report describes a technique for determining numbers of oospores of *S. sorghi* in soil and provides estimates of oospore densities which occur in naturally infested soils of south Texas. The assay technique, and data obtained from it, may be useful in programs of investigation and control of downy mildew in four ways: (i) to predict potential severity of downy mildew if susceptible cultivars of sorghum or corn are grown in infested soils; (ii) to assay soils of breeding and screening nurseries in order to evaluate selection pressures applied to entries and probabilities of escapes; (iii) to simulate field conditions in greenhouse experiments or screening programs; and (iv) to assess effects of biological and cultural control treatments on numbers of oospores in soil.

The most important feature of the assay technique is that oospores are concentrated within a fraction containing soil particles significantly smaller than the spores, so that counting of spores is thereby facilitated. In evaluating the technique with assays of artificially infested soils, oospores were observed in suspensions containing coarse sand and fine sand particles in addition to silt. However, counts in the suspensions containing sand are arduous and time-consuming. Counts in suspensions containing primarily silt particles, in contrast, are accomplished much more rapidly and are therefore better suited to routine assays of field soils.

Results of assays of oospore densities in naturally infested soils and observations of disease severity suggest that, for fine-textured soils, the potential for severe seedling disease in a susceptible crop of sorghum or corn might be considered slight with less than 20 oospores/g soil, moderate with 20-40 oospores/g, and high with more than 40 oospores/g (Table 3). However, oospores in soil at high densities do not always cause severe disease in susceptible plants, and this indicates that information on inoculum density is not sufficient to describe inoculum potential (2).

To fully describe the inoculum potentials of *S. sorghi* in various soils, information also would be required on percentages of viable and germinable versus nonviable, mycoparasitized, or dormant oospores; influences of soil environment upon germination of oospores; and the extent to which populations of *S. sorghi* might be specialized in virulence to susceptible host cultivars. Some or all of these factors may have affected the level of correlation obtained between estimates of oospore densities and incidence of downy mildew in sorghum seedlings grown in pots. Storage of soil samples at 4 C prior to planting to sorghum also may have reduced infection by inducing dormancy of oospores (13) and thereby contributed to the poor correlation between oospore densities and disease incidence. In spite of these limitations, however, knowledge of oospore densities in soil still provides an important additional parameter for explaining incidence of downy mildew in sorghum and corn seedlings. Previously, such disease usually could be explained only from known cropping and disease histories of soils, dates of planting, and host resistance or susceptibility (4).

Differences in resistance and susceptibility of sorghum cultivars in growers' fields undoubtedly influenced the low correlation between oospore densities and disease incidence. When portions of all soils were grown to seedlings of the same susceptible cultivar in pots, a higher correlation coefficient was obtained, but this was still not significant at $P = 0.05$. In some soils with high oospore densities (including the highest), taken from fields with a high incidence of downy mildew, few or no plants were infected in pots (Table 3). This suggests that populations of *S. sorghi* might be specialized in virulence to susceptible host cultivars; apparent specialization to corn and sorghum has been reported for *S. sorghi* (15). Regardless of the reason, however, it is apparent that growth of plants of susceptible cultivars in potted soil does not always provide a reliable indication of the disease potential of the soil.

In Nueces County, most soils are fine-textured, and consequently only four of the 18 samples were low in clay content. In two of these four, ratios of infected field plants to oospore densities were far greater than those obtained for any of the soils with high clay contents (Fig. 3).

Additional samples should be taken from sandy soils to further document this apparent influence of soil texture on the inoculum potential of oospores. If correct, it suggests that fewer oospores are required to produce disease in sandy soils than in clay soils, and that severity of disease will increase more rapidly from year to year in sandy soils planted to susceptible sorghum than in clay soils.

Most techniques for assaying populations of plant pathogenic fungi in soil require growth of colonies on agar media (9, 19) and therefore cannot be applied to *S. sorghi* or other obligate pathogens. Techniques previously described for assaying populations by physical separation of spores or sclerotia from soil were based on flotation (8, 12, 20). Results of the present study show that populations of pathogens in soil may also be assayed by washing and sedimentation of spores from soil suspensions.

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