Factors Affecting Oospore Germination in Phytophthora cactorum, the Incitant of Apple Collar Rot

Z. Banihashemi and J. E. Mitchell

Associate Professor, Department of Plant Protection, College of Agriculture, Pahlavi University, Shiraz, Iran; and Professor, Department of Plant Pathology, University of Wisconsin, Madison 53706.

Research supported by the College of Agricultural and Life Sciences, University of Wisconsin, Madison, and by Hatch Project No. 1281.

Accepted for publication 10 September 1975.

ABSTRACT

BANIHASHEMI, Z., and J. E. MITCHELL. 1976. Factors affecting oospore germination in Phytophthora cactorum, the incitant of apple collar rot. Phytopathology 66: 443-448

Oospores of *Phytophthora cactorum* produced in cultures grown in the dark required light for germination. A few oospores produced under continuous light germinated in the dark, but light was required for good germination. Germination increased with increasing light intensity up to 4,330 lux. Germination was greatest in light passing an indigo filter (440 nm) and lowest in that passing an orange filter (575 nm). The optimum temperature for oospore germination was 20 C and oospores failed to germinate on water agar at 28 C, the optimum temperature for mycelial growth. Both aging and treatment with 1% Glusulase (glucuronidase and sulfatase) increased oospore germination. Germination was decreased by adding $CaCl_2$ at concentrations above 25 μg/ml. Germination was not affected by agar concentration, by 100 μg/ml Tergitol NPX, or by 200 μg/ml vancomycin. Germination was decreased when pimaricin concentration exceeded 7.5 μg/ml and was only 17% of the control with 100 μg/ml pimaricin. Likewise, germination was decreased 50% by 0.5% D-glucose and 1% sucrose, and 40% by 200 μg/ml polymyxin B.

Additional key words: Malus sylvestris, soil-borne pathogen, light, soil extract.

Oospores are important survival propagules, especially in homothallic species of *Phytophthora,* and are the major potential source of variation in nature (24). One of the major problems encountered in the study of oospores in species of *Phytophthora* has been their low level of germination. Blackwell (3) in 1943 stated the difficulties she had experienced for many years in attempting to germinate oospores of *Phytophthora cactorum.* She found that aging and chilling increased germination of oospores. Since then, many workers have studied the germination of oospores of homothallic as well as heterothallic species of *Phytophthora.* Conditions influencing oospore formation (4, 7, 10, 11, 12, 13, 16, 19) and germination (2, 6, 9, 10, 13, 15, 16, 17, 20, 21) have been studied during the past decade.

Light appeared to be one of the most important environmental conditions affecting the formation of oospores in *Phytophthora* spp. Harnish (7) studied the effect of light on oospore and sporangium formation in ten species of *Phytophthora* and found that in most species, white light at high intensity reduced or inhibited oospore formation and stimulated sporangium formation. Abundant oospores were formed in continuous darkness in all species tested. Daylight and blue light stimulated the production of sporangia, whereas darkness and red light favored oospore formation in *P. cactorum* and *P. capsici.* The action spectrum effective in inhibiting oospore production in these two species was found to be between 390 and 600 nm. Savage (19) found that green and blue light inhibited oospore production in some *Phytophthora* spp., whereas under red light, abundant oospores were formed. Klisiewicz (13) found that *P. drechsleri* produced many oospores in the dark, but very few in continuous white light. He found that continuous darkness or darkness alternated with light was required for sexual reproduction.

Romero and Gallegly (16) reported that oospores of *P. infestans* germinated best in blue and green light and that very little germination occurred in light passing a red filter. Berg and Gallegly (2) later showed that maximum germination of oospores of *P. cactorum* occurred under blue (400-480 nm) and far-red (700-1,000 nm) filters. Very few oospores had germinated in the dark, even after 30 days of incubation.

Very little work has been done on effect of light intensity on either oospore formation or germination in *Phytophthora* spp. Huguenin and Boccas (11) found that the rate of sexual reproduction in *P. palmivora* decreased as a function of light intensity. Hebert and Kelman (8) working with the resting sporangia of *Physoderma maydis* found that light intensity from 0-130 lux increased germination significantly, but that higher light intensity did not.

