Germination of Oospores of Sclerospora sorghi in the Presence of Growing Roots of Host and Nonhost Plants

R. G. Pratt

Assistant Professor, Texas Agricultural Experiment Station, Texas A&M University Agricultural Research and Extension Center, P.O. Box 10607, Corpus Christi, TX 78410. Present address: Agricultural Research, Science and Education Administration, U.S. Department of Agriculture, and Department of Plant Pathology and Weed Science, Mississippi State University, P.O. Drawer PG, Mississippi State, MS 39762.

Accepted for publication 8 June 1978.

ABSTRACT

PRATT, R. G. 1978. Germination of oospores of Sclerospora sorghi in the presence of growing roots of host and nonhost plants. Phytopathology 68: 1606-1613.

Oospores of *Sclerospora sorghi* maintained between porous membranes in soil germinated at low frequencies adjacent to growing roots of sorghum, corn, oats, wheat, soybeans, and cotton. Germination occurred at similar frequencies in the presence of roots of sorghum seedlings of cultivars both resistant and susceptible to downy mildew, and also in nontreated field soil, autoclaved soil, and sand. No germination was observed in the absence of plant roots. Germination always resulted in formation of single, broad, coenocytic germ tubes which were seldom branched and elongated up to 1.25 mm prior to autolysis. Germination occurred consistently with oospores stored at 25 C for 8 mo, but not with oospores stored at 4 C; however, when oospores were transferred from 4 C to 25 C, the frequency of germination increased steadily after 2, 4, and 6 wk. Most germination occurred within 3 days after growth of roots adjacent to oospores. In all experiments, numerous instances of "false" germination were observed, due to growth of hyphae of mycoparasitic fungi from within oospore walls. Criteria for distinguishing true and false germination of oospores of *S. sorghi* are discussed.

Sclerospora sorghi Weston & Uppal is the causal organism of downy mildew of sorghum and corn. This disease has been very destructive in North, Central, and South America, Africa, and Asia (6). Susceptible plants which become systemically infected in the seedling stage by germ tubes from oospores or conidia often grow to maturity but produce no grain or aborted ears. Oospores are formed between veins of leaves of infected plants beginning in midseason and are added to soil as a result of natural leaf shredding prior to harvest or mechanical shredding of leaves and stalks after harvest.

Oospores of *S. sorghi* are believed to germinate in soil and initiate infection in roots (3, 5, 14, 18). Numerous studies have demonstrated that sorghum seedlings grown in soil infested with oospores develop systemic downy mildew in the absence of conidial inoculum (3, 5, 14, 18). However, in spite of the ease of obtaining infection with oospore inoculum, few investigators have induced and observed oospore germination. Weston and Uppal (18) reported germination of oospores of *S. sorghi* after incubation on moist blotting paper in high humidity for 48 hr. Germ tubes were illustrated originating from oospores with homogeneous internal contents and were stated to be continuous with oospore walls, 4.4 μm average thickness, and usually branched. Other investigators did not obtain germination by this method (3, 14). Neither water from washings of sorghum seedlings grown in sand nor β-glucuronidase induced germination (17). Sansome (15) described oospore nuclei of *S. sorghi* during their first and second divisions but did not state whether these occurred during germination. Safeeulla (14) reported germination of oospores in mixtures of soil and host-root extracts and also of oospores maintained in distilled water following a cold shock. He further stated that germination occurred with oospores in contact with roots of seedlings of susceptible, but not resistant, sorghum and maize cultivars (14).

Downy mildew of sorghum and corn is presently controlled almost exclusively by using resistant cultivars (6, 14). The potential for cultural or biological control is largely undefined because little is known of how oospores survive, germinate, and cause infection in soil. The purposes of this study, therefore, were to induce germination of oospores of *S. sorghi* and to evaluate factors which influence germination.

MATERIALS AND METHODS

Collection, storage, and concentration of oospores.—Leaves of sorghum plants infected with *S. sorghi*, collected from two susceptible cultivars, were used to supply oospores in all experiments. Only leaves with necrotic stripes and incipient natural shedding were collected. Tissue of leaves was air-dried for 4 wk, stripped from midribs, shredded into sections less than 1 cm^2, and stored in paper bags at either 4 C or 25 C for 6-10 mo. To obtain oospores, 2.0 g of leaf pieces were comminuted in 100 ml of distilled water for 60 sec and the oospore suspension was filtered through a double-layer of cheesecloth. Oospores were concentrated by removing

00032-949X/78/000290$3.00/0

upper portions of suspensions settled for 10-15 min in beakers. Oospores from only one cultivar were used in any given experiment.

