Influence of Polychromatic Light, Carbohydrate Source, and pH on Conidiation of Botryotinia squamosa

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Based on a portion of a Ph.D. thesis by the senior author.

Accepted for publication 16 February 1972.

ABSTRACT

Botryotinia squamosa (*Botrytis squamosa*) does not produce conidia readily in vitro when grown in pure culture under fluorescent or incandescent irradiation, fluorescent plus incandescent irradiation, or diffuse sunlight. It sporulates on necrotic onion leaf apices in the field during midsummer in New York State. Abundant conidiation in vitro occurred in 5 to 7 days when the fungus, grown on potato extract-mineral salts medium at 18 C, was exposed simultaneously to BLB near-ultraviolet (near-UV) and cool-white fluorescent lamps for a 14-hr photoperiod. When supplemented during the first 4 hr with cyclic incandescent lighting (1 sec light, 1 sec dark), the quantity of conidia produced was increased significantly. For conidiation, juvenile mycelium (1 week old or less) was sensitive to near-UV and daylight fluorescent lamps; older mycelium was practically insensitive. Irradiation of sclerotia followed by cold-dormancy stimulated sporulation from sclerotia at 6 to 9 C in 90 days, whereas irradiation of juvenile mycelium at 18 to 23 C stimulated the juvenile mycelium to sporulation in 7 days. Neither the morphology nor the pathogenicity of the conidia was altered. Maximum sporulation was at pH 5.0. Aged soluble starch, dextrin, or potato extract in the medium aided maximum conidiation, whereas mono- or disaccharides were less effective.

Repression of sexual reproduction by exposure to near-UV occurred. In paired cultures of compatible matings of *B. squamosa*, the apothecial initials aborted and conidiation commenced on the stipe tissue. The initiation and inhibition of both sexual and asexual reproductive processes were dependent on length of exposure and quality of irradiation.

Phytopathology 62:889-895.

Additional key words: spore formation.

Botryotinia squamosa Viennot-Bourgin (*Botrytis squamosa* Walker) does not readily produce conidia on potato-dextrose agar (PDA) or any other media tested under either fluorescent lamps or diffuse sunlight in vitro. When conidia are produced, they are quite sparse. Abundant conidiation occurs between mid-June and mid-July on necrotic onion leaf apices in New York (6, 13), when the incidence of near-ultraviolet (near-UV) wavelengths is higher and days are longer (18). Since the stimulation of conidiation in some fungi is due almost entirely to ultraviolet irradiation (1, 8, 17), this source was investigated for induction of conidiation of *B. squamosa*.

The objectives of this study were: (i) to develop a simple technique for inducing conidiation of *B. squamosa* in vitro; and (ii) to determine by comparison with various light, carbohydrate sources, and pH treatments, the optimum conditions necessary for conidiation.

MATERIALS AND METHODS.—*Cultures utilized and maintenance.*—Wild-type sclerotial isolate A-9 and asclerotial mutant A-64 of *B. squamosa* were utilized in this study. Isolate A-9 was grown from a single ascospore from an apothecium of the cross N.Y. 66-6 × Cronshey (2). Mutant A-64 dark sporulator likewise was selected from a fungal hybridization program involving backcrosses of morphological mutants (2).

The stock cultures were maintained on PDA in the dark at 9 C. Transfers from these were incubated in the dark at 18 C for 4 days prior to exposing them to light in Pyrex glass petri dishes (15 mm high × 60 mm diam; four plates/replicate with the lids on). The photoperiod, carbohydrate source, and pH are reported in connection with individual experiments.

Polychromatic light, photoperiod, and cyclic lighting.—Sylvania F 40 BLB near-UV (340 to 380 nm), CW 40 cool-white fluorescent lamps (425 to 625 nm), and 40-w incandescent (575 to 1,060 nm) lamps were used as sources of irradiation in these studies at a distance of 45 cm from the cultures. The spectral distributions and intensities for the separate lamps were measured with a Spectroradiometer Model Sr (Instrument Specialties Co., Lincoln, Neb.) and are presented in Fig. 3. Similar data for General Electric lamps of these types is presented by Jagger (7). Leach (8) reported that the BLB lamps do not emit far-ultraviolet irradiation, and that Pyrex glass transmits near-UV irradiation. Six polychromatic light combinations with a 14-hr photoperiod were studied. There were: two incandescent lamps; four fluorescent lamps; two fluorescent plus two incandescent lamps; four near-UV lamps; two near-UV plus two fluorescent lamps; and two near-UV plus two fluorescent plus two incandescent lamps. Comparisons were made with the last two polychromatic light combinations at 11 different photoperiods varying from 8 to 18 hr to determine the optimum photoperiod for conidiation.