The purpose of the present investigation was to study conditions affecting germination of oospores of *P. cactorum,* the incitant of apple collar rot. A preliminary report of this work appeared earlier (1).

MATERIALS AND METHODS

Single zoospore cultures of *P. cactorum* obtained from diseased apple trees were used throughout the experiment. The pathogen was grown in 140-ml medicine bottles containing 20 ml of cleared V-8 broth supplemented with 30 mg/liter of beta sitosterol (6). Bottles were incubated on their sides in the dark at 20-22 C for 2-4 months, unless otherwise specified. When oospores were needed, mycelial mats from one or more bottles were removed and sonicated for 30 seconds in 8-10 ml of sterile distilled water. The suspension, which consisted mostly of oospores, was frozen for 24 hours at −20 C to kill mycelial fragments and sporangia (18). After thawing, the oospores were washed twice with sterile distilled water by centrifugation at 4,000 *g* for 15 minutes. A part of the suspension was diluted with sterile distilled water and used for germination studies and the remainder was stored at 4 C until used. For enzyme treatment, 1 ml of undiluted oospore suspension was mixed with 1 ml of 2% Glusulase (a mixture containing 181,500 units glucuronidase and 84,180 units sulfatase per milliliter, Endo Laboratories, Inc., Garden City, New York) in sterile distilled water. The mixture was incubated for 24 hours in conical glass centrifuge tubes in the dark at 24 C (17). Oospores free of mycelium sedimented to the bottom of the tubes and the supernatant was decanted. The sedimented oospores were diluted with sterile distilled water to the desired concentration.

Oospore germination was studied on 2% water agar or in sterile distilled water unless otherwise indicated. The concentration of oospores in each case was adjusted so that about one to five oospores could be observed in each × 100 microscope field. One drop of oospore suspension was placed in a 60-mm diameter plastic petri plate containing 10 ml of sterile distilled water, or 1 ml of a more diluted oospore suspension was spread over the surface of water agar in a 90-mm diameter plate. Plates were incubated for 3-7 days under 2,150-2,480 lux illumination at 21-22 C unless otherwise specified.

The light source in both light intensity and light filter experiments was a combination of cool-white fluorescent and incandescent lights. Temperature on the agar surface was measured by means of a thermocouple and remained within the optimum range.

The desired light intensity was obtained by varying the number of layers of cheesecloth on the top of the boxes. An opening in one side covered with several layers of cheesecloth provided the ventilation required to minimize temperature differences at the various light intensities. To study the effect of light spectra on germination of oospores, plastic filters with the following transmission peaks were used: violet (380 nm), indigo (440 nm), blue (two peaks at 410 and 550 nm), green (550 nm), yellow (575 nm), orange (575 nm), and red (625 nm).

For temperature studies, plates were incubated in water baths that provided constant temperatures of 16, 20, 24, and 28 C in a growth chamber with an ambient temperature of 16 C and with 4,630 lux of cool-white fluorescent illumination. Thermocouples were inserted in the agar to monitor the temperatures during the experiment.

Soil extracts were obtained by mixing 1 kg of orchard soil and 1 liter of glass-distilled water by periodic hand stirring for 30 minutes. This was allowed to settle overnight at room temperature and the supernatant was passed through double layers of cheesecloth and then centrifuged at 4,000 rpm for 15 minutes. The supernatant was used after (a) no further treatment, (b) autoclaving for 20 minutes, (c) further centrifuging at 10,000 *g* for 30 minutes, or (d) filtering through 0.25-μm pore size filter.

Oospore germination was observed with an inverted microscope at × 100 magnification. The internal structure of oospores changed during the germination process before the formation of germ tubes. After incubation, oospores were classified as (i) unchanged oospores with thick wall, a smooth surface and glossy appearance, (ii) activated oospores with a thin wall and contents having a light-brown color with granular appearance and sometimes swollen, but without a germ tube, or (iii) germinated oospores; i.e., with a germ tube and generally with a sporangium. About 150-200 oospores were counted in each of three or four replicate plates and the percentages of activated oospores and of germinated oospores were calculated. All experiments were repeated at least twice.

