Parasitism of Oospores of Phytophthora megasperma var. sojae, P. cactorum, Pythium sp., and Aphanomyces euteiches in Soil by Oomycetes, Chytridiomycetes, Hyphomycetes, Actinomycetes, and Bacteria

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ABSTRACT

SNEH, B., S. J. HUMBLE, and J. L. LOCKWOOD. 1977. Parasitism of oospores of Phytophthora megasperma var. sojae, P. cactorum, Pythium sp., and Aphanomyces euteiches by oomycetes, chytridiomycetes, hyphomycetes, actinomycetes, and bacteria. Phytopathology 67: 622-628.

Oospores of *Phytophthora megasperma* var. *sojae*, *P. cactorum*, *Pythium* sp., and *Aphanomyces euteiches* in natural soil were infected with oomycetes, chytridiomycetes, hyphomycetes, actinomycetes, and bacteria. The oomycetes were *Pythium* sp. and *Leptolegnia* sp. The hyphomycetes were *Dactylella spermatophaga*, *Diheterospora chlamydosporia*, *Humicola fuscoatra*, *Fusarium oxysporum*, *Cephalosporium* sp., and *Alternaria alternata*. One isolate with nonseptate sterile mycelia was not identified. The chytrids were identified as *Rhizidiomycopsis japonicus*, *Canteriomyces stigeoclonii*, and *Hyphochytrium catenoides*. The actinomycete was *Actinoplanes missouriensis*. Two bacterial isolates were identified as *Pseudomonas* spp. In flooded soils, oospores were parasitized primarily by chytrids, oomycetes, *A. missouriensis*, and bacteria, whereas in soil with moisture levels below water-holding capacity, hyphomycetes predominated. Parasitism may have a significant potential for reducing populations of oospores in soil.

During a study of the behavior of *Phytophthora megasperma* var. *sojae* in natural soil, numerous oospores of the pathogen were found to contain fungal and bacterial parasites. Although mycoparasitism is a well known phenomenon (2, 5, 11, 18), parasitism of fungal resting structures, including oospores in soil, is less well understood. Drechsler identified *Dactylella* spp., *Trinacrium subtile*, and *Trichothecium* spp. as parasites of oospores of *Pythium* spp. (12, 13, 14, 15, 16). He also observed oospore predation by amebae, nematodes, rhizopods, and arthropods (12). Kenneth et al. (19) found oospores of *Sclerospora sorghi* parasitized by *Phlyctochytrium* sp., and Honour and Tsao (14) found those of *Phytophthora parasitica* parasitized by streptomycetes.

The purposes of the present work were to determine the extent of oospore parasitism in *P. megasperma* var. *sojae* and other root-infecting phycomycetes in soil, and to identify the parasitic microorganisms.

MATERIALS AND METHODS

Oospore preparation, incubation in soil, and observation.—Oospores of *Phytophthora megasperma* (Drechs.) var. *sojae* Hildb., *Phytophthora cactorum* Leb. & Cohn (Schroet.), *Pythium* sp., and *Aphanomyces euteiches* Drechs. were produced in cultures grown for 4-7 wk in darkness in V-8 juice broth supplemented with 30 μg/ml cholesterol (1). The cultures were air-dried to kill the mycelium. The oospores were harvested by homogenizing the mycelial mats in water, using a tissue grinder. Mycelial fragments were removed from some oospore preparations with enzymes (22). Incubation conditions and methods for observing oospores were described previously (23). Briefly, about 10^3 oospores from aqueous suspensions were applied to Nuclepore (polycarbonate) membrane filters (13 mm diameter, 0.4-μm pore size). Excess water was removed by applying a slight vacuum to the membrane filter apparatus. Conover loam soil was placed in 10 cm diameter petri dishes to a depth of about 1 cm. The soil then either was flooded or adjusted to soil moisture levels of less than saturation. The membranes with oospores were floated on the flooded soil samples, or were covered with a nylon net (0.4-mm pore size) and placed about 5 mm deep in the soil at moisture levels below saturation. After 4 to 10 days of incubation at 23 $\pm$ 2 C, the oospores were transferred from the membranes to water agar disks on microscope slides (23). Water and cover slips were applied for microscopic examination. The slides were kept in a moist chamber for 3 to 20 hr to allow further development of hyperparasites in the infected oospores.

Isolation of oospore parasites.—*Bacteria.*-Individual infected oospores were transferred to a drop of sterile water on a sterile glass slide and were crushed with a needle. The contents were streaked onto nutrient agar (per liter: 10 g glucose, 5 g peptone, 5 g yeast extract, and 20 g agar).

Filamentous fungi.—Individual infected oospores were transferred to acidified PDA. Isolates were maintained on V-8 juice agar.

Chytrids and actinomycetes.—Zoospores were released from sporangia produced in or on infected oospores within 3-5 hr of slide preparation. Zoospore suspensions were streaked on Miller's M_3 agar (20), containing 20 μg Benlate (50% benomyl) per ml to inhibit growth of contaminating fungi.