Incubation of oospores adjacent to roots in soil.—Oospores from stirred suspensions were deposited evenly with a pipette over one-half of the surface of a nuclepore membrane (47 mm diameter, 2.0 μm pore size) on a paper towel. Water was drawn into the towel while oospores were retained. A second membrane was added to cover the oospores, and each pair of membranes with oospores sandwiched between was applied to the inside edge of a six-ounce (178-ml capacity) styrofoam cup with bottom drainage holes (Fig. 1). Sandy clay loam soil from a sorghum field was added and watered immediately to saturation. After drainage, six seeds of sorghum (Pioneer 846 or as specified) or other plant species were placed on the soil surface adjacent to the inside edge of the double membrane and covered with additional soil. Cups were maintained at a 45-degree angle to promote growth of roots of seedlings adjacent to the membranes. After 4-20 days in continuous fluorescent light (1,000 lx) with watering at 4-day intervals, edges of cups were cut away with a razor blade and sections (3 mm wide) of double membrane against which individual roots were appressed (Fig. 1) were removed with a scissors and gently rinsed in a stream of water. Single-membrane sections were separated under a dissecting microscope, mounted beneath coverslips on slides in distilled water with oospores on the upper surfaces, and examined throughout at ×100. The number of germinated oospores per cm^2 of 2-4 cm^2 total double membrane area from each cup was determined. Three replicate cups were examined for each treatment in all experiments.

RESULTS

Oospores of *S. sorghi* germinated only on portions of membranes against which roots of sorghum or other plants were appressed. Germination always was less than 1% of the total number of spores and up to 3% of those that appeared viable [with well-defined walls, finely granular cytoplasm, and circular globules (Fig. 1)]. When membrane sections were examined immediately after removal from cups, germinated oospores were observed. After several hours, additional germinations occurred, suggesting that washes of membranes in water stimulated germination. Newly germinated oospores (with short germ tubes without vacuoles) seldom were observed after 10 hr, and older germinated oospores (with long vacuolate germ tubes with partially lysed walls) then became difficult to observe. Therefore, all counts of germination were made 3-5 hr after mounting of membrane sections on slides. In each experiment, replicate cups of different treatments were observed in rotating order.

Morphology of germinating oospores and germ tubes.—Immediately prior to germination, contents of oospores appeared slightly clumped, swollen, and homogeneous (Fig. 2-H). Germination occurred only by germ tubes which penetrated dissoluted portions of oospore walls (Fig. 2-E, F). Germ tubes often penetrated oospore and oogonial walls through narrow channels (Fig. 2-I, J). Occasionally cytoplasm from germinated oospores partially filled spaces between oospore and oogonial walls (Fig. 2-G), but most often oospore walls were confluent with oogonial walls at points of emergence of germ tubes (Fig. 2-E, F, H).

Germ tubes were coenocytic, broad (mean of 20 = 5.5 μm wide, range = 4-6 μm), and grew in a straight, curved, or slightly undulating course (Fig. 3-D, G). Not more than one germ tube ever originated from a single oospore. Apices of germ tubes were hemispherical (Fig. 3-D, E, H). Branching occurred in a minority of germ tubes and was never accomianied by septation (Fig. 3-H). Bulbous swellings sometimes developed after germ tubes emerged through oogonium walls (Fig. 3-D). One young germ tube elongated from 143 to 220 μm in 25 min (185 μm/hr) but subsequent elongation was at a slower rate.

Germination of oospores of *S. sorghi* appeared to involve the translocation of cytoplasm from within oospores to germ tubes with no net increase in quantity. As cytoplasm flowered into germ tubes, vacuoles developed adjacent to oospore walls opposite germ tubes (Fig. 2-H, I), and these gradually enlarged and filled oospore cavities (Fig. 3-A, B). Germ tubes ceased elongating shortly after cytoplasm was evacuated from oospores, and the cytoplasm within them then became fragmented which produced a beaded appearance (Fig. 3-F). Subsequently, all cytoplasm disintegrated and germ tubes became difficult to observe (Fig. 3-B, C). Maximum lengths of 20 germ tubes ranged from 300-1,250 μm.

Factors influencing oospore germination.—In all

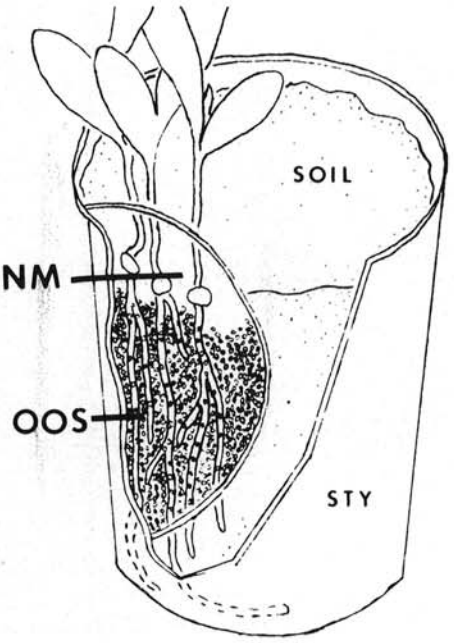

Fig. 1. Experimental unit for studies of germination of oospores of *Sclerospora sorghi* in the presence of plant roots: double Nuclepore membranes (NM) with oospores (OOS) sandwiched in between are applied to the inside wall of a styrofoam cup (STY) which is filled with soil and planted with seed behind the membranes. The cup is maintained at a 45-degree angle to promote growth of roots against the membranes. After 4 or more days, side of cup is cut away and sections of membranes against which the roots are appressed are excised and examined microscopically.

