Interaction of Light and Sterol on Sporangium and Chlamydospore Production by *Phytophthora lateralis*

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ABSTRACT

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Chlamydospore production by *Phytophthora lateralis* was most abundant in V8 broth with 20 μg/ml β-sitosterol, and maximum sporangium production occurred with 10 μg/ml. Growth (dry weight) was not enhanced by sterol concentrations ranging from 1 to 200 μg/ml. Cultures grown on V8 sterol agar or broth, and illuminated (680 μW cm^{-2}, combined Blacklight Blue and Cool White fluorescent lamps) either continuously or 12 hr daily, produced at least four times as many sporangia as were produced by cultures in the dark on sterol media, or in the light or dark on media not amended with sterol. Chlamydospores were produced most abundantly in the dark on V8 sterol agar or broth, with production greatly reduced by continuous or 12 hr of light daily. Chlamydospore production was suppressed by all light intensities tested (85, 170, 340, 680 μW cm^{-2}) compared with production in the dark. Few chlamydospores formed in cultures on media without sterol, whether incubated in the light or dark. Growth (dry weight or colony size) was not affected by illumination. None of numerous regimes of diurnal temperature cycles enhanced sporulation more than constant temperatures. Optimal sporangium production requires incubation on media with sterol at 14–16 C in the light; optimal chlamydospore production requires incubation at 24–25 C in the dark on media with sterol.

Additional key words: soil fungi, sporulation, reproduction.

Phytophthora lateralis Tucker and Milbrath is the causal agent of a root rot disease affecting native stands of *Chamaecyparis lawsoniana* (Murr.) Parl. along the Pacific coast of Oregon and California and numerous horticultural cultivars of *Chamaecyparis* distributed by the ornamental plant industry (8,10). In the spectrum of growth rates characteristic of the various *Phytophthora* spp., that of *P. lateralis* may be classified among the slowest (14). Host resistance and fungal survival studies, which require quantities of inoculum, have been impeded by the time consuming process of inoculum production.

Sterols play an important role in the development and reproduction of several pythiaceous fungi. The literature on this subject is abundant (4). The reproduction of numerous *Phytophthora* spp. is influenced by light (7,15,17)

The relationship of light and sterol on sporulation of *Phytophthora* spp. was investigated. Hendrix (3) studied sporulation by two *Phytophthora* spp. and found that sporangium production on a medium with sterol was higher in illuminated than in unilluminated cultures. Merz and Vickers (6) reported partial reversal of the inhibitory effect of light on oospore formation by four *Phytophthora* spp. when sterol was added to the culture medium; at any of the concentrations of sterol tested, production of oospores was never as great in the light as in the dark. Englander and Turbitt (1) found that near-ultraviolet light stimulated production of chlamydospores by *P. cinnamomi* only when the culture medium contained sterol. None of the concentrations of sterol tested (1–200 μg/ml) enhanced chlamydospore production in the dark.

In view of the significant effects of light and sterols on other pythiaceous species, their effects on *P. lateralis* were examined.

MATERIALS AND METHODS

Isolates. *P. lateralis* isolate PL 11 was used in all experiments reported here. Three other isolates, PL 12, 14, and 17, also were included in the final experiment. All *P. lateralis* isolates were from diseased, native *C. lawsoniana,* and their pathogenicity was confirmed by inoculating rooted *C. lawsoniana* cuttings in the greenhouse.

Media. V8 broth and agar were prepared with commercial V-8 juice (Campbell Soup Co., Camden, NJ 08101) and clarified by centrifugation (1,000 *g* for 10 min) and filtration through Whatman GF/A glass-fibre paper (Whatman, Inc., Clifton, NJ 07014). V8 agar and broth contained clarified V-8 juice, 100 ml; $CaCO_3$, 0.1 g; Difco agar, 17 g (deleted in broth); and distilled water, 900 ml. V8 sterol agar and broth were prepared as above, except with only 890 ml distilled water and, unless otherwise indicated, 0.02 g β-sitosterol (Sigma Chemical Co., St. Louis, MO 63178) dissolved in 10 ml hot 95% ethanol. Control media in some experiments contained ethanol (95%, 10 ml/L) without sterol. Media were autoclaved 20 min at 121 C, and 7-ml aliquots were pipetted into 6-cm-diameter plastic petri dishes.