Identification of the parasites.—Two bacterial isolates were grown on various media for physiological tests, Gram-stained, and their motility and colony morphology was determined. Final identification was according to Bergey's manual (7). *Actinoplanes missouriensis* was identified according to the key of Cross and Goodfellow (10). Chytrids and oomycetes were identified according to Sparrow (24, and *personal communication*). Hyphomycetes were identified using Barron's book (3), and by personal communication with G. L. Barron. *Fusarium oxysporum* was identified by T. Kommedahl. Other hyphomycetes were identified by the Centraalbureau voor Schimmelcultures, Baarn, The Netherlands.

Oospore inoculation with the parasites.—To test for parasitic potential, oospores of *P. megasperma* var. *sojae*, *P. cactorum*, *Pythium* sp., and *A. euteiches* were reinoculated with chytrids and *Actinoplanes*. Only oospores of *P. megasperma* var. *sojae* were reinoculated with hyphomycetes, oomycetes, and bacteria. Nuclepore membrane filters bearing oospores were floated on soil extract made from a 1:1 (w/v) soil-water suspension that had been standing on the laboratory bench for 24 hr. The filtered suspension was autoclaved and placed in 10-cm diameter petri dishes. For fungal hyperparasites, penicillin-G (K+) and streptomycin sulfate (500 μg/ml each) were added to inhibit bacterial contaminants. For chytrids and actinomycetes, 20 μg Benlate/ml was added to inhibit nonpythiaceous filamentous fungi. One drop of

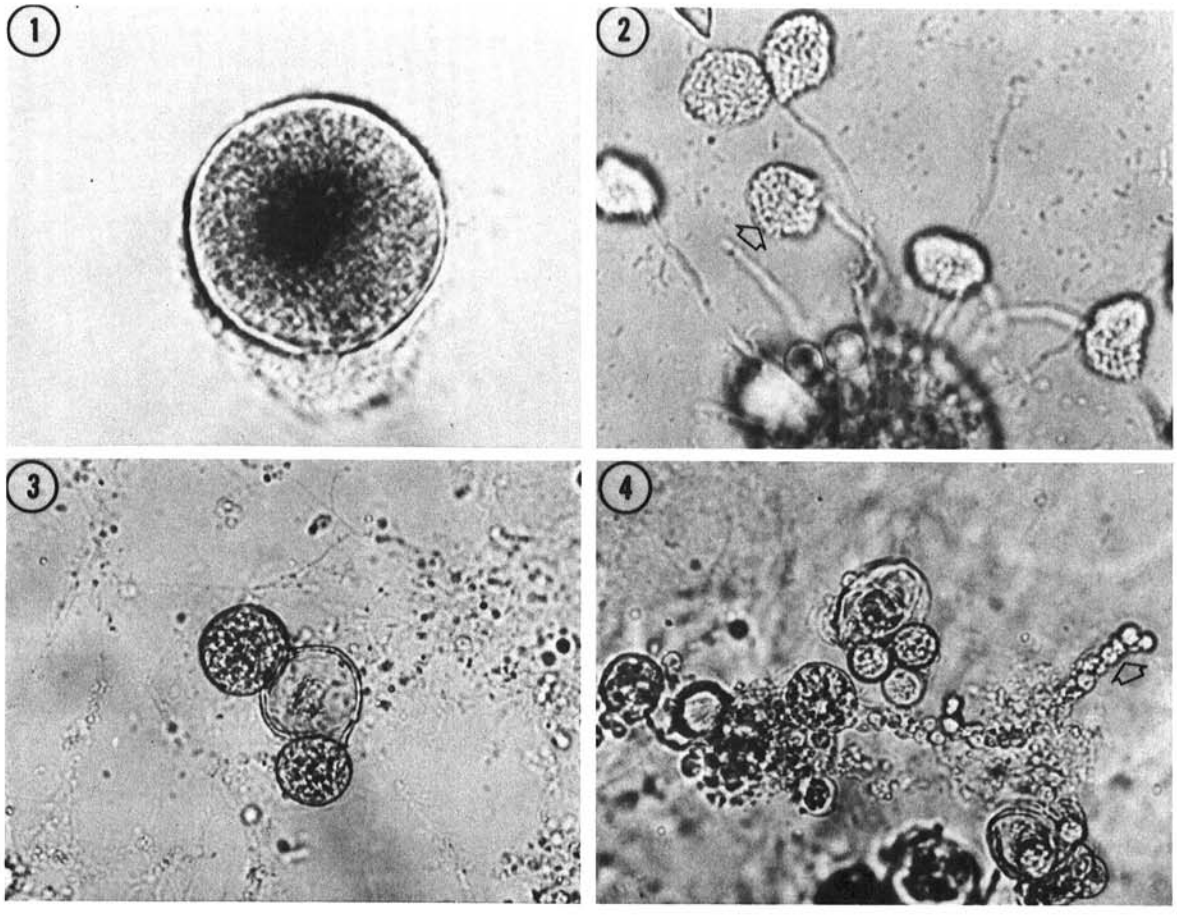

Fig. 1-4. Oospores of *Phytophthora megasperma* var. *sojae* parasitized by bacteria and chytridiomycetes. **1)** *Pseudomonas* sp. (×1,000). **2)** *Actinoplanes missouriensis* with terminal sporangia (arrow); zoospores are being differentiated within the sporangia, which are borne on thin sporangiophores emerging from the infected oospore (×1,000). **3)** *Rhizidiomycopsis japonicus*, with epibiotic thalli on the surface of an empty oospore (×400). **4)** *R. japonicus* with a discharge tube containing zoospores (arrow) (×400).

