Effects of Oxygen and Carbon Dioxide Tensions on Sporangium and Oospore Formation by Phytophthora spp.

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ABSTRACT

The effects of aeration on sporangium production and oospore production by several species of *Phytophthora* were determined by incubating cultures in continuous-flow (100 ml/min) atmospheres containing 0, 5, 15, or 30% CO_2 plus 1, 5, or 20% O_2. Sporangium production was examined after growing cultures of *P. cactorum, P. capsici, P. cinnamomi, P. citrophthora, P. palmivora,* and *P. parasitica* in a glucose-nitrate-sterol liquid medium for 72 hr, washing the resulting mats with sterile deionized water, and incubating the suspended mats in open petri plates in aerated plexiglass chambers exposed to fluorescent light at 24 C for 24 hr. Oospore production by *P. cactorum, P. megasperma* var. *sojae,* and in pairings of the opposite mating types of *P. capsici, P. cinnamomi, P. drechsleri,* and *P. palmivora* was evaluated after 12 days' growth on glucose-nitrate agar with sterol in open petri plates in aerated chambers at 20 C in darkness.

Sporangium formation was reduced by decreasing O_2 concentration or increasing CO_2 levels from those in air. Oospore production was greater at O_2 concentrations of 1% and 5% than in air, but decreased with increasing CO_2 concentrations when the O_2 level was 1, 5, or 20%. Phytopathology 61:807-812.

Since species of *Phytophthora* may produce spores in environments such as infected plant tissue or plant debris in soil which often contain atmospheres with lower O_2 and higher CO_2 levels than air (4, 14, 15, 18, 20), studies on the effects of O_2 and CO_2 on sporulation may provide information on the development of these plant pathogens. Sporangium formation by *Phytophthora* spp. generally requires good aeration, whereas oospores and chlamydospores are typically formed under conditions of poor aeration (e.g., in agar culture at the bottom of a petri plate). Tsao (22) demonstrated that sporangium production by *P. parasitica* can be induced by incubating washed mycelial mats in a shallow layer of water at relatively high temperatures (25 C); when identically prepared mats are incubated in deep water at relatively low temperatures (15-18 C), chlamydospores are produced on the submerged mats. It was concluded that reduced aeration prevented sporangium formation and favored chlamydospore production (22). No investigations on the opt CO_2 and O_2 concentrations for the production of chlamydospores, oospores, or sporangia have been reported. Medeiros & Alvim (16), however, did observe that sporangium formation by *P. palmivora* on cacao pod husks was inhibited when CO_2 accumulated in desiccators containing infected pods, or in pod piles in the field. Uppal (23) in 1926 reported that *P. colocasiae, P. infestans, P. palmivora,* and *P. parasitica* formed zoospores in cultures from which O_2 had been removed.

The objective of this study was to determine the effects of various concentrations of O_2 and CO_2 on the formation of sporangia and oospores by several species of *Phytophthora* under defined conditions of temperature, light, relative humidity, hydrogen ion concentration, and nutrition.

MATERIALS AND METHODS.—The cultures studied were obtained from the collection of *Phytophthora* species of the Department of Plant Pathology, University of California, Riverside (Table 1). For tests on the production of oospores, single zoospore cultures of the following species were studied: *P. cactorum* (P-472); *P. megasperma* var. *sojae* (P-405); *P. capsici* (P-504 mated with [×] P-505); *P. cinnamomi* (67 × SB-216-1); *P. drechsleri* (P-208 × P-209); and *P. palmivora* (P-253 × P-255). Species of *Phytophthora* used for studies on sporangium production included *P. cactorum* (P-472), *P. capsici* (P-504 and P-505); *P. cinnamomi* (SB-216-1); *P. citrophthora* (P-479), *P. palmivora* (P-253 and P-255), and *P. parasitica* (T-131).