RESULTS

Preparation of oospore suspension.—Sonication of mycelial mats resulted in a good fragmentation of mycelium and release of oospores, but it did not kill all sporangia and mycelial fragments. Freezing at −20 C for 24 hours killed all sporangia and mycelial fragments without adverse effect on oospore germination.

Effect of light on oospore germination.—To determine the effect of culture age and Glusulase treatment on oospore viability, three single-zoospore isolates of *P. cactorum* were incubated at room temperature in diffuse fluorescent light. Oospores were harvested weekly after 2 weeks of incubation and a suspension was prepared. A portion of each oospore suspension was treated with 1% Glusulase. Both enzyme-treated and nontreated oospores were incubated in sterile distilled water for 7 days at 22 C under 2,480 lux of cool-white fluorescent light and germination was counted. All isolates responded similarly. Oospore germination increased with age of culture from 14 - 38%. Glusulase treatment increased germination in younger oospore populations, but no differences in ultimate germination were observed when cultures 5 weeks or more of age were pretreated with enzyme. There was a difference in rate of germination, for a higher percentage of treated than untreated oospores had germinated when counts were made after 3 - 4 days instead of 7 days of incubation.

Preliminary experiments confirmed earlier reports that light was required for oospore germination. Oospores obtained from cultures grown under darkness and diffuse light and also oospores from dark-grown cultures treated with 1% Glusulase did not germinate in the dark (Table 1). Occasionally, as many as 1% of oospores grown in alternating dark and light germinated after prolonged incubation in the dark. In the light there were 3 - 5% activated oospores which had not yet germinated, but none in the dark treatments.

The duration of exposure of oospores to light during the germination process was also important (Table 2). When oospores were exposed to light for various periods

TABLE 1. Effect of light and enzyme treatment on germination of oospores of *Phytophthora cactorum*

Light treatment during		Oospore treatment before germination	Germinated oospores (%)	Activated oospores[b] (%)
Growth[a]	Germination			
Dark	Light	Freezing	49.3[c]	4.1[c]
Dark and light	Light	Freezing	62.1	5.4
Dark	Light	Freezing and enzyme	76.1	3.5
Dark	Dark	Freezing	0.0	0.0
Dark and light	Dark	Freezing	0.6	0.0
Dark	Dark	Freezing and enzyme	0.0	0.0

[a]Cultures were grown in the dark or in diffuse light at 20-22 C for approximately 4 months.
[b]Nongerminated oospores which have undergone the initial changes in internal structure which precede germ-tube development.
[c]Percent of total population of oospores in the specified states after incubation in sterile distilled water for 4 days with 2,165 lux of continuous cool-white fluorescent illumination.

TABLE 2. Effect of duration of exposure to light on germination of oospores of *Phytophthora cactorum*

Initial light period (hours)	Subsequent dark period (hours)	Germinated oospores (%)[b]	Activated oospores[a] (%)[b]
108	0	91.2	4.1
96	12	88.9	2.3
84	24	91.4	2.0
72	36	87.4	2.5
60	48	82.6	2.4
48	60	69.7	2.5
36	72	26.6	1.4
24	84	3.1	1.2
12	96	0.3	0.3
6	102	0.0	0.0
0	108	0.0	0.0

[a]Nongerminated oospores which have undergone the initial changes in internal structure which precede germ-tube development.
[b]Percent of total population of oospores in the specified states after incubation in sterile distilled water at 22 C for designated periods with 2,594 lux continuous cool-white fluorescent illumination and then in the dark.