suspension containing bacteria, mycelial fragments, spores of hyphomycetes, or zoospores of the chytrids or actinomycetes was placed on each of the membranes. After 3-10 days incubation at 23 ± 2 C, the oospores were recovered and examined for infection by the parasites.

Quantitative evaluation of oospore infection by parasites in soil.—Two soil samples from an apple orchard in Wisconsin were used. One, a sandy loam with pH 6.0, was taken from an area with apparently healthy trees. The other, a silt loam with pH 5.9, was taken from an area where trees were infected with *P. cactorum*. Oospores of *P. megasperma* var. *sojae*, *P. cactorum*, *Pythium* sp., and *A. euteiches* were incubated in soils at 25, 50, and 150% of water-holding capacity. As before, membranes bearing oospores were floated on the flooded soil samples or buried in the soils when moisture contents were below saturation. In each treatment, 200 oospores were observed on each of four membrane filters.

All experiments were repeated two to four times with similar results.

RESULTS

Oospores of *P. megasperma* var. *sojae* incubated in 10 soils collected from different areas in Michigan were parasitized by a wide range of soil microorganisms, including oomycetes, chytridiomycetes, hyphomycetes, actinomycetes, and bacteria.

Infection of oospores by bacteria.—Bacteria frequently infected the oospores on flooded soil. Of the two identified, one was a fluorescent *Pseudomonas* sp., and the other a nonfluorescent *Pseudomonas* sp. (Fig. 1). The bacterial cells were motile within the infected oospore, and completely digested the cytoplasm and the oospore wall, leaving an empty 'ghost' of the oogonial wall. Bacteria also invaded oospores infected by other parasites.

Oospore infection by an actinomycete.—A zoospore-producing actinomycete, *Actinoplanes missouriensis* Couch, frequently infected the oospores on flooded soil (Fig. 2). The walls of infected oospores were lysed, and the