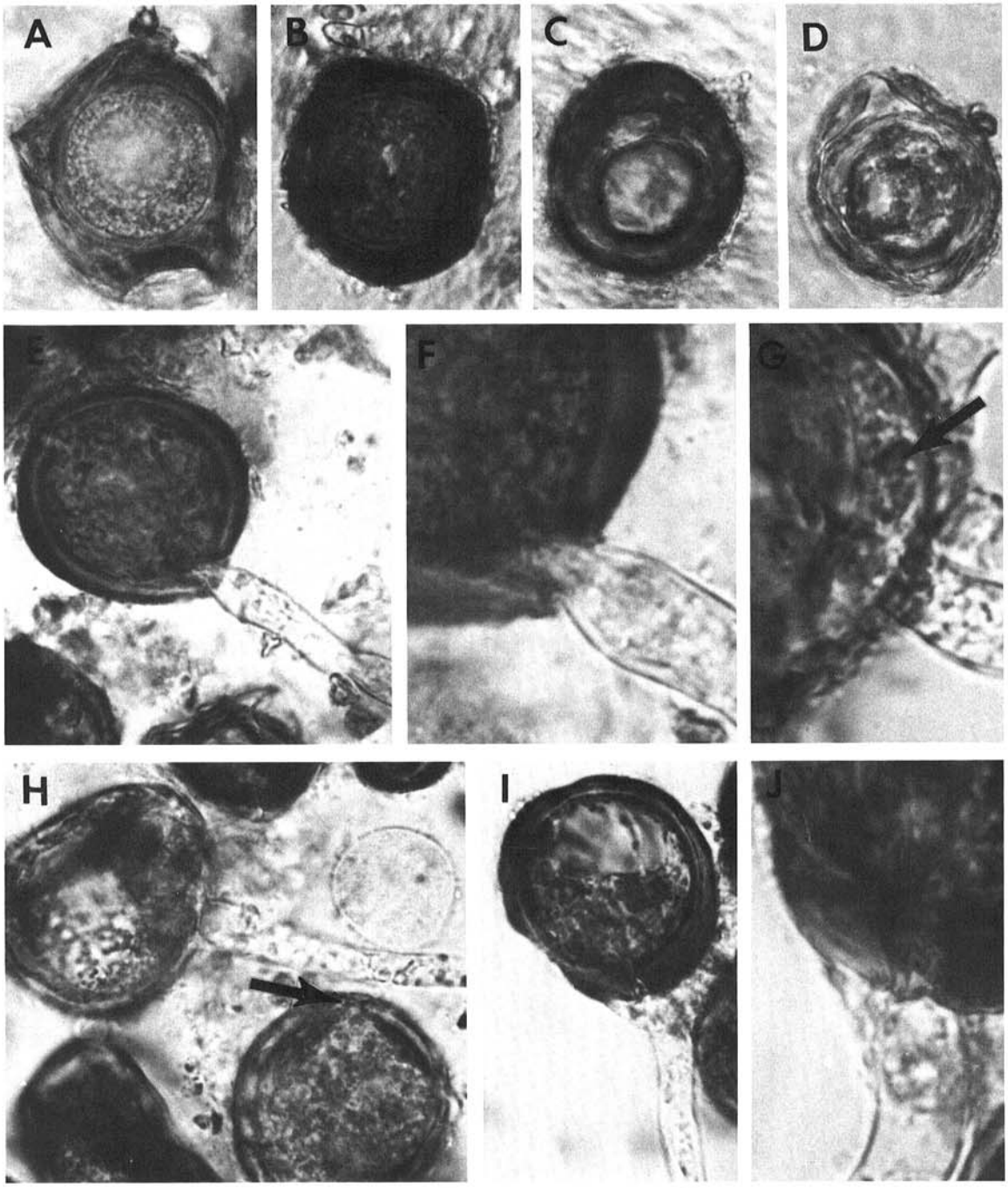

Fig. 2-(A to J). Viable-appearing, aborted, and newly germinated oospores of *Sclerospora sorghi*. **A and B)** Viable-appearing oospores with granular cytoplasm, circular globules and differences in pigmentation of oogonial walls. **C and D)** Aborted oospores with refractory and agglutinated contents and overly thickened walls. **E)** Newly germinated oospore with homogeneous contents and a single, stout germ tube. **F)** Closer view of (E) showing break in the oospore wall and continuity of cytoplasm from spore to germ tube. **G)** Example of occasional flow of cytoplasm between oospore and oogonial walls (arrow) during germination. **H)** Germinated oospore with developing vacuole and oospore with homogeneous contents and dissolution in wall immediately prior to germination (arrow). **I)** Germinated oospore with developing vacuole and narrow channel through oospore and oogonial wall. **J)** Closer view of (I) showing continuity of cytoplasm through narrow channel from oospore to germ tube. All photomicrographs are of nonstained spores and germ tubes.