TABLE 3. Effect of light intensity on germination of oospores of *Phytophthora cactorum*

Light intensity (lux)	Germinated oospores (%)[b] after		Activated oospores[a] (%)[b] after	
	70 hours	92 hours	70 hours	92 hours
104	0.0	3.9	2.8	12.6
544	0.3	30.3	7.4	18.5
1,080	0.3	27.1	7.0	24.2
2,165	8.8	66.0	22.7	11.9
3,240	40.2	87.9	19.8	1.3
4,330	55.3	86.7	15.9	1.7
6,480	47.6	74.4	9.6	3.7
10,830	29.9	66.4	12.4	4.5

[a]Nongerminated oospores which have undergone the initial changes in internal structure which precede germ-tube development.
[b]Percent of total population of oospores in the specified states after incubation on 2% water agar under cool-white fluorescent and incandescent bulbs at 20-24 C for indicated time.

and then placed in the dark, germination increased with an increase in time of light exposure up to 60 hours. No oospores germinated after exposure to 6 hours of light, followed by 102 hours of dark incubation; and 24 hours of incubation in light resulted in only 3% germination of oospores. However, when oospores were incubated in the light for 48 hours and then in the dark for 60 hours, 70% had germinated and most had sporangia. A few additional spores had been activated, but had not germinated. The light effect appears to be on the activation process, because no germination had occurred at the end of the 48-hour light period.

Preliminary results showed that under cool-white fluorescent illumination germination of oospores increased as light intensity increased. Very little effect was found from 104-2,165 lux, but there was a sharp increase at 2,165 lux. The range in intensities was expanded in an experiment in a controlled-environment growth chamber under fluorescent and incandescent light using light intensities from 0 to 10,830 lux. Temperatures on agar

TABLE 4. Effect of light color on germination of oospores of *Phytophthora cactorum*

Light color (spectral peak)	Germinated oospores (%)[b]	Activated oospores[a] (%)[b]
Violet (380 nm)	36.1	15.1
Indigo (440 nm)	42.7	17.5
Blue (410 and 550 nm)	30.8	15.5
Green (550 nm)	25.2	18.0
Yellow (575 nm)	31.0	14.1
Orange (575 nm)	1.6	0.9
Red (625 nm)	5.5	2.7

[a]Nongerminated oospores which have undergone the initial changes in internal structure which precede germ-tube development.

[b]Percent of total population of oospores in the specified states after incubation on 2% water agar at 20 C under continuous cool-white fluorescent and incandescent light for 92 hours.

under various intensities were measured by thermocouple and the air flow past the cultures in the growth chamber was adjusted so the temperature at the agar surface was comparable at all light intensities. Intensities above 10,830 lux could not be used due to the rise of temperature on the agar surface. Germination of oospores increased with increased intensity up to 4,330 lux and then declined at higher intensities (Table 3). A sharp increase was noticed at about 3,242 lux. Very little germination occurred at 104 lux, even after 92 hours of incubation. Under suboptimal light conditions, substantial numbers of oospores were activated, but had not yet germinated.

The effect of light spectra was investigated using seven color filters under fluorescent and incandescent bulbs. The temperature on agar under the filters was maintained between 22-24 C. The highest rate of germination occurred under the indigo filter (Table 4). The lowest germination occurred under the orange filter, but increased slightly under the red filter. The effectiveness of the shorter wave lengths was emphasized by the lack of correlation between germination and intensity of incident radiation. The lowest light intensity (868 lux) and radiant energy (0.2×10^5 erg/cm^2/sec) and the highest light intensity (16,235 lux) and radiant energy (2×10^5 erg/cm^2/sec) were detected under the indigo and yellow filters, respectively.

The effect of exposure of cultures to light during oospore formation and maturation on subsequent germination of oospores was determined by growing cultures for 60 days at 22-24 C in the dark and with 104, 544, 1,075, and 2,165 lux under cool-white fluorescent bulbs. Oospores produced under continuous darkness were processed in the dark during sonication, freezing, and incubation for germination. For germination studies, oospores were incubated for 7 days at 22 C either in the dark or under 2,600 lux illumination from cool-white fluorescent bulbs. Maximum oospore formation occurred in continuous darkness and the number of oospores formed decreased as light intensities increased. Exposure to light during oospore development had a relatively small effect compared with similar exposure during germination. Oospores from cultures grown under 530 lux germinated 8% in the dark and 74% in the light. Those grown in the dark germinated 0.3% in the dark and 99% in the light. The same relationship held when intensities were increased fourfold.