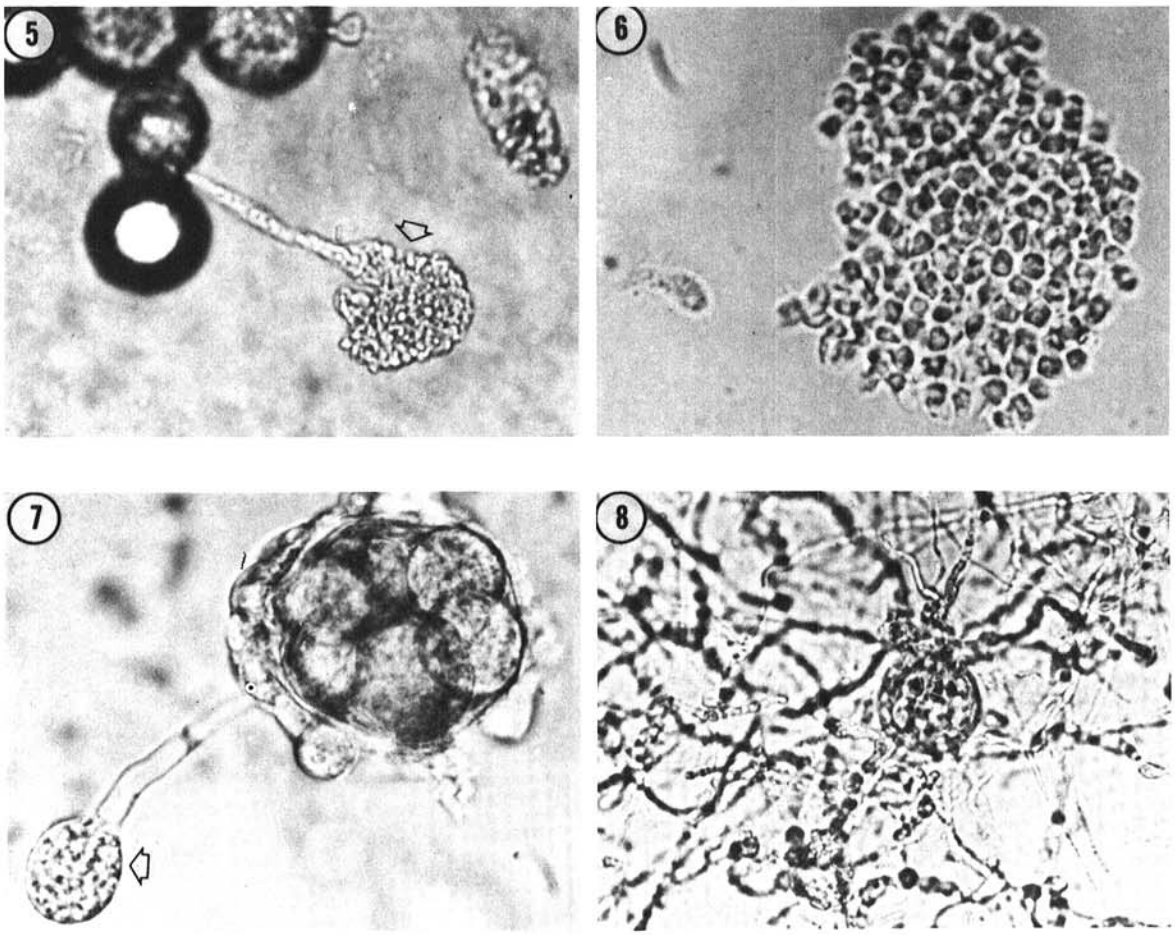

Fig. 5-8. Oospores of *Phytophthora megasperma* var. *sojae* parasitized by chytridiomycetes. **5)** *Canteriomyces stigeoclonii*, with an undifferentiated mass of protoplasm (arrow) being discharged through a tube from an infected oospore (×400). **6)** Differentiation of *C. stigeoclonii* zoospores 15-25 min after discharge of protoplasm (×1,000). **7)** *Hyphochytrium catenoides*, with discharge tube emerging from an infected oospore and terminating in a vesicle (arrow) (×1,000). **8)** Sterile mycelial isolate growing from an infected oospore (×400).

contents usually became disorganized and concentrated in the center of the oospore. Hyphae with terminal sporangia extended from the infected oospores. In the presence of free water, tiny zoospores (1.5 μm in diameter) were differentiated within the sporangia, and were released within 1-3 hr.

Oospore infection by chytridiomycetes.—Oospores incubated in flooded soil were infected with epibiotic and endobiotic chytrids. The following three species were identified: (i) *Rhizidiomycopsis japonicus* Kobaiashi & Oukubo (Fig. 3) is an epibiotic parasite. Anteriorly uniflagellate and spherical zoospores encysted on the outer surface of the oospores and infected the oospores by means of rhizoids. The thalli grew exteriorly and developed into sporangia. In the presence of free water, zoospores were differentiated within the sporangia. In aerobic conditions, zoospores were discharged through one to three pores, whereas in microaerophilic conditions they exited through a discharge tube (Fig. 4) (F. K. Sparrow, *personal communication*). (ii) *Canteriomyces stigeoclonii* (De Wild.) Canter. Infected oospores contained one or more endobiotic thalli. In the presence of free water, the undifferentiated protoplasm was released through a discharge tube (Fig. 5), and within 15-30 min uniflagellate elongated zoospores were differentiated (Fig. 6). On Miller's M_3 medium (20), individual zoospores encysted and developed into single thalli. Zoospores were released only in nutrient-deprived conditions; i.e., in sterile distilled water. (iii) *Hyphochytrium catenoides* Karling also is an endobiotic parasite. Oospores infected with *H. catenoides* resembled those infected with *C. stigeoclonii*, except that the thalli of *H. catenoides* developed into sporangia. Zoospores similar to those of *C. stigeoclonii* frequently differentiated within the sporangium, and were released via a discharge tube terminating in a vesicle (Fig. 7). Zoospores placed on agar media grew into hyphal colonies with typically swollen cells, each of which became a sporangium when the culture was flooded with water. A culture isolated from oospores of *A. euteiches* by W. A. Ayers (U. S. Department of Agriculture, Beltsville, MD 20705) and another isolated from microsclerotia of *Verticillium dahliae* by W. J. Tolmsoff (U.S. Department of Agriculture, Agricultural Research Service, National Cotton Pathology Research Laboratory, College Station, TX 77840) infected