Fungus culture. Petri dishes with agar medium were seeded by inverting a 5-mm-diameter disk of corn meal agar cut from the periphery of a 7- to 12-day-old colony of *P. lateralis*. Broth cultures were seeded by adding a homogeneous suspension of *P. lateralis* (prepared from 9- to 15-day-old colonies grown on V8 broth and comminuted in a Servall Omnimixer [Sorvall Instruments, Newtown, CT 06470]) to autoclaved, cooled medium prior to dispensing it to petri dishes.

Measurement of growth and sporulation. Dry weights of colonies in liquid medium were determined by vacuum filtration on tared Whatman No. 1 filter papers, flushing unassimilated nutrients with measured amounts of water, and drying the filters to a constant weight at 75 C. Growth as increase in colony area was determined on agar cultures by periodically marking the peripheries of the colonies on the bottoms of the petri dishes and later tracing these outlines with a planimeter.

Production of chlamydospores and sporangia was determined directly on cultures grown in agar or from samples of comminuted colonies when cultures were in liquid medium. After the prescribed incubation period, cultures were killed and fixed by flooding with a thin layer of FAA (formaldehyde, 48 ml; acetic acid, 40 ml, 95% ethanol, 352 ml; and distilled water, 360 ml). In each agar culture spores were counted in 20 microscope fields, delineated by an ocular counting grid (each field 0.5 mm^2), spaced uniformly along radii drawn below each colony, so that no preference was given to hyphae of a particular age. Colonies from broth cultures were transferred to an 8-ml-capacity Servall Omnimixer cannister containing 5 ml of water and comminuted for 30 sec at 70% (rheostat-controlled) line voltage. The resultant suspension was

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diluted to 250 ml in a volumetric flask and, immediately following agitation, four 0.1-ml samples were pipetted onto depression slides. Sporangia and chlamydospores were counted microscopically.

Criteria for counting spores were: sporangia at least 20 μm long, symmetrical, and containing cytoplasm and chlamydospores at least 20 μm in diameter, and containing cytoplasm. Occasionally, chains of swollen cells, resembling sporangia, but shorter ($<20\ \mu$m) and irregularly shaped, were observed in some treatments. These were not included in spore counts. Frequently, clusters of small (5–10 μm maximum dimension) asymmetric structures, devoid of cytoplasm, were found. These were considered to be undeveloped or abortive chlamydospores and were not included in spore counts. There were three or four replicate cultures in each treatment except in the alternating temperature experiment in which, due to the unique temperature regime at any given location on the temperature gradient device (5), replication was not possible. Each experiment was conducted at least twice, although in some experiments, where noted, a different medium (V8 agar instead of V8 broth) was used.

Temperature and light. The effect of temperature was determined by incubation of cultures on temperature gradient devices (5). These devices are sheets of metal with thermostatically controlled temperatures individually maintained at each edge, providing rows of isothermal lines which allow the replication of cultures at selected temperatures. In experiments with diurnal temperature regimes, a temperature gradient was alternately established in one direction for 12 hr, and then switched to a direction perpendicular to the previous direction of the gradient for 12 hr, after which the cycle was repeated. Thus, cultures at each location on this device were subjected to unique diurnal temperature cycles. Temperatures on gradient devices were monitored with thermocouples attached to the metal sheets at various locations and readings were made periodically with a calibrated temperature potentiometer (Leeds and Northrup Co., North Wales, PA 19454). Throughout the incubation period on gradient devices maintaining a temperature gradient in one direction only, variation in temperature on any given isothermal line was typically ≤ 0.5 C on unilluminated cultures, and ≤ 1.5 C on illuminated cultures. Variation on the device providing diurnal temperature regimes was typically ≤ 1.0 C in the dark and ≤ 1.5 C under illumination.