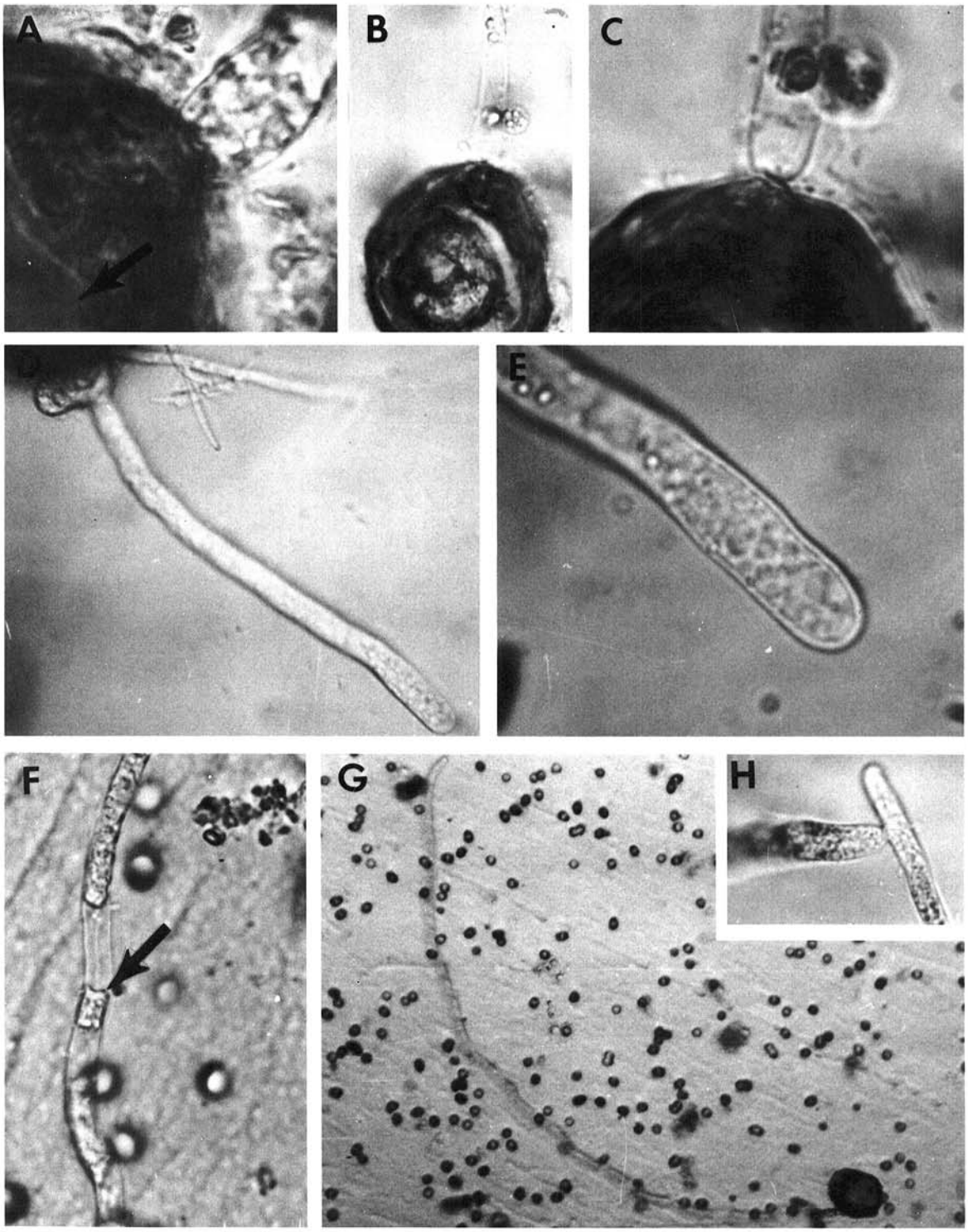

Fig. 3-(A to H). Old germinated oospores and germ tubes of *Sclerospora sorghi*. **A)** Final flow of cytoplasm from oospore to germ tube with vacuole (arrow) almost completely filling oospore cavity. **B)** Germinated oospore and basal portion of germ tube after evacuation of cytoplasm. **C)** Closer view of (B) showing walls and point of attachment of germ tube. **D)** Newly formed germ tube with basal swelling at point of emergence from oogonium and with smaller hyphae of contaminant fungi in background. **E)** Closer view of (D) showing hemispherical tip of germ tube and densely packed cytoplasm. **F)** Old germ tube with fragmented cytoplasm (arrow) producing beaded appearance. **G)** Final length and configuration of a germ tube which penetrated pore in membrane immediately after emergence and grew on opposite side. **H)** Branching of a germ tube with cessation of growth by the original apex. All photomicrographs are of nonstained spores and germ tubes.