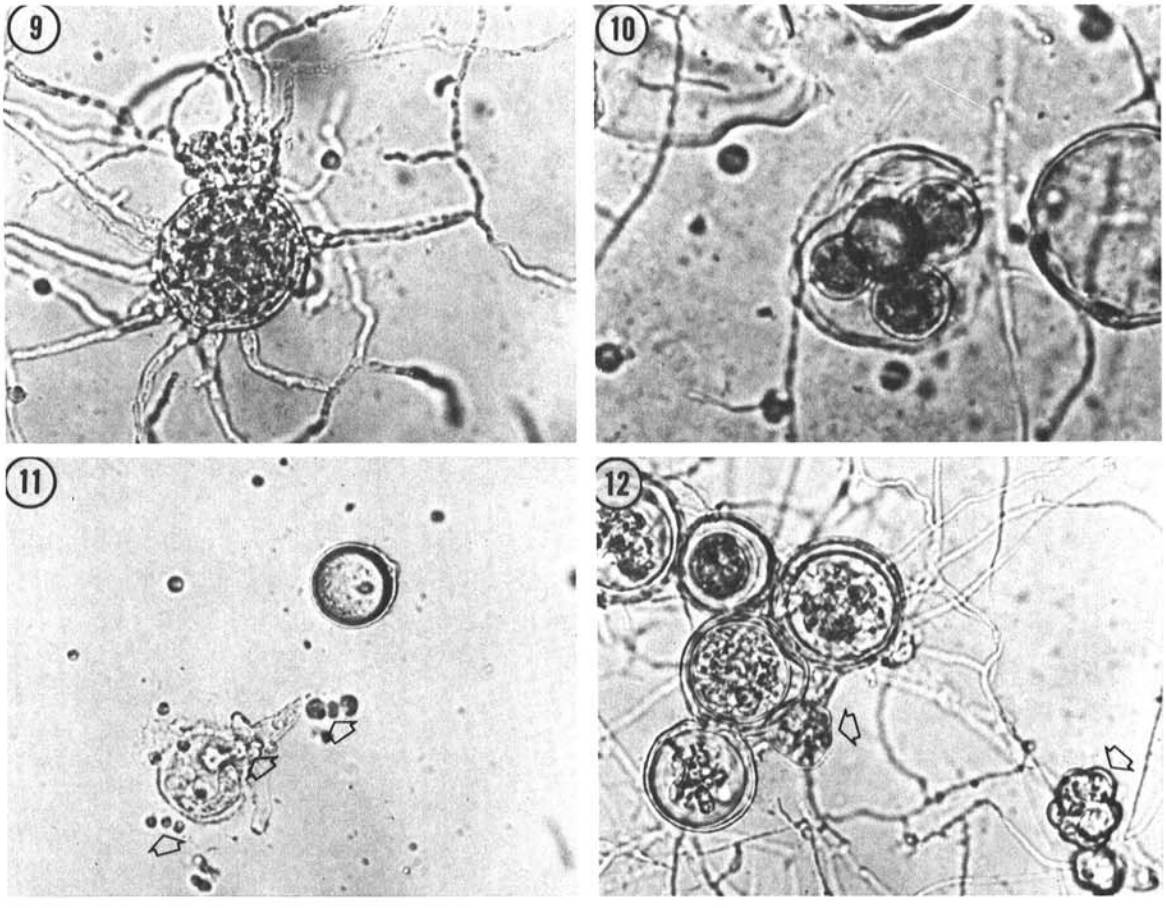

Fig. 9-12. Oospores of *Pytophthora megasperma* var. *sojae* parasitized by oomycetes and hyphomycetes. **9)** Hyphae of *Pythium* sp. growing from an oospore (×600). **10)** Oospores of *Pythium* sp. within an infected oospore (×760). **11)** *Leptolegnia* sp., with spherical zoospores (arrows) (×400). **12)** Chlamydospores of *Diheterospora chlamydosporia* (arrows) (×760).

oospores of *P. megasperma* var. *sojae* and *P. cactorum* in a manner similar to our isolate.

Oospore infection by oomycetes.—In flooded soil, the following oomycetes were observed infecting oospores: (i) A nonseptate, slow-growing isolate with sterile mycelium, and presumably an oomycete (Fig. 8). (ii) An isolate of *Pythium* sp. was very destructive to oospores of *P. megasperma* var. *sojae* when free water required for zoospore production was present. Hyphal growth of the parasite from an infected oospore often was abundant (Fig. 9). The parasite produced small oospores (14 μm in diameter), usually within the host (Fig. 10), but occasionally outside it. (iii) *Leptolegnia* sp. In the presence of free water, the hyphae of this parasite emerged from the host and became sporangia. Spherical zoospores developed in a linear array and were released terminally (Fig. 11).

Oospore infection by hyphomycetes.—At soil moisture levels below saturation, oospores were infected with the following hyphomycetes: (i) *Humicola fuscoatra* Traaen. The hyphae of this parasite penetrated the oospores, consumed their contents, and formed aleurospores in or near the host (Fig. 12). (ii) *Diheterospora chlamydosporia* (Komischko) Barron & Onions. Contents of infected oospores disintegrated and became granular in appearance (Fig. 13). This fungus, which has a *Verticillium* sp. conidial stage, produces four- to 10-celled chlamydospores. (iii) *Fusarium oxysporum* (Schlecht.) Snyd. & Hans. frequently infected oospores (Fig. 14) and produced chlamydospores either outside or within the host oospore. Less frequently, microconidia and macroconidia were produced externally. (iv) *Cephalosporium* sp. produced chlamydospores within the host oospores, and abundant hyphae extended from the host (Fig. 15). (v) *Alternaria alternata* Fr. (Keissl.) produced typical conidia on hyphae growing from infected oospores (Fig. 16). (vi) *Dactylella spermatophaga* Drechs., which was described by Drechsler (12) as a parasite of oospores of *Pythium* spp., was isolated from oospores of *P. megasperma* var. *sojae* and *P. cactorum*.