Effect of temperature and nutrients.—The optimum temperature for oospore germination was lower than the optimum for mycelial growth. The latter increased uniformly between 16 and 28 C, while germination at 16, 20, 24, and 28 C was 41, 88, 62, and 0%, respectively. The optimum temperature for germination of oospores is believed to be about 22 C. Slower germination occurred at 16 C. The germination of oospores at 20 and 28 C after 3 days of incubation in autoclaved soil extract on water agar under optimum light conditions was 90% and 6%, respectively.

There was also an effect of certain nutrients on germination. Calcium was found to accelerate the rate of oospore germination over that in glass-distilled water. Germination in double glass-distilled deionized water at 67 hours and 96 hours was 3 and 50%, respectively, while that with 1 μg/ml $CaCl_2$ was 50 and 80% after the same intervals. Maximum stimulation occurred in the presence of 1 μg/ml of $CaCl_2$ and inhibition was observed above 25 μg/ml.

Although the rate of oospore activation increased substantially in the presence of 1 μg/ml of $CaCl_2$, it was still considerably lower than that in soil extracts. High germination occurred in soil extract prepared with various treatments (Table 5). Autoclaving the extract did not reduce the activity, but filtration through a 0.2-μm

TABLE 5. Effects of soil extract on germination of oospores of *Phytophthora cactorum*

Treatments	Germinated oospores (%)[b]	Activated oospores[a] (%)[b]
Glass-distilled water	1.3	19.5
Glass-distilled water + 1 μg/ml $CaCl_2$	29.7	37.7
Soil extract, nonautoclaved	82.6	4.4
Soil extract, autoclaved	81.5	2.0
Soil extract, nonautoclaved, but centrifuged at 10,000 *g*	76.7	14.1
Soil extract, nonautoclaved, but filtered through 0.2-μm pore size	65.7	0.2

[a]Nongerminated oospores which have undergone the initial changes in internal structure which precede germ-tube development.

[b]Percent of total population of oospores in the specified states after incubation for 4 days in test solutions at 21 C and 2,150 lux continuous cool-white fluorescent illumination.

pore-size filter appeared to reduce activity somewhat. This might be due to the adsorption of low amounts of nutrient present in soil extract.

Other substances used in culture media were tested for their effect on germination. Pimaricin at 100 μg/ml reduced oospore germination by 80%, but had little effect at 50 μg/ml or less. Greatest germination was obtained when less than 10 μg/ml pimaricin was used. Pimaricin at 100 μg/ml inhibited activation of oospores less than half as much as it did germination. Germination was not affected by agar concentration from 1.5-4.0%, by Tergitol NPX at 100 μg/ml or by vancomycin at 200 μg/ml. Germination was decreased 40% by polymyxin B at 200 units per milliliter, 50% by 0.5% glucose, and 50% by 1% sucrose.

DISCUSSION

Formation, development, and germination of oospores of *Phytophthora* species are known to be influenced by various environmental factors. In the present investigation, we have shown that a high proportion of oospores of *P. cactorum* would germinate if certain conditions were provided and that external conditions, as well as internal factors, influenced the extent of oospore germination.

Light was the most critical external factor that affected germination of oospores of *P. cactorum*. It was shown that both light quality and quantity affected the rate and amount of oospore germination. While Hebert and Kelman (8) reported that resting sporangia of *Physoderma maydis* did not respond to light if intensity was higher than 104 lux, in the present study, little germination of oospores occurred at 104 lux, and intensities of 3,242-4,330 lux were required for maximum germination. Whether this response to light intensity is general among *Phytophthora* species remains to be determined. The increase in germination at higher intensities might be due to the increased requirement for energy or to other triggering mechanisms involved during the germination process.