preparations of oospores, including those obtained before and after storage of leaf pieces, some spores appeared viable and others appeared to be aborted or parasitized. Oospores that appeared viable had well-defined walls, finely granular cytoplasm, and circular globules (Fig. 2-A, B). Oospores that appeared aborted or parasitized had overly thickened or poorly defined walls and irregular, agglutinated or refractory contents (Fig. 2-C, D). Percentages of viable-appearing oospores from leaf pieces of one sorghum cultivar stored at 25 C and 4 C were similar (approximately 25%) after 10 mo. However, in several experiments, oospores stored at 25 C germinated consistently (at low frequency) while no germination occurred with oospores stored at 4 C for 6-10 mo. When leaf pieces containing oospores were transferred from 4 C to 25 C for 2, 4, and 6 wk prior to testing, germination increased with each time interval (Table 1). No germination occurred with oospores freshly collected from plants in the field. All evaluations of oospore germination with resistant and susceptible sorghum cultivars (Table 2), host and nonhost plants (Table 3), soil or sand, or different incubation times and watering schedules were conducted with spores from leaf pieces stored only at 25 C for 6-10 mo.

In most experiments, germinated oospores were observed more frequently at 4 days after planting of seed than at 8 days (Table 3). In one experiment, sections of membrane adjacent to roots were examined at 4-day intervals up to 20 days after planting; germinated oospores were observed only after 4 and 8 days. Daily watering of soil in cups (versus watering at 4-day intervals) did not increase numbers of germinated oospores up to 20 days in this experiment, and it significantly decreased oospore germination at 4 days in another experiment.

Similar numbers of oospores germinated on membranes when nontreated soil, autoclaved soil (1-liter quantities in paper bags at 121 C for 20 min), or sand was added to cups and planted to sorghum. No germination was observed on sections of membranes from similar cups without seedlings. Observations were greatly facilitated with autoclaved soil due to fewer hyphae of fungi from soil present among oospores.

Oospore germination (evaluated at 4 days) was induced by seedlings of three sorghum cultivars highly resistant to downy mildew as well as by seedlings of three predominantly susceptible cultivars. Two susceptible cultivars stimulated the highest and lowest germination, and these were the only significantly different values (Table 2). The second highest amount of germination occurred on membranes from cups planted to seedlings of a highly resistant cultivar (Table 2).

TABLE 1. Germination of oospores of *Sclerospora sorghi* on porous membranes in soil adjacent to roots of sorghum seedlings at four intervals following transfer from 4 C to 25 C

Storage time at 25 C following transfer from 4 C[y]	Oospore germination (no. per cm^2 of membrane area adjacent to roots[z])
0	0.09 a
2	1.05 a
4	3.89 b
6	5.29 b

[y]Oospores in infested sorghum leaf pieces stored at 4 C for 47, 45, 43 and 41 wk prior to removal to 25 C. Germination of oospores from all storage intervals was tested simultaneously.

[z]Oospores between porous membranes were added to cups with soil planted to sorghum seedlings (cultivar Pioneer 846). Sections of membranes against which roots were appressed were excised, measured, and observed for oospore germination 4 days after planting. Values were means of oospores germinated per unit membrane area in each of three replicate cups. Means followed by same letter are not significantly different according to Duncan's multiple-range test ($P = 0.05$).

TABLE 2. Germination of oospores of *Sclerospora sorghi* on porous membranes in soil adjacent to roots of sorghum seedlings of cultivars resistant and susceptible to downy mildew

Sorghum cultivar	Downy mildew reaction	Oospore germination (no. per cm^2 of membrane area adjacent to roots)[z]
Pioneer 846	susceptible	4.85 a
Northrup King 233	resistant	3.43 ab
Funks G2163 DMR	resistant	1.26 ab
Taylor-Evans Total	susceptible	1.21 ab
Pioneer 8308B	resistant	0.63 ab
Taylor-Evans-TE-Y-101	susceptible	0.51 b

[z]Oospores between porous membranes were added to cups with soil planted to seedlings of six sorghum cultivars. Sections of membranes against which roots were appressed were excised, measured, and observed for oospore germination 4 days after planting. Values are means of oospores germinated per unit membrane area in each of three replicate cups. Means followed by the same letter are not significantly different according to Duncan's multiple-range test ($P = 0.05$).

TABLE 3. Germination of oospores of *Sclerospora sorghi* on porous membranes in soil adjacent to roots of host and nonhost plants

Plant[y]	Oospore germination (no. per cm^2 of membrane area adjacent to roots[z]) Day 4	Day 8
Hosts:		
Sorghum	1.31	0.43
Corn	0.22	0.93
Nonhosts:		
Wheat	1.03	0.00
Oats	0.00	0.18
Cotton	0.07	0.10
Soybeans	1.16	0.30

[y]Sorghum (Pioneer 846) and corn (Funks G5820) are hosts of *S. sorghi*; the other plants are nonhosts.