Illumination was supplied by a combination of equal numbers of Cool White fluorescent (F40 CW) and Blacklight Blue fluorescent (F40 BLB) tubes. Unless otherwise stated, light intensity at colony level was 680 μW cm^{-2}. In experiments to test the effect of light intensity on sporulation, layers of gauze were arranged between lights and cultures to adjust intensity to the desired levels. Measurements were made with a combination Quantum/Radiometer/Photometer (Lambda Instruments, Lincoln, NE 68504). Dark incubation was on a gradient device in an opaque enclosure.

TABLE 1. Production of chlamydospores, sporangia, and growth by *Phytophthora lateralis,* incubated in V8 broth with various concentrations of sterol

Concentration of supplemental sitosterol (μg/ml)	Dry weight growth (mg)[v]	Chlamydospores[w] (no.)	Sporangia[x] (no.)
0	21 b[y]	44,000 e[y]	5,000 c[y]
0 + E[z]	38 a	36,000 e	900 d
1 + E	37 a	80,000 d	8,000 c
2 + E	37 a	207,000 c	7,000 c
10 + E	36 a	476,000 b	53,000 a
20 + E	44 a	782,000 a	41,000 b
100 + E	40 a	567,000 ab	40,000 b
200 + E	42 a	660,000 ab	39,000 b

[v] Average dry weight per culture, derived from four replicate cultures, measured after 14 days of incubation in the dark.

[w] Average number of chlamydospores per culture, derived from four replicate cultures, measured after 19 days of incubation in the dark.

[x] Average number of sporangia per culture, derived from four replicate cultures, measured after 19 days of incubation in the dark and 7 days in the light.

[y] Any given pair of values in a column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

[z] E = 95% ethanol, as sterol solvent or solvent control, present in the medium at 1% total volume.

RESULTS

Effect of sterol concentrations on growth and sporulation. *P. lateralis* colony dry weights were determined at 2-day intervals from cultures grown in the dark at 20 C in V8 broth, either unamended, or amended with ethanol (sterol solvent), or with various concentrations of β-sitosterol dissolved in ethanol. By the 6th day similar dry weights were obtained from all treatments in which the medium had sterol and in the medium with ethanol, and these were substantially greater than weights obtained from the unamended V8 broth. This differential was consistent throughout the 14th day of incubation when sampling was terminated (Table 1). Beginning on the 4th day, occasional chains of swollen cells appeared along the hyphae, but only in cultures in media with $\leq 10\ \mu$g/ml supplemental sterol. By the 6th day these structures were evident in all media, but in cultures grown in media with 20 μg/ml supplemental sterol there were also some terminally located, lightly pigmented, large chlamydospores. After 8 days, numerous large, heavily pigmented intercalary chlamydospores were evident