The duration of exposure of oospores to light also was important for germination. Very little germination (3%) occurred when oospores were exposed to light for 24 hours. An exposure of 48 hours or more was required for good germination (70% or higher). This period of exposure to light seemed to be required for some physiological and structural changes that must precede germ-tube and sporangium development. Light is not required after activation has occurred. The light requirement at this stage could not be replaced by enzyme treatment or by incubation in soil extract. Recently, Sneh and McIntosh (22) showed that when oospores of *P. cactorum* either were added to soil surface in petri dishes or mixed with the soil, some oospores germinated and produced sporangia. However, they did not indicate the light condition which prevailed during incubation. Whether the light requirement for germination of oospores can be satisfied by one or more soil factors is not known. Production of sporangia and germ tubes was not light dependent, since activated oospores could germinate in the dark. Klisiewicz (13) reported that germination of oospores of *P. drechsleri* produced under continuous light was similar in the presence and absence of light.

Effect of light quality was not clear from our results. Germination was greatest in the low intensity light passing an indigo filter, while very little germination occurred under the higher intensity light passing an orange filter. Germination tended to increase again under the red filter. While the results agree in general with those reported by others (2, 10, 16), a comparison needs to be made with light in narrow band widths of equal energy.

Optimum temperature for oospore germination (22 C) was found to be lower than for the mycelial growth of the pathogen (28 C). Germination was delayed 72 hours at 16 C. Very little or no germination occurred at 28 C when oospores were incubated on water agar or in sterile distilled water, but 16% germinated at this temperature in soil extract. This suggests that under natural soil conditions, oospores may germinate at all temperatures permitting mycelial growth. The activity of an oospore could be expected to begin at a temperature below 16 C and reach a peak at 20-24 C. Germination of oospores at low temperatures would be an important factor for infection early in the season with less competition from other soil microorganisms (5). This would suggest that any soil treatment aimed at disease control should be applied early in the season, if it is to markedly affect oospore germination and reduce infection of the susceptible host.

Stanghellini and Russell (23) reported that calcium was required during the pregermination stage of oospores of *Pythium aphanidermatum* and that calcium at 10-200 μg/ml induced endospore wall absorption. In the present investigation, we found that calcium at 1 μg/ml greatly accelerated the rate of oospore activation and was inhibitory at concentrations above 25 μg/ml. Oospores of *P. cactorum* germinated better in soil extract obtained from soil around apple trees than in glass-distilled water with and without 1 μg/ml of $CaCl_2$. Autoclaving, Millipore filtration, or high-speed centrifugation of soil extract did not affect appreciably its effectiveness in stimulating germination. The nutritional value of soil extract to germ-tube production may be of significance in the biology of the pathogen. Due to the ability of oospores of *P. cactorum* to germinate in sterile distilled water, on water agar, and in natural soil extract which usually contain low amounts of nutrient, it is reasonable to assume that they are relatively insensitive to a general soil fungistasis brought about by nutrient depletion (14).

Certain physiological changes apparently must occur before oospore germination is possible. Increases in oospore germination of *P. cactorum* have been obtained by incubation in soil for 30-60 days (22) or by passage through live water snails (20). In the present investigation, both aging the culture and treating oospores with Glusulase increased the rate of oospore germination. The aging period was shortened, however, when oospores were treated with enzyme.

Finally, it was shown that various components of culture media such as antibiotics, sugars, amino acids, and growth retardants also may influence the extent and rate of oospore germination.

These results contribute to our understanding of conditions that influence the germination of oospores, to the development of a means to isolate the organism from soil on selective agar media, and to our knowledge of the behavior of the pathogen in soil.