[z]Oospores between porous membranes were added to cups with soil planted to seedlings of indicated plants. Sections of membranes against which roots were appressed were excised, measured, and observed for oospore germination 4 and 8 days after planting. Values are means of oospores germinated per unit membrane area in three replicate cups. Means of treatments at 4 days or 8 days did not differ significantly according to Duncan's multiple-range test, $P = 0.05$.

Germination of oospores of *S. sorghi* in the presence of roots of corn, wheat, oat, cotton, and soybean seedlings also was evaluated and compared with germination induced by sorghum seedlings. Wheat, oats, cotton, and soybeans are not hosts of the pathogen. Although the overall amount of germination was low in this experiment, some germinated oospores were observed on membranes from cups containing seedlings of all crop species after 4 or 8 days (Table 3). Morphological features of germinated oospores and germ tubes produced in the presence of roots of all crops were identical.

Growth of mycoparasitic fungi from within oospores.—In all experiments, instances of "false" germination (growth of hyphae of other fungi from within former oospores and oogonia of *S. sorghi*) were observed. These always were more frequent than true germination. Hyphae of mycoparasitic or contaminant fungi arose from within oogonia in which oospore walls were not discernible (Fig. 4-E) or from within clearly defined oospore walls (Fig. 4-C, F). In addition to hyphae, motile zoospores and multiple spherical bodies suggestive of resting structures of chytridiomycetous fungi were observed within oospore cavities.

Hyphae of other fungi which developed from within oogonia or oospores were usually multiple (Fig. 4-A, B, C, D, F) and septate (Fig. 4-A, D), but sometimes septa