Oospore infection by chytrids in two soils.—Chytrids parasitized oospores of *P. cactorum*, *P. megasperma* var. *sojae*, *Pythium* sp., and *A. euteiches* in both orchard soils

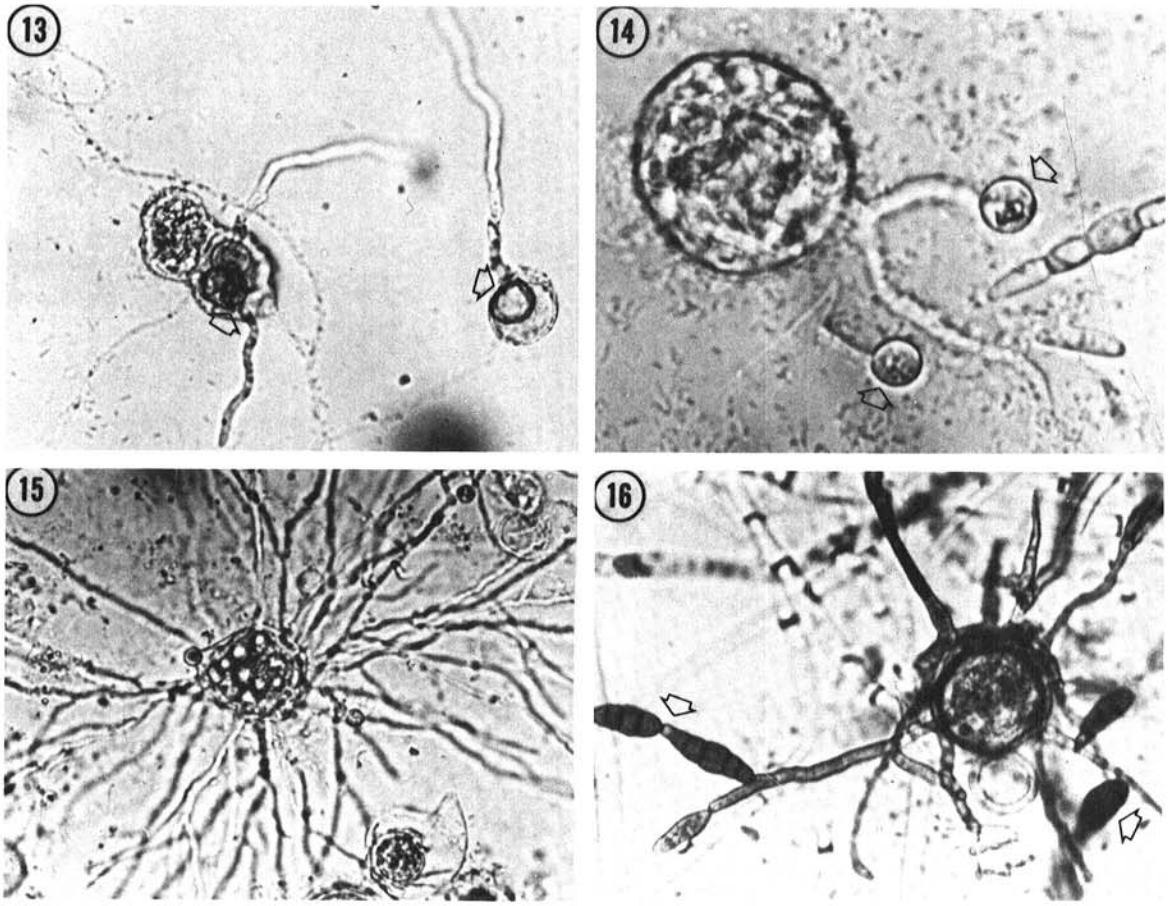

Fig. 13-16. Oospores of *Phytophthora megasperma* var. *sojae* parasitized by hyphomycetes. **13)** Germinated aleurospores of *Humicola fuscoatra* in an infected oospore (arrows) (×400). **14)** *Fusarium oxysporum*, with chlamydospores (arrow) and macroconidia that are formed on the hyphae (×1,000). **15)** *Cephalosporium* sp. hyphae growing from an infected oospore (×400). **16)** *Alternaria alternata* hyphae and conidia (arrows) growing from an infected oospore (×400).

(Fig. 17). Five-40% of the oospores were parasitized within 1 week, and 12-58% in 3 weeks. More ospores of *P. megasperma* var. *sojae* and *P. cactorum* were infected than were those of the other two species. Oospore infection of all four species was significantly higher in soil collected near healthy apple trees than in soil collected near trees infected with *P. cactorum* (e.g., 58% vs. 24% oospore infection for *P. cactorum*, respectively).

In another experiment, the frequency of infection of oospores of *P. cactorum* and *P. megasperma* var. *sojae* was determined after 2 weeks' incubation in the same two soils at 25%, 50%, and 150% of water-holding capacity. In flooded soil, many oospores of both species were parasitized by chytrids, whereas only a few were parasitized by hyphomycetes and bacteria (Table 1). By contrast, at soil moistures below saturation there was no infection by chytrids, but many oospores were infected by hyphomycetes. The most frequently occurring and destructive species were *F. oxysporum*, *D. chlamydosporia*, *H. fuscoatra*, and *D. spermatophaga*. Oospore infection either by chytrids or hyphomycetes in soil collected near apparently healthy apple trees was greater than that in the soil near apple trees that were infected by *P. cactorum*. Relatively few oospores were infected by bacteria in either soil.