The glucose-nitrate agar (GNA) medium used for studies on the production of oospores was modified from that of Leal et al. (12) and contained per liter: KNO_3, 0.154 g; glucose, 5.0 g; β-sitosterol, 0.03 g; 2-(N-morpholino)-ethanesulfonic acid (MES) as a buffer (9), 5.3 g; thiamine hydrochloride, 0.001 g; $MgSO_4 \cdot 7H_2O$, 0.2 g; $FeSO_4 \cdot 7H_2O$, 0.001 g; KH_2PO_4, 0.5 g; $CaCl_2 \cdot 2H_2O$, 0.01 g; and 1 ml of a minor element mixture which provided, in the final solution, 1 ppm of Zn ($ZnSO_4 \cdot 7H_2O$) and 0.02 ppm each of Cu ($CuSO_4 \cdot 5H_2O$), Mo ($NaMoO_4 \cdot 2H_2O$), and Mn ($MnCl_2 \cdot 4H_2O$); and Difco purified agar, 15 g. All ingredients except sucrose and β-sitosterol were dissolved in 775 ml of deionized water, the pH was adjusted to 6.2 by titration with 6 N KOH before adding agar, and the final volume brought to 800 ml. Beta-sitosterol was dissolved in 40 ml of dichloromethane, which evaporated upon autoclaving, and was added to the medium. Sucrose was added to 200 ml of deionized water in a separate flask, and the components were mixed after autoclaving at 121 C at 15-lb. pressure for 12 min. The single zoospore

TABLE 1. Sources of *Phytophthora* cultures

Phytophthora spp.	Isolate no.	Mating type	Source	Origin
P. cactorum (Leb. & Cohn) Schroet.	P-472	Homothallic	Pear	California
P. capsici Leonian	P-504	A^1	Pepper	Mexico
	P-505	A^2	Pepper	Mexico
P. cinnamomi Rands	67	A^1	Camellia	California
	SB-216-1	A^2	Avocado	California
P. citrophthora (R.E. Sm. & E.H. Sm.) Leonian	P-479	Sterile	Lemon	California
P. drechsleri Tucker	P-208	A^1	Pepper	Mexico
	P-209	A^2	Pepper	Mexico
P. palmivora (Butl.) Butl.	P-253	A^1	Cacao	Mexico
	P-255	A^2	Cacao	Costa Rica
P. parasitica Dast.	T-131	A^1	Citrus	California
P. megasperma (Drechs.) var. *sojae* A.A. Hildeb.	P-405	Homothallic	Soybean	Mississippi

stock cultures were maintained on GNA. Cultures used for studies on sporangium production were grown in a glucose-nitrate liquid (GNL) medium that differed from GNA only in the omission of agar and the higher KNO_3 concentration (3.08 g/liter).

Cultures examined for oospore production were mated by placing 7-mm plugs of the two mating types of each species on opposite sides of 100- × 15-mm petri plates containing 15 ml of GNA/plate. For cultures of homothallic species, plates of GNA were each inoculated with a single mycelial plug. Half the plates were used as ambient air controls. The remaining plates were placed in a plexiglass chamber after the lids had been removed aseptically, and the chamber was aerated with the desired atm at a rate of 100 ml/min. The cultures were incubated for 12 days in the dark at 20 C. The production of oospores was evaluated by counting 10 fields from each of three replicate plates in a standardized manner under a compound microscope (×12.5 objective and ×16 ocular) fitted with a net reticule in the ocular which outlined a field of 0.48 mm^2. The relative abundance of oospores is reported as 0 = none; I = 1-5; II = 6-10; III = 11-15; IV = 16-20; V = 21-30; VI = 31-40; and VII = 41-50/field.