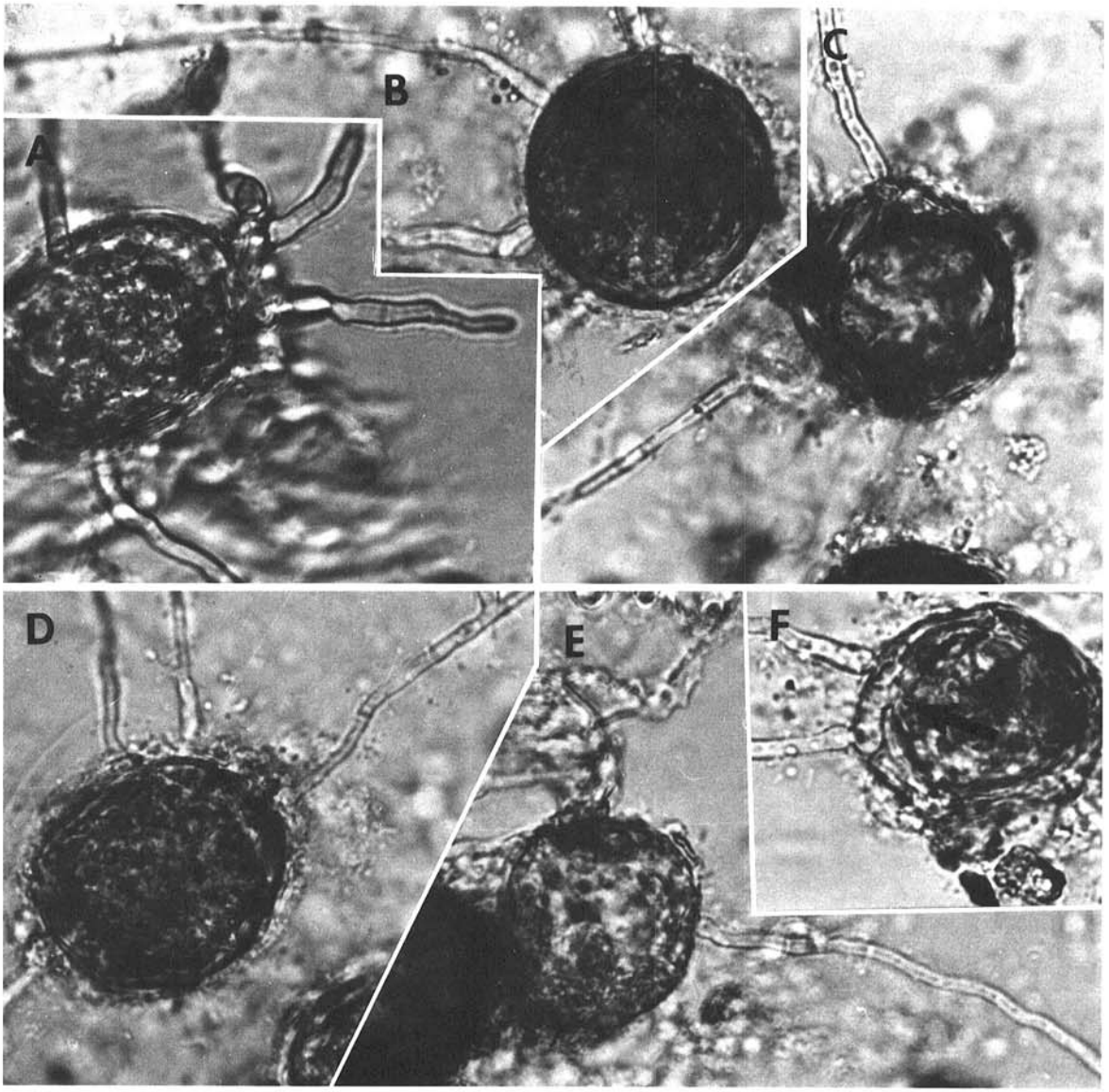

Fig. 4-(A to F). Growth of hyphae of mycoparasitic fungi from within former oogonia and oospores of *Sclerospora sorghi*. **A, D, and E)** Hyphae with septa clearly visible. **A, B, and D)** Parasitized oospores with portions of walls still visible. **C and F)** Parasitized oospores with walls largely intact. **E)** Growth of hypha of parasite from within former oogonium with oospore walls absent. **F)** Hyphae of parasite emerged through gap in former oospore wall (arrow) and partially filling the oogonial cavity prior to emergence through the oogonial wall. All photomicrographs are of nonstained spores and hyphae.

were difficult to observe or hyphae were coenocytic. Usually they were more narrow than germ tubes of *S. sorghi* (Fig. 3-D, Fig. 4) and frequently branched (Fig. 4-A, D). Apices of hyphae of other fungi were usually acuminate rather than hemispherical. Identities of mycoparasitic fungi were not determined.

DISCUSSION

Results of this study demonstrate that oospores of *S. sorghi* germinate in soil in response to stimuli from plant roots, and that germination stimuli are associated with roots of resistant and susceptible sorghum cultivars and also nonhost plants. The results also indicate that host-induced germination of oospores in soil is significantly influenced by temperature during prior storage and by moisture levels in the soil, but not by the presence of other soil microorganisms. Although oospores germinated at low frequencies in these experiments, some germination was obtained consistently with oospores stored at room temperature and also with those from low-temperature storage after dormancy was alleviated by returning them to storage at 25 C (Table 1). This consistent germination allowed both qualitative and quantitative evaluation of factors which influenced it. The membrane technique described here, and that previously used with *Aphanomyces euteiches* (12), may be useful for investigating oospore germination in other downy-mildew fungi and also in species of *Pythium* and *Phytophthora*, for which most information has been obtained only from in vitro studies.

The germinated oospores observed here were not used to infect sorghum seedlings to obtain downy mildew. Nevertheless, evidence that these represent true oospore germination is as follows: (i) the germ tubes were uniformly coenocytic and broader than hyphae of other fungi which originated from within oospores; (ii) the germ tubes were always single; (iii) they always ceased growth and degenerated several hours after emergence. Germinated oospores and germ tubes observed here were very similar to those originally described by Weston and Uppal (18), who noted that germ tubes of spores germinated on moist blotting paper were hyaline, unseptate, and originated from spores in which globules were no longer present. They illustrated only single germ tubes arising from oospores. Their range of widths of germ tubes encompasses that observed here, although the mean size is smaller (4.4 versus 5.5 μm). Weston and Uppal stated that germ tubes usually were branched, but they also described and illustrated nonbranched germ tubes similar to those observed here. It is not known how these authors obtained germination of oospores of *S. sorghi* in the apparent absence of host stimuli; other investigators were unable to repeat their results (3, 14). With *S. philippensis*, oospores were reported to germinate readily on moist filter paper and to produce single, stout germ tubes (10).

The characteristics of germinating oospores and germ tubes noted here are not in complete agreement with those recently described by Safeeulla (14). He reported that some oospores germinated by multiple germ tubes; this feature never was observed with oospores of *S. sorghi* from Texas. However, it is possible that the apparent multiple germ tubes may actually have originated from swellings produced after single germ tubes emerged (Fig. 3-D) and been favored by incubation of spores in host extract. The emergence of spherical bodies from oospores (14), in contrast, appears to represent an example of mycoparasitism by a chytridiomycete. Other authors have described parasitism of oospores of *S. sorghi* by a chytrid (8), and such parasitism is also well documented for oospores of *Pythium* and *Phytophthora* (16).

The frequent examples of invasion of oospores by filamentous fungi (Fig. 4), similar to those described for other oomycetes (16), indicates that the mere emergence of hyphae from within oospore walls is not a sufficient criterion for oospore germination (17). The emergence of multiple, septate, or narrow ($\leqslant 3$ μm wide) hyphae from within oospores, in face, may be safely considered to represent false germination.

The low frequencies of oospore germination in all experiments may have occurred because only a small percentage of oospores were germinable at any one time, or because limited pore areas on membranes impeded movement of stimuli from roots to spores. It also appears likely that stimuli for germination were released only briefly as root tips grew past spores on membranes. Most studies of root exudation, and of germination of spores in the rhizosphere (9), indicate that exudates are released primarily near growing root tips. The fact that most oospore germination occurred within 4 days from planting of the seed, with little germination observed after 8-20 days, suggests that stimuli for germination were released only briefly in the vicinity of individual spores by root tips.