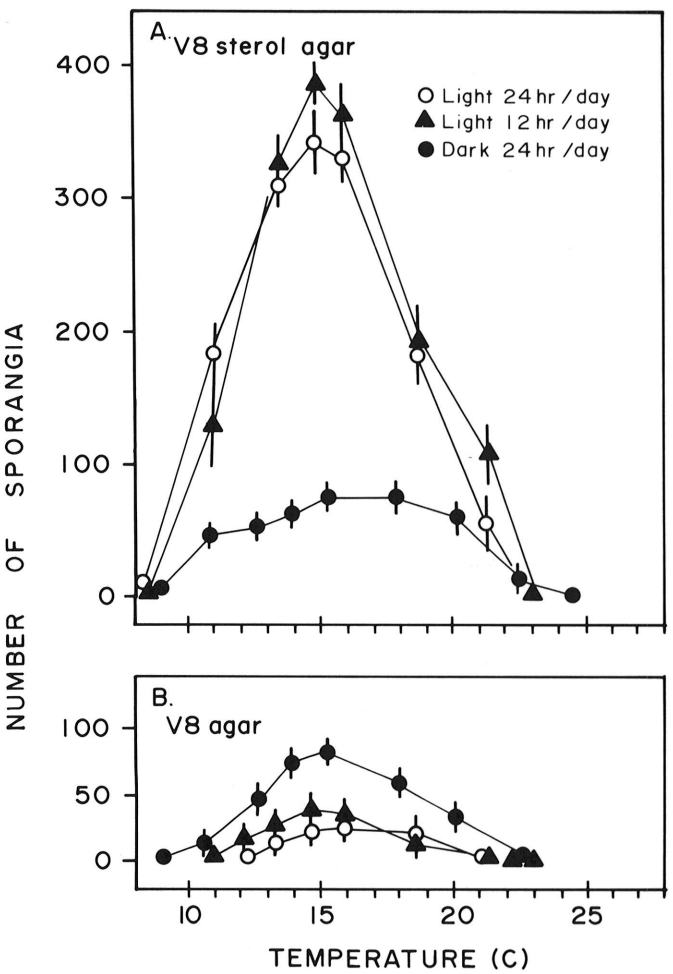

Fig. 1. Production of sporangia by *Phytophthora lateralis* after incubation for 11 days at various temperatures in the light (680 μW cm^{-2}, combined Cool White and Blacklight Blue fluorescent light) or in the dark. Culture medium was V8 agar, **A,** amended with 20 μg/ml sitosterol, or **B,** not amended with supplemental sterol. Each point represents the number of sporangia per 10 mm^2 of colony surface area (average of four replications). Vertical bars through data points designate confidence intervals, $P = 0.05$.

throughout colonies growing in medium with 20 μg/ml supplemental sterol, with a few spores of this type occurring in all other media amended with sterol. A few well formed, pigmented chlamydospores were seen in unamended media on the 14th day. At that time, numerous mature chlamydospores had formed on cultures in media amended with 1 or 2 μg/ml but only at the margins of colonies, whereas numerous chlamydospores were uniformly distributed throughout the colonies in media amended with $>2 \leqslant 10$ μg/ml sterol. After 19 days, chlamydospore production was significantly higher when at least 2 μg/ml supplemental sterol was present in the medium, and highest numbers of spores were found in medium with 20 μg/ml supplemental sterol (Table 1).

Sporangia were not observed in cultures in which chlamydospores were counted after 19 days of incubation. Remaining cultures from each treatment medium above were incubated at room temperature (18–20 C) under fluorescent light for 7 days, after which sporangia were found in all treatments. Production was significantly higher in medium with $\geqslant 10$ μg/ml supplemental sterol (Table 1).

Interaction of light and sterol. Since illumination so markedly affected initiation of sporangium formation, further studies were made on the effect of illumination on sporangium and chlamydospore production. Highest numbers of sporangia were produced by cultures grown on V8 sterol agar (supplemented with 20 μg/ml sitosterol) in the light, either illuminated continuously or 12 hr daily, compared to cultures incubated on V8 agar not amended with sterol, either in the light or dark (Fig. 1). This interaction of light and sterol, stimulating production of sporangia, occurred over a range of temperatures (approximately 12–18 C), with the optimum at approximately 15 C. Chlamydospores were produced most abundantly by cultures grown in the dark on V8 sterol agar with the optimum temperature being approximately 24–25 C (Fig. 2). The number of chlamydospores was greatly reduced in cultures on V8 sterol agar in either continuous or 12 hr of light daily. Few chlamydospores were observed in cultures on V8 agar without supplemental sterol, either in the light or in the dark.

Evaluations of sporangium and chlamydospore production were repeated in similar illumination regimes and incubation temperatures, but with cultures in liquid media (V8 broth and V8 sterol broth). The same temperature optima and similar relationships between spore production, illumination treatments, and sterol were obtained in liquid media as on agar media.

Growth, measured as dry weight, was similar over a broad range of temperatures (approximately 11–24 C), whereas colony size increased with increasing temperatures between approximately