For studies on sporangium production, 15 ml of GNL were added to 100- × 15-mm petri plates, and each plate was inoculated with four 7-mm discs from the margin of a 5-day-old culture. Cultures were incubated in the dark at room temperature (22-25 C) for 72 hr. The mycelia were then washed twice by decanting the fluid from the mycelial mats in the plates and replacing it with 25 ml portions of deionized water, after which the colonies were suspended in 10 ml of deionized water. Half the replicates prepared as described above were used as controls. After determining that no sporangia had been produced by the colonies during the growth and wash periods, the lids of the remaining plates were removed and the cultures immediately placed in a plexiglass chamber through which a flow of 400 ml/min of the desired atm was passed. The rate of flow was adjusted to 100 ml/min after 1 hr of flushing at the higher rate, and the treated and control plates were irradiated for 24 hr at 25 C in an incubator equipped with 4 fluorescent lamps (General Electric cool-white F20T12) with a light intensity of 200 ft-c at the level of the cultures. To determine that the sporangia formed were functional, half of the treated cultures and half of the control cultures were incubated at 15 C for 30 min, then returned to room temperature to induce zoospore swarming. Three drops of methylene blue were added to each of the remaining plates and sporangia counted on a steroscopic microscope (×12 objective and ×12.5 ocular) fitted with a net reticule which outlined a field of 0.71 mm^2. Three fields were counted at the margin of each of the four colonies in each plate, and the relative abundance of sporangia was reported as 0 = none; I = 1-10; II = 11-20; III = 21-30; IV = 31-40; V = 41-50; VI = 51-100; VII = 101-200; VIII = 201-300/field.

Atmospheres used for studies on oospore production in GNA contained 0, 5, 15, or 30% CO_2 plus 1, 5, or 20% O_2. For studies on sporangium production, the cultures were exposed to atm of 0, 5, or 15% CO_2 plus 1, 5, 20, or 40% O_2. Gases were either purchased as mixtures of O_2, CO_2, and N_2 from the Matheson Co., or were premixed from O_2, CO_2, and high-purity N_2 with a series of microflow valves and flowmeters (17). Effluent gases from the plexiglass chambers were periodically analyzed by gas chromatography to determine the concentrations of O_2, CO_2, and N_2. The flow rates of the gas streams through the chambers were sufficient to maintain constant levels of O_2 and CO_2.

RESULTS.—*Oospore production.*—More oospores were produced by all species of *Phytophthora* after 12 days in nitrogen atm containing 1 or 5% O_2 than in air (Table 2). While the production of oospores of *P. cinnamomi* and *P. palmivora* was only slightly greater in low O_2 atm, oospore production by *P. capsici, P. drechsleri, P. cactorum,* and *P. megasperma* var. *sojae* was greatly increased.

The number of oospores decreased with increasing CO_2 concentrations when the O_2 levels were 1, 5, and 20%. With the exception of *P. capsici* and *P. drechsleri,* both of which formed a few oospores in an atm

TABLE 2. Effects of oxygen and carbon dioxide concentrations of atmosphere above culture on oospore formation by *Phytophthora* spp.

Species and isolates	Oospore formation[a,b] at various gas concentrations (% O_2: % CO_2)												
	1:0	1:5	1:15	1:30	5:0	5:5	5:15	5:30	20:0	Air	20:5	20:15	20:30
P. capsici P-504 × P-505	VII	VII	V	I	V	IV	VI	0	II	II	II	II	0
P. cinnamomi 67 × SB-216-1	III	II	II	0	III	I	0	0	II	II	0	0	0
P. drechsleri P-208 × P-209	VII	VII	V	I	VII	VI	IV	0	V	V	III	III	0
P. palmivora P-253 × P-255	III	I	I	0	II	I	I	0	I	I	I	0	0
P. cactorum P-472	VII	IV	0	0	A[c]	I	0	0	IV	IV	I	0	0
P. megasperma var. *sojae* P-405	VII	I	I	0	V	I	I	0	III	III	II	0	0

[a] Based on three experiments with three replications/experiment.
[b] Relative abundance of oospores is recorded as 0 = none; I = 1-5; II = 6-10; III = 11-15; IV = 16-20; V = 21-30; VI = 31-40; and VII = 41-50/field of 0.48 mm².
[c] A = Masses of oospores so dense that counts could not be made.

containing 1% O_2 plus 30% CO_2, no oospores were observed in cultures in atm containing 30% CO_2 plus 1, 5, or 20% O_2. *Phytophthora palmivora* and *P. megasperma* var. *sojae* formed few or no oospores under any of the CO_2 levels tested. *Phytophthora cactorum* formed as many oospores in an atm containing 1% O_2 plus 5% CO_2 as in air; oospore production, however, was greatly reduced by 5% CO_2 in combination with 5 or 20% O_2, and was completely inhibited at higher CO_2 levels. *Phytophthora cinnamomi* produced more oospores in the presence of 5 or 15% CO_2 in an atm containing 1% O_2 than in atm containing 5 or 20% O_2. Oospore production by *P. capsici* and *P. drechsleri* was unaffected or only slightly affected by the addition of 5% CO_2 to 1% or 5% O_2 in comparison to production in the respective atm of 1% or 5% O_2 without CO_2. Oospore formation by these two species in atm containing 1 or 5% O_2 plus 15% CO_2 was equal to or greater than that in air.