Oospore germination was significantly less with daily watering of soil in cups to saturation for 4 days than with only initial watering, and daily watering up to 20 days did not stimulate germination. This suppressive effect of excess soil moisture on oospore germination is in agreement with results of a previous study (1) in which incidence of downy mildew in sorghum was suppressed by high soil moisture during 16 days after planting in soil infested with oospores.

Among the downy-mildew fungi, oospores have been reported to germinate readily and at high percentages in *S. graminicola* (11) and *S. philippinensis* (10), but only sporadically and at low frequencies or over long intervals in *Plasmopara* and *Peronospora* (2, 4, 7, 13). The membrane technique described here for *S. sorghi*, or the similar technique described for *A. euteiches* by Percich and Mitchell (12), also might be used to induce oospore germination in these and other species. Knowledge of factors which affect oospore germination may provide guidelines for development of cultural and biological controls. Results of the present study with nonhost plants suggest that trap or decoy crops might be grown in infested soil to stimulate germination of oospores of *S. sorghi* and thereby provide biological control of downy mildew in sorghum and corn.

LITERATURE CITED

1. BALASUBRAMANIAN, K. A. 1974. Role of date of seeding, soil moisture, temperature, and pH in the incidence of downy mildew of sorghum. Plant Soil

41:233-241.
2. BERRY, S. A., and G. N. DAVIS. 1957. Formation of oospores by Peronospora destructor and their possible relation to epiphytology. Plant Dis. Rep. 41:3-6.
3. COSPER, J. W. 1969. Inoculation, infection and reproduction of Sclerospora sorghi (Kulk.) Weston and Uppal in sorghum. M.S. Thesis, Texas A&M University, College Station, Texas. 46 p.
4. DUNLEAVY, J., and G. SNYDER. 1962. Inhibition of germination of oospores of Peronospora manshurica. Proc. Iowa Acad. Sci. 69:118-121.
5. FREDERIKSEN, R. A., A. J. BOCKHOLT, L. E. CLARK, J. W. COSPER, J. CRAIG, J. W. JOHNSON, B. L. JONES, P. MATOCHA, F. R. MILLER, L. REYES, D. T. ROSENOW, D. TULEEN, and H. J. WALKER. 1973. Sorghum downy mildew: a disease of maize and sorghum. Texas Agric. Exp. Stn. Res. Monog. 2. 32 p.
6. FREDERIKSEN, R. A., and B. L. RENFRO. 1977. Global status of maize downy mildew. Annu. Rev. Phytopathol. 15:249-275.
7. GREGORY, C. T. 1912. Spore germination and infection with Plasmopara viticola. Phytopathology 2:235-249.
8. KENNETH, R. G., and G. SHAHOR. 1975. Pathological aspects of sorghum downy mildew disease (Sclerospora sorghi) on maize and sorghums. Pages 125-127 *in* Proceedings Symposium on Downy Mildew of Maize, Tropical Agric. Res. Center, March, 1975, Nishigahara, Japan. 259 p.
9. MITCHELL, J. E. 1976. The effect of roots on the activity of soilborne plant pathogens. Pages 104-128 *in* Heitefuss, R., and P. H. Williams, eds. Physiological plant pathology. Encyclopedia of Plant Physiology N. S. Vol. 4. Springer-Verlag, New York. 890 p.
10. NAPI-ACEDO, G., and O. R. EXCONDE. 1967. Note: oospores of Sclerospora philippinensis Weston from corn leaf tissue. Philipp. Agric. 51:279-282.
11. PANDE, A. 1972. Germination of oospores in Sclerospora graminicola. Mycologia 64:426-430.
12. PERCICH, J. A., and J. E. MITCHELL. 1976. Germination of oospores of Aphanomyces euteiches in soil in contact with roots. Proc. Am. Phytopathol. Soc. 3:280 (Abstr.).
13. PERSON, L. H., and G. B. LUCAS. 1953. Oospore germination in Peronospora tabacina. Phytopathology 43:701-702.
14. SAFEEULLA, K. M. 1976. Biology and control of the downy mildews of pearl millet, sorghum, and finger millet. Wesley Press, Mysore, India. 304 p.
15. SANSOME, E. 1966. Meiosis in the sex organs of the oomycetes. Pages 77-83 *in* First Oxford Chromosome Conf. on Chromosomes Today. Oxford, England, July, 1964. 274 p.
16. SNEH, B., S. J. HUMBLE, and J. L. LOCKWOOD. 1977. Parsitism of oospores of Phytophthora megasperma var. sojae, P. cactorum, Pythium sp., and Aphanomyces euteiches in soil by oomycetes, chytridiomycetes, hyphomycetes, actinomycetes, and bacteria. Phytopathology 67:622-628.
17. VUDHIVANICH, P. 1975. Studies on oospore germination, chemical control, and cultural control of Sclerospora sorghi Weston and Uppal in sorghum. M.S. Thesis, Texas A&M University, College Station, Texas. 36 p.
18. WESTON, W. H., JR., and B. N. UPPAL. 1932. The basis for Sclerospora sorghi as a species. Phytopathology 22:573-586.