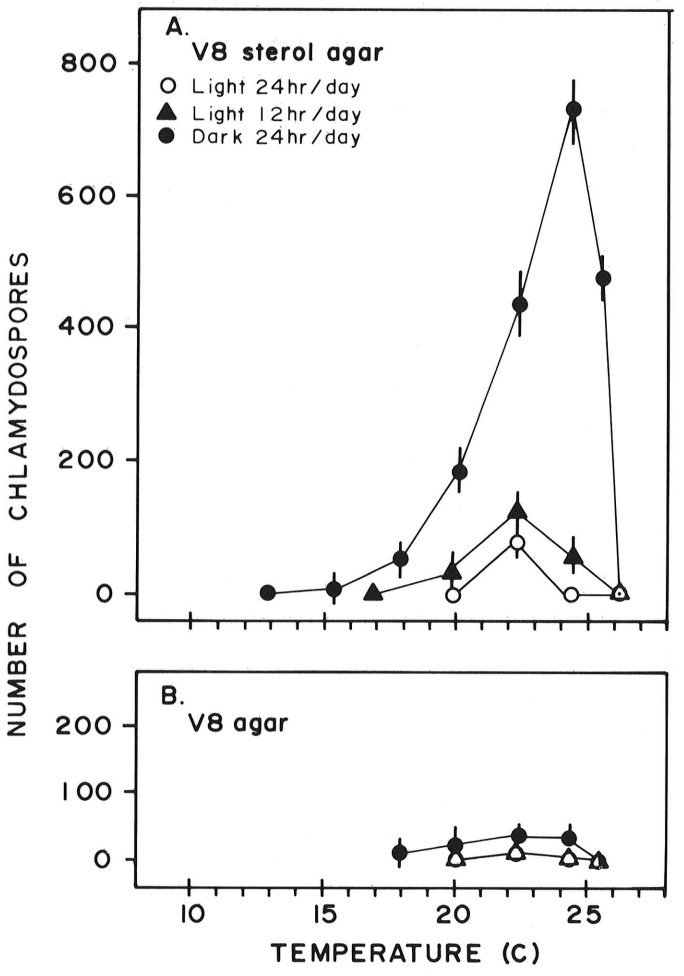

Fig. 2. Production of chlamydospores by *Phytophthora lateralis* after incubation for 11 days at various temperatures in the light (680 μW cm^{-2}, combined Cool White and Blacklight Blue fluorescent light) or in the dark. Culture medium was V8 agar, **A,** amended with 20 μg/ml sitosterol, or **B,** not amended with supplemental sterol. Each point represents the number of chlamydospores per 10 mm^2 of colony surface area (average of four replications). Vertical bars through data points designate confidence intervals, $P = 0.05$.