A variation of less than 0.1 unit from the initial pH of 6.2 was observed when the final pH of the cultures was recorded after 12 days of growth.

Sporangium production.—Maximum sporangium production under the conditions employed in this study occurred in air (Table 3). Sporangium production by *P. parasitica* (T-131), *P. palmivora* (P-255), and *P. capsici* (P-504) was as abundant in a nitrogen atm containing 5% O_2 as in air; the formation of sporangia by *P. palmivora* (P-253), *P. citrophthora* (P-479), and *P. capsici* (P-505) was only slightly less at 5% O_2. Sporangium production by *P. cactorum* (P-472), however, was greatly reduced at 5% O_2. *Phytophthora cinna-*

TABLE 3. Effects of oxygen and carbon dioxide concentrations of atmosphere above culture on sporangium formation by *Phytophthora* spp.

Species and isolates	Sporangium formation[a,b] at various gas concentrations (% O_2: % CO_2)												
	1:0	1:5	1:15	5:0	5:5	5:15	20:0	Air	20:5	20:15	40:0	40:5	40:15
P. cactorum P-472	0	0	0	II	0	0	V	V	I	I	V	I	I
P. capsici P-504	VI	I	F[c]	VIII	I	F	VIII	VIII	II	II	VIII	II	II
P. capsici P-505	III	0	0	IV	I	0	VI	VI	II	II	VI	II	II
P. cinnamomi SB-216-1	0	0	0	0	0	0	F	F	0	0	0	0	0
P. citrophthora P-479	III	I	0	IV	I	0	VI	VI	I	0	VI	I	0
P. palmivora P-253	VII	II	F	VII	II	F	VIII	VIII	II	I	VIII	II	I
P. palmivora P-255	VII	II	0	VII	I	0	VII	VII	II	I	VII	II	I
P. parasitica T-131	0	0	0	III	I	0	III	III	I	0	III	I	0

[a] Based on two experiments with two replications/experiment.
[b] Relative abundance of sporangia reported as 0 = none; I = 1-10; II = 11-20; III = 21-30; IV = 31-40; V = 41-50; VI = 51-100; VII = 101-200; VIII = 201-300/field of 0.71 mm².
[c] F = less than 10 sporangia formed/plate.

momi (SB-216-1) formed only one or two sporangia/culture in any of the gas combinations tested. When the O_2 concentration in the atm over the mats was reduced to 1%, T-131 and P-472 formed no sporangia, and P-253, P-479, P-504, and P-505 formed fewer sporangia than in air. P-255 produced as many sporangia at 1% O_2 as it did at 5% O_2 or in air.

The number of sporangia decreased with increasing concentrations of CO_2 when the O_2 concentrations were 1, 5, and 20%. P-253 and P-504 were able to form at least a few sporangia in all the gas mixtures tested. Sporangia were produced by T-131 and P-505 in an atm containing 5% O_2 and 5% CO_2, but none were formed under any other combination of CO_2 and 1 or 5% O_2. While P-255 and P-479 did not produce sporangia in atm containing 1 or 5% O_2 plus 15% CO_2, a few sporangia were formed when the CO_2 content was reduced to 5%. No sporangia were formed by P-472 when 5 or 15% CO_2 was added to 1 or 5% O_2.

A few sporangia were formed by P-253, P-255, P-472, P-504, and P-505 in an atm containing 20% O_2 plus 5 or 15% CO_2. T-131 and P-479 were able to form sporangia in gas combinations containing 20% O_2 plus 5% CO_2, but no sporangia were formed when the CO_2 concentration was increased to 15%.