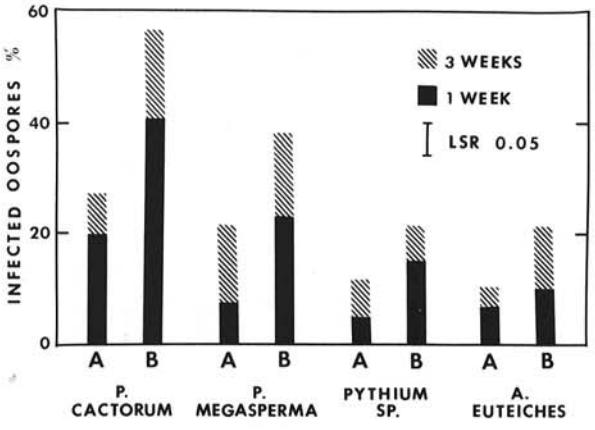

Fig. 17. Infection of oospores of *Phytophthora cactorum*, *P. megasperma* var. *sojae*, *Pythium* sp., and *Aphanomyces euteiches* by chytrid parasites in two soils: soil A is from a portion of an apple orchard in which trees were infected with *P. cactorum*, and soil B is from a portion in which trees apparently were free of infection with *P. cactorum*.

DISCUSSION

Oospores of *P. megasperma* var. *sojae*, *P. cactorum*, *Pythium* sp., and *A. euteiches* were parasitized by a great diversity of soil microorganisms including oomycetes, hyphomycetes, chytridiomycetes, actinomycetes, and bacteria. There may be a succession of oospore infections by different groups of parasites as soil moisture conditions change. In relatively dry soil, streptomycetes (14) and hyphomycetes appeared to dominate, whereas in wet soil oomycetes, chytridiomycetes, and *Actinoplanes missouriensis* predominated.

Members of the Actinoplanaceae have not been reported previously as fungal parasites, although they have been isolated from nonliving keratinous and chitinous materials (9, 10, 24).

Many different chytrids have been found to parasitize algal filaments and hyphae of aquatic Phycomycetes. For example, *Rosella* sp. and *Allomyces* sp. (24), and *Pleolpidium inflatum* (25) were parasitic upon the hyphae

TABLE 1. Effect of soil moisture on infection of oospores of *Phytophthora* spp. by hyphomycetes, chytrids, and bacteria after incubation for 2 wk in two soils.

Oospores of	Soil[a]	Soil moisture (% of waterholding capacity)	Oospores parasitized[b] by:		
			Hyphomycetes (%)	Chytrids (%)	Bacteria (%)
P. cactorum	A	25	15	0	0
		50	19	0	4
		150	0	6	5
	B	25	26	0	0
		50	41	0	7
		150	0	39	3
P. megasperma var. *sojae*	A	25	56	0	0
		50	64	0	4
		150	3	63	7
	B	25	66	0	0
		50	80	0	3
		150	9	78	2

[a]Soil A is from a portion of an apple orchard infected with *P. cactorum*; Soil B is from a portion of the same orchard apparently free of infected trees.

[b]Membrane filters bearing oospores were floated on the flooded soil, or were buried in the soil at moistures below saturation. Upon recovery from soil, 200 oospores on each of four membranes were observed for each treatment. LSR = Least significant range by Tukey's 'w' procedure was 7.0 ($P = 0.05$).

of *Pythium* and *Phytophthora* spp. However, there are few reports of oogonial or oospore parasitism by chytrids. *Rhizidiomycopsis japonicus* infected oogonia of *Aplanes* sp. in water (24), and *Phlyctochytrium* sp. parasitized oospores of *Sclerospora sorghi* in soil (19). In the present study, the endobiotic parasites, *C. stigeoclonii* and *H. catenoides*, were found more frequently than the epibiotic parasite, *R. japonicus*. *Canteriomyces stigeoclonii* [syn. *Olpidium* sp. and *Anisolpidium stigeoclonii* (8, 24)], also is a parasite of the algae *Stigeoclonium* sp. and *Draparnaldia* sp. (24). *Hyphochytrium cantenoides* also is a weak parasite of *Zea mays*, *Nitella flexilis*, and *Chara coronata* (24).

Oospores also were parasitized by species of the oomycete genera *Pythium* and *Leptolegnia*, and by the hyphomycete genera *Dactylella*, *Diheterospora*, *Fusarium*, *Cephalosporium*, and *Alternaria*; species of the hyphomycete genera *Dactylella*, *Trinacrium*, and *Trichothecium* previously were reported to parasitize oospores of *Pythium* spp. (12, 13, 14, 15, 16); a *Fusarium* sp. previously was found to be parasitic on the hyphae of species of the mucorales and on *Rhizoctonia solani* (21); and *Diheterospora chlamydosporia* previously was found parasitizing snail eggs (3, 4).