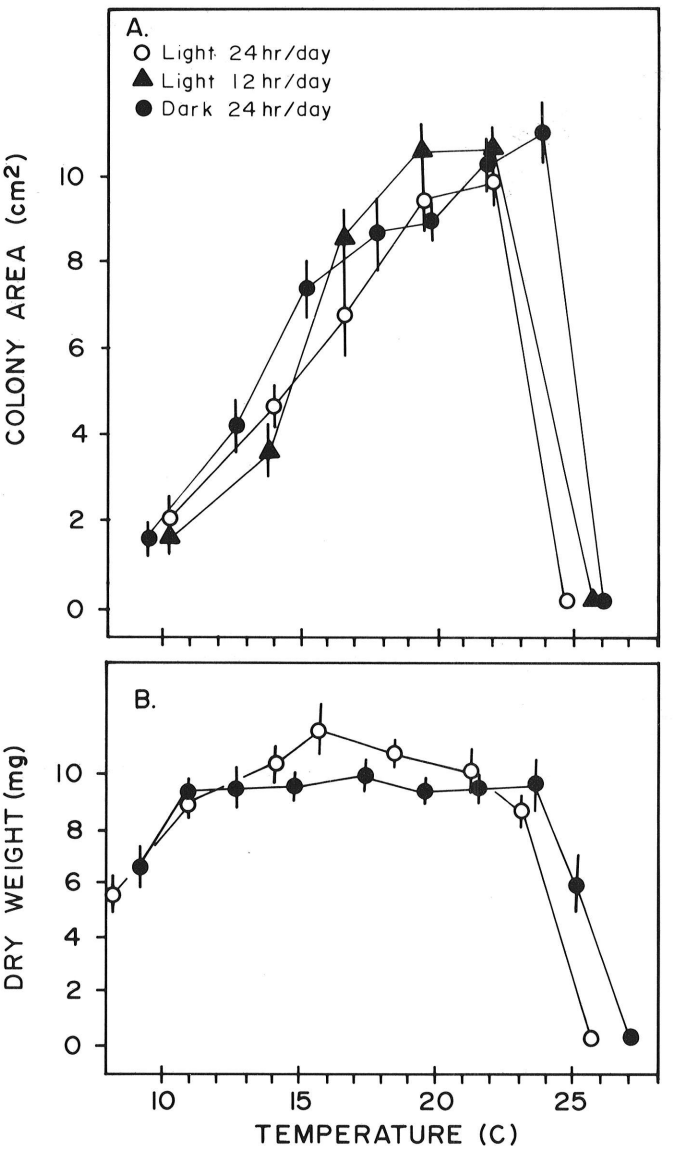

Fig. 3. Growth of *Phytophthora lateralis* at various temperatures in the light (680 μW cm^{-2}, combined Cool White and Blacklight Blue fluorescent light) or dark. Growth was measured as, **A,** increase in colony area (square centimeters) between the 5th and 10th day of incubation on V8 sterol agar, or **B,** dry weight (mg) after 14 days of incubation in V8 sterol broth. Vertical bars through data points designate confidence intervals, $P = 0.05$.

10–22 C (Fig. 3). There were no differences in growth due to incubation in the light or dark at most temperatures tested, however, there was a slight increase in the maximum temperature for growth on dark-incubated cultures (approximately 26 C) from that measured on illuminated cultures (approximately 25 C).

Diurnal light and temperature regimes. The effect on sporulation of diurnal temperature and light regimes was investigated by incubating cultures on alternating temperature gradient devices. There was no distinct optimum temperature regime for sporangium production, but at least three times as many sporangia were produced on illuminated (12 hr daily) cultures at the 18.6/16.2 C cycle than on cultures incubated continuously in the dark at any temperature regime (Table 2). Frequently, abortive sporangia (described above) formed, primarily on cultures incubated continuously in the dark at temperatures between 15–20 C; these spores were not included in the data in Table 2. When this experiment was repeated, sporangia were most prevalent on illuminated cultures, in regimes with temperatures between 15.0–19.5 C.

Chlamydospores were produced sparsely on illuminated cultures, and these primarily at cycles with 22.0–24.6 C during either the illuminated or dark period (Table 3). However, large numbers of chlamydospores developed on cultures incubated continuously in the dark in a wide range of diurnal temperature regimes. Chlamydospore production was most abundant at a constant temperature of approximately 26 C. Large numbers of chlamydospores were produced on colonies incubated in some of the regimes in which one of the temperatures in the diurnal cycle was approximately 26 C, although comparable production occurred in various other cycles. Numerous small, poorly developed chlamydospores (described above) formed on cultures in cycles in which at least one temperature was below approximately 19 C, and the other temperature was below approximately 23 C; data representing these spores were not included in Table 3. When this experiment was repeated, the greatest numbers of chlamydospores were found on cultures incubated continuously in the dark in a diurnal temperature regime of approximately 24.5–25.5 C. In the dark, cultures in regimes with one or both temperatures below approximately 24 C supported only sparse spore production. As before, chlamydospore production was negligible in cultures illuminated 12 hr daily, regardless of the temperature regime.

Chlamydospore production at various light intensities. The inhibitory effect of light on chlamydospore production reported here for *P. lateralis* may be due to high light intensity, whereas lower intensities might not affect, or may stimulate, production of these spores.

Cultures were incubated on V8 sterol agar at 25 C in the dark or in light with intensities of 85, 170, 340, and 680 μW cm^{-2}. Chlamydospore production at 85 μW cm^{-2} was only 38% of that produced by dark-incubated cultures, and even fewer chlamydospores were produced at higher light intensities (Table 4).

Isolates. Three other isolates of *P. lateralis* were similar to isolate PL 11 in their responses to light and supplementation of V8 agar with sitosterol (Table 5). All isolates produced more sporangia in light on medium with added sterol than in the dark or on medium without added sterol. All isolates produced more chlamydospores on sterol-amended medium in the dark than on medium not amended with sterol or on sterol-amended medium incubated in the light. While temperature optima among isolates were not studied and may vary as with other *Phytophthora* spp. (9,16), these results indicate that the behavior of isolate PL 11 is typical of isolates of *P. lateralis*.