All isolates produced ca. the same number of sporangia in the presence of 40% O_2 in a nitrogen atm as in air. As the concentration of CO_2 was increased in the presence of 40% O_2, production of sporangia decreased.

Zoospore release from sporangia formed on mycelial mats under any of the atm tested was observed after chilling the cultures. Even when sporangium production was extremely poor, the few sporangia formed were still capable of indirect germination.

DISCUSSION.—*Oospore production.*—Most *Phytophthora* species formed greater numbers of oospores at O_2 concentrations of 1 or 5% than in air. While no work has been reported previously on the effects of O_2 on oospore formation by *Phytophthora* species, low O_2 levels have been observed to enhance the production of spores by other fungi. Wilson (24) noted that macroconidium production by *Fusarium oxysporum* f. sp. *cubense,* as evaluated 2 days after the removal of cultures from controlled atm, was greatest at concentrations of 0.01 to 5.0% O_2. Ascospore formation by *Saccharomyces cerevisiae* was stimulated over that in air by atmospheres containing 0 to 12% O_2 (1). Oospores of *Aqualinderella fermentans* were formed only under anaerobic conditions (10).

Most species of *Phytophthora* were able to form oospores in atm containing up to 15% CO_2. While oospore formation by all species was reduced with increasing CO_2 concentrations, the effects of increasing CO_2 concentrations were generally more inhibitory when the O_2 concentration was 5 or 20% than when the O_2 level was 1%.

From the methods used in this study, it can be concluded that species of *Phytophthora* are capable of forming oospores in atm that contain levels of O_2 and CO_2 that might be found in infected plant tissue.

Sporangium production.—The results of this study show that the formation of sporangia on washed mycelial mats after 24 hr in atm containing different O_2 and CO_2 concentrations was optimum in air. Conditions of the experiments reported here were not favorable for the production of sporangia by *P. cinnamomi;* thus, few sporangia were produced in any of the treatments. This species requires either the use of soil extract (25) or extensive washing of young hyphae followed by incubation in a salt solution (5) for sporangium production. None of the O_2 or CO_2 treatments substituted for these conditions. Sporangium production by the other species was generally reduced at 1% O_2, as compared to the controls in air. The production of asexual spores by other fungi has been observed to decrease with decreasing levels of O_2 (6, 7, 11, 19).

Sporangium production by all of the isolates in this study was more sensitive to the CO_2 concentration in the atm over the mats than was growth (17). Medeiros & Alvim (16) observed that when unmeasured amounts of CO_2 accumulated in desiccators containing pieces of cacao husks infected with *P. palmivora,* sporangium formation was reduced or completely prevented, whereas mycelial growth was stimulated. The formation of many different types of spores by other fungi is usually more readily inhibited by CO_2 than is vegetative growth (2, 3, 6, 8, 13, 19, 21).

Although sporangium formation by species of *Phytophthora* typically occurs in the presence of light after nutrients required for vegetative growth have been depleted (22), this study demonstrates that aeration conditions in which CO_2 does not accumulate and in which an adequate supply of O_2 is maintained must also be provided for sporangium production. Medeiros & Alvim (16) reported that the inhibition of sporangium formation by CO_2 levels higher than that of air also occurs in nature. While sporangia were formed abundantly by *P. palmivora* on cacao pods at the surface of husk piles and on scattered, individual pods, sporangia were not produced inside piles of cacao husks. It was concluded that high levels of CO_2 resulting from respiration accumulated inside the husk piles and prevented sporangium production. They apparently did not consider that the lack of sporangium production could have resulted from the absence of light or the presence of toxic compounds instead of the accumulation of CO_2.

While the formation of sporangia is reduced or prevented in environments with lower levels of O_2 and greater levels of CO_2 than in normal air, any sporangia formed would probably be capable of indirect germination, even in the most poorly aerated environments, in the presence of water. Sporangia formed in any of the tests in this study were capable of forming and releasing zoospores. Uppal (23) observed that sporangia formed by *P. colocasiae, P. infestans, P. palmivora,* and *P. parasitica* were able to germinate indirectly, but not directly by germ tubes, in the absence of O_2.

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