An important question is whether oospores were alive at the time they were invaded by the hyperparasites. In other work (Sneh and Lockwood, *unpublished*), oospores of *P. megasperma* var. *sojae* from the same cultures as those used in the present work showed at least 70% germinability. The percentage viability probably was greater than 70%, since virtually all the oospores contained apparently living protoplasm, but may have been dormant. In any case, when the incidence of parasitism exceeded 30%, living oospores certainly were being parasitized; in some instances as many as 89% of the oospores were parasitized (Table 1).

Our results indicate that soils contain a large number and great diversity of oospore parasites, which may have the potential to reduce populations of plant pathogenic Phycomycetes in soil. Their presence may be a factor in the suppressiveness of some soils towards these pathogens (6). Further work is needed to correlate oospore parasitism and disease incidence in other soils, and to evaluate the significance of oospore parasitism in soil under natural conditions. Such oospores may become melanized and possibly more resistant to parasitic invasion than those produced in vitro (17). Moreover, oospores produced in plant tissues may be afforded some protection by residues of those tissues.

LITERATURE CITED

1. AYERS, W. A., and R. D. LUMSDEN. 1975. Factors affecting production and germination of oospores of three Pythium species. Phytopathology 65:1094-1100.
2. BARNETT, H. L. 1963. The nature of mycoparasitism by fungi. Annu. Rev. Microbiol. 17:1-14.
3. BARRON, G. L. 1968. The genera of Hyphomycetes from soil. Williams and Wilkins, Baltimore, Maryland. 364 p.
4. BARRON, G. L., and A. H. S. ONIONS. 1966. Verticillium chlamydosporium and its relationships to Diheterospora, Stemphyliopsis and Paecilomyces. Can. J. Bot. 44:861-869.
5. BOOSALIS, M. G. 1964. Hyperparasitism. Annu. Rev. Phytopathol. 2:363-376.
6. BROADBENT, P., and K. F. BAKER. 1974. Behaviour of Phytophthora cinnamomi in soils suppressive and conducive to root rot. Austr. J. Agric. Res. 25:121-137.
7. BUCHANAN, R. E., and N. E. GIBBONS. 1974. Bergey's manual of determinative bacteriology. 8th ed. Williams and Wilkins, Baltimore, Maryland. 1,246 p.
8. CANTER, H. M. 1953. Annotated list of British aquatic chytrids. Trans. Br. Mycol. Soc. 36:278-303.
9. COUCH, J. N. 1963. Some new genera and species of the Actinoplanaceae. J. Elisha Mitchell Sci. Soc. 79:53-70.
10. CROSS, T., and M. GOODFELLOW. 1973. Taxonomy of the actinomycetes. Pages 11-112 *in* G. Sykes and F. A. Skinner, eds. Actinomycetales: characteristics and practical importance. Academic Press, London and New York. 339 p.
11. DEVAY, J. E. 1956. Mutual relationships in fungi. Annu. Rev. Microbiol. 10:115-140.
12. DRECHSLER, C. 1938. Two hyphomycetes parasitic on oospores of root-rotting Oomycetes. Phytopathology 28:81-103.
13. DRECHSLER, C. 1943. Another hyphomycetous fungus parasitic on Pythium oospores. Phytopathology 33:227-233.
14. DRECHSLER, C. 1952. Another nematode-strangulating Dactylella parasitic on Pythium oospores. Mycologia 44:533-556.
15. DRECHSLER, C. 1961. Two additional species of Dactylella parasitic on Pythium oospores. Sydowia 15:92-97.
16. DRECHSLER, C. 1963. A slender-spored Dactylella parasitic on Pythium oospores. Phytopathology 53:1050-1052.
17. HONOUR, R. C., and P. H. TSAO. 1973. Lysis of Phytophthora parasitica oospores in soil. Abstract No. 36 *in* Abstracts of papers. 2nd Int. Congr. Plant Pathol., 5-12 September 1973, Minneapolis, Minnesota, (unpaged).
18. KARLING, J. S. 1942. Parasitism among the chytrids. Am. J. Bot. 29:24-35.
19. KENNETH, R., E. COHEN, and G. SHAHOR. 1975. A species of Phlyctochytrium attacking nematodes and oospores of downy mildew fungi. Phytoparasitica 3:70 (Abstr.).
20. MILLER, C. E. 1967. Isolation and pure culture of aquatic Phycomycetes by membrane filtration. Mycologia 59:524-527.
21. RAYBAUD, L. 1921. Sur un Fusarium parasité de quelques Mucorinnees. C. R. Soc. Biol. Paris 84:213-215.
22. SNEH, B. 1972. Use of cellulase and hemicellulase for the separation of Phytophthora cactorum oospores from mycelium mats. Can. J. Bot. 50:2685-2686.
23. SNEH, B. 1976. A method for observation and study of living fungal propagules incubated in soil. Soil Biol. Biochem. 9:65-66.
24. SPARROW, F. K. 1960. Aquatic Phycomycetes. University of Michigan Press, Ann Arbor. 1,187 p.
25. WATERHOUSE, G. M. 1940. A chytrid allied to Pleolpidium inflatum Butler. Trans. Br. Mycol. Soc. 24:7-19.