TABLE 2. Effects of 12-hr temperature alternation cycles with and without illumination on sporangium formation by *Phytophthora lateralis* in V8 sterol agar

Light-dark cycles[a] (12-hr)	Second cycle temp (C)	Sporangia produced[b] with first cycle temperatures (C) at:							
First cycle illuminated		31.9	27.9	25.0	22.0	18.6	15.3	10.6	6.1
Second cycle dark	29.5	0	0	0	0	0	0	0	0
	27.0	0	0	0	0	0	0	0	0
	24.6	0	0	0	0	40	25	0	0
	21.9	0	0	3	4	103	77	6	0
	19.1	0	0	1	57	261	86	4	0
	16.2	0	0	0	134	333	126	2	0
	13.8	0	0	2	81	42	106	2	2
	11.4	0	0	11	27	7	0	0	0
First cycle dark		30.2	26.1	22.4	19.0	15.5	12.5	8.8	4.6
Second cycle dark	29.2	0	0	0	0	0	0	0	0
	26.1	0	0	0	4	8	3	0	0
	23.0	0	0	8	6	94	19	4	0
	19.9	0	0	65	37	50	44	0	0
	16.9	0	9	77	15	27	38	10	0
	14.0	0	0	21	24	6	18	9	0
	10.9	0	0	1	4	24	3	2	4
	7.9	0	0	1	6	7	7	0	0

[a] Illumination was supplied by a combination of equal numbers of Cool White (F40 CW) and Blacklight Blue (F40 BLB) fluorescent tubes, with light intensity of 680 μW cm^{-2} at colony level.
[b] Number of sporangia per 10 mm^2 colony surface area on each 14-day-old culture.

TABLE 3. Effects of 12-hr temperature alternation cycles with and without illumination on chlamydospore formation by *Phytophthora lateralis* in V8 sterol agar

Light-dark cycles[a] (12-hr)	Second cycle temp (C)	Chlamydospores produced[b] with first cycle temperatures (C) at:							
First cycle illuminated		31.9	27.9	25.0	22.0	18.6	15.3	10.6	6.1
Second cycle dark	29.5	0	0	0	0	0	0	0	0
	27.0	0	0	0	9	0	15	0	0
	24.6	0	0	0	66	27	16	8	0
	21.9	0	0	5	24	0	0	0	3
	19.1	0	0	0	7	0	2	0	0
	16.2	0	0	0	10	0	0	0	0
	13.8	0	0	0	0	0	0	2	0
	11.4	0	0	0	10	0	0	0	0
First cycle dark		30.2	26.1	22.4	19.0	15.5	12.5	8.8	4.6
Second cycle dark	29.2	0	0	24	0	6	0	0	0
	26.1	0	447	48	191	74	136	46	0
	23.0	0	377	102	161	160	151	72	15
	19.9	0	283	38	15	73	143	144	9
	16.9	0	389	87	11	124	113	43	0
	14.0	0	286	52	61	132	157	0	0
	10.9	0	266	86	90	83	117	0	0
	7.9	0	211	117	74	51	31	0	0

[a] Number of chlamydospores per 10 mm^2 of colony surface area on each 14-day-old culture.
[b] Illumination was supplied by a combination of equal numbers of Cool White (F40 CW) and Blacklight Blue (F40 BLB) fluorescent tubes, with light intensity of 680 μW cm^{-2} at colony level.

TABLE 4. Chlamydospore production by *Phytophthora lateralis* grown on V8 sterol agar at 24 C in the dark or at various light intensities

Light intensity[a] (μW cm^{-2})	Chlamydospores[b] (no.)
0	152 ± 19[c]
85	57 ± 12
170	36 ± 7
170	36 ± 7
340	9 ± 4
680	11 ± 5

[a] Illumination was supplied by a combination of equal numbers of Cool White (F40 CW) and Blacklight Blue (F40 BLB) fluorescent tubes, and intensity was adjusted with layers of gauze.
[b] Number of chlamydospores per 3 mm^2 of colony surface area (average of three replications) on 14-day-old cultures.
[c] Confidence intervals, $P = 0.05$.