LITERATURE CITED

1. BANIHASHEMI, Z., and J. E. MITCHELL. 1974. Germination of oospores of Phytophthora cactorum. Annu. Proc. Am. Phytopathol. Soc. for 1974. 1:57-58. (Abstr.).
2. BERG, L. A., and M. E. GALLEGLY. 1966. Effect of light on oospore germination in species of Phytophthora. Phytopathology 56:583 (Abstr.).
3. BLACKWELL, E. 1943. On germinating the oospores of Phytophthora cactorum. Trans. Br. Mycol. Soc. 26:93-103.
4. BRASIER, C. M. 1969. The effect of light and temperature on reproduction of two tropical species of Phytophthora. Trans. Br. Mycol. Soc. 52:105-113.
5. BRAUN, H., and I. NIENHAUS. 1959. Fortegefuhrte Untersuchungen uber die Kragenfaule des Apfels (Phytophthora cactorum). Phytopathol. Z. 36:169-208.
6. ERWIN, D. C., and W. H. MC CORMICK. 1971. Germination of oospores produced by Phytophthora megasperma var. sojae. Mycologia 63:972-977.
7. HARNISH, W. N. 1965. Effect of light on production of oospores and sporangia in species of Phytophthora. Mycologia 57:85-90.
8. HEBERT, T. T., and A. KELMAN. 1958. Factors influencing the germination of resting sporangia of Physoderma maydis. Phytopathology 48:102-106.
9. HENRY, A. W., and D. STELFOX. 1968. Comparative behavior of the oospore and oogonia of Phytophthora citricola during germination on an artificial medium. Can. J. Bot. 46:1419-1421.
10. HUGUENIN, B. 1972. Influence de la lumier blanche sur les phases précoces de la gametogénese chez le Phytophthora palmivora. Butl. C. R. Acad. Sci., Ser. D, Paris 274:3214-3217.
11. HUGUENIN, B., and B. BOCCAS. 1971. Role de qualques facteurs dans la formation et la germination des oospores chez le Phytophthora palmivora Butl. Ann. Phytopathol. 3:353-371.
12. HUGUENIN, B., and R. JACQUES. 1973. Establissement du spectra d'action de la lumiere sur la sporogénese et l'oogénese de sourches du Phytophthora palmivora Butl. C. R. Acad. Sci., Ser. D, Paris 276:725-728.
13. KLISIEWICZ, J. M. 1970. Factors affecting production and germination of oospores of Phytophthora drechsleri. Phytopathology 60:1738-1742.
14. KO, W. K., and J. L. LOCKWOOD. 1967. Soil fungistasis: relation to fungal spore nutrition. Phytopathology 57:894-901.
15. LEAL, J. A., and B. GOMEZ-MIRANDA. 1965. The effect of light and darkness on the germination of the oospores of certain species of Phytophthora on some synthetic media. Trans. Br. Mycol. Soc. 48:491-494.
16. ROMERO, S., and M. E. GALLEGLY. 1962. The influence of temperature and light on formation and germination of oospores of Phytophthora infestans. Phytopathology 52:165 (Abstr.).
17. SALVATORE, M. A., F. A. GRAY, and R. B. HINE. 1973. Enzymatically induced germination of oospores of Phytophthora megasperma. Phytopathology 63:1083-1084.
18. SATOUR, M. M., and E. E. BUTLER. 1968. Comparative morphological and physiological studies of the progenies from interspecific matings of Phytophthora capsici. Phytopathology 58:183-192.
19. SAVAGE, E. J. 1966. Effect of light quality on the production of oospores from inter- and intra-specific pairings of Phytophthora isolates. Phytopathology 56:898 (Abstr.).
20. SHAW, D. S. 1967. A method of obtaining single oospore cultures of Phytophthora cactorum using live water snails. Phytopathology 57:454.
21. SMOOT, J. J., F. J. GOUGH, H. A. LAMEY, J. J. EICHENMULLER, and M. E. GALLEGLY. 1958. Production and germination of oospores of Phytophthora infestans. Phytopathology 48:165-171.
22. SNEH, B., and D. L. MC INTOSH. 1974. Studies on the behavior and survival of Phytophthora cactorum in soil. Can. J. Bot. 52:795-802.
23. STANGHELLINI, M. E., and J. D. RUSSELL. 1973. Germination in vitro of Pythium aphanidermatum oospores. Phytopathology 63:133-137.
24. ZENTMYER, G. A., and D. C. ERWIN. 1970. Development and reproduction of Phytophthora. Phytopathology 60:1120-1127.