TABLE 5. The effect of sterol and illumination on sporangium and chlamydospore production on four isolates of *Phytophthora lateralis*

Isolate	Sporangium production at 15 C (no.)[b]				Chlamydospore production at 24 C (no.)[b]			
	+ sterol[a]		− sterol		+ sterol[a]		− sterol	
	light	dark	light	dark	light	dark	light	dark
PL 11	263 ± 29	69 ± 10	39 ± 8	58 ± 6	97 ± 13	620 ± 41	24 ± 11	31 ± 8
PL 12	114 ± 20	21 ± 9	51 ± 16	18 ± 4	91 ± 7	337 ± 17	56 ± 5	78 ± 14
PL 14	197 ± 12	85 ± 6	79 ± 13	63 ± 18	49 ± 6	508 ± 38	62 ± 15	95 ± 11
PL 17	343 ± 17	101 ± 19	64 ± 15	75 ± 21	23 ± 8	212 ± 58	19 ± 7	27 ± 13

[a] 20 μg/ml sitosterol added to V8 agar.
[b] Number of sporangia or chlamydospores per 10 mm^2 of colony surface area (average of three replications) on 14-day-old cultures. Values are followed by the confidence intervals, $P = 0.05$.

DISCUSSION

We found an interaction between light and sterol in the production of sporangia and chlamydospores by *P. lateralis*. Illumination of colonies greatly enhances production of sporangia, and inhibits chlamydospore formation, but only when the fungus is grown on media with sterol.

P. lateralis appears to produce sporangia in response to light and sterol similarly to two species studied by Hendrix (3). In V8 agar and broth media not supplemented with sterol, chlamydospore production by *P. lateralis* was sparse, irrespective of the illumination treatment, whereas chlamydospore production in media supplemented with sterol increased slightly in the light and substantially in the dark. This phenomenon appears similar to the partial reversal by sterol of light inhibition of oospore formation in four *Phytophthora* spp. (6).

Hendrix (2) reported a sterol requirement for chlamydospore and sporangium formation by *P. lateralis* in synthetic media. We obtained both types of asexual spores in unamended V8 broth and agar, probably due to sterol present in this natural medium. However, significant increase in numbers of chlamydospores occurred with increasing concentrations of β-sitosterol between 1, 2, 10, and 20 μg/ml, provided that cultures were incubated in the dark. Sitosterol at concentrations of $\geqslant$ 10 μg/ml significantly stimulated production of sporangia. Trione (12) found that sporangium production of *P. lateralis* was better in media low in nutrients. Our successful production of abundant sporangia in a complex natural medium is attributed to the inclusion of adequate sterol in the medium, and illumination during incubation.

Light strongly influences the sporulation physiology of *P. lateralis*. Reduced chlamydospore production in light, a previously unreported phenomenon, and increased sporangium production in light, are important with respect to culture identification, inoculum production, and in vitro physiological studies. Considering the presumably subterranean sites of chlamydospore production, the role of light in their formation is uncertain. However, the stimulation by light of sporangium production is consistent with the hypothesis of Zentmyer and Ribeiro (17) that sporulation is more likely to be light-dependent for aerial pathogens than for those which sporulate in the soil. Under certain climatic conditions, *P. lateralis* may cause aerial infections (8,11,13), and may produce sporangia on colonized cedar foliage litter on the soil surface (11).

The in vitro temperature parameters reported here for sporulation and growth by *P. lateralis* may be correlated with the epidemiology of the root rot disease on native *C. lawsoniana*. In the coastal regions where the disease is epidemic, probably the conditions least favorable for development of both the host and fungus occur during the warm, dry summer weather, whereas active development of both the pathogen and host are presumed to be most favored by the mild, wet winters. We found that sporangia were produced prolifically over a broad range of temperatures between approximately 10 and 20 C, encompassing ambient and soil temperatures typical of the winter months in the Pacific Northwest coastal regions. The optimum temperature for chlamydospore production was 24–25 C, which is approximately the maximum temperature for linear growth and dry weight increase. Apparently, chlamydospores are produced as a mechanism for survival in high temperatures, and this supports Trione's (11) hypothesis that chlamydospores are an important means of oversummering for *P. lateralis*.

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