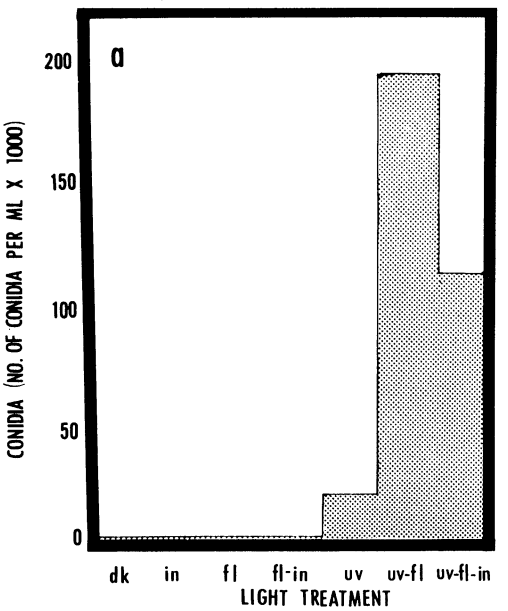
Cyclic lighting from incandescent lamps was tested for its stimulatory effect on conidiation from juvenile mycelium (1 week old or less) as a supplement to the 14-hr period of fluorescent and near-UV irradiation. The cyclic lighting was achieved by means of a cam-operated microswitch programmed for continuously alternating exposure of 1 sec dark and 1 sec of light. It was utilized during the first 4 hr of the 14-hr period of fluorescent and near-UV irradiation for 1 to 7 days. At 1-day intervals, four replicate cultures in each series were removed to a 14-hr photoperiod of fluorescent and near-UV light for the remainder of the 7-day period.

To determine when it would be most beneficial to apply either noncyclic or cyclic incandescent lighting to the 14-hr period of fluorescent and near-UV irradiation during each photoperiod for a period of 7 days, 4 hr of continuous or cyclic lighting was applied to (i) the first 4 hr of the light period; (ii) the middle 4 hr; or (iii) to the last 4 hr.

The temperature during irradiation was 18 C during darkness and 20 to 23 C during the light period. Preliminary studies indicated that temperatures above 26 C inhibited conidiation, whereas no growth of *B. squamosa* occurred above 32 C. Additional studies were conducted in a controlled environmental chamber with (i) a day temperature of 23 C and a night temperature of 18 C and (ii) a day and night temperature of 18 C.

Carbohydrates and basal medium.—Fructose, galactose, glucose, xylose, rhamnose, lactose, maltose, sucrose, trehalose, dextrin, soluble starch, and potato broth extract were utilized as carbohydrate sources. Twenty-year-old soluble starch (J. T. Baker Chemical Co., Phillipsburg, N.J.) and a 1-year-old soluble starch (Mallinckrodt Chemical Works, St. Louis, Mo.) were compared. Potato broth was prepared by autoclaving 200 g of peeled potatoes in 1,000 ml of water for 30 min. Each liter of media was supplemented with 250 mg NH_4Cl, 500 mg KH_2PO_4, 500 mg $MgSO_4 \cdot 7H_2O$, 1.45 mg $Fe(NO_3) \cdot 9H_2O$, 0.88 mg $ZnSO_4 \cdot 7H_2O$, 0.41 mg $MnSO_4 \cdot 4H_2O$, 4 μg H_3BO_3, 4 μg H_3MoO_3, 0.004 mg $CuSO_4$, 1 mg thiamine, 0.5 mg biotin, and 20 g agar. The medium minus the carbohydrate had a pH of 4.7 prior to adding 20 g of carbohydrate and autoclaving. The 12

Fig. 1. Influence of polychromatic light, photoperiod, pH, carbohydrate source, and cyclic lighting on conidiation of *Botryotinia squamosa*. **a)** Comparison of continuous darkness (dk) to 14-hr photoperiods of incandescent (in), fluorescent plus incandescent (fl-in), near-ultraviolet plus fluorescent (uv-fl), or near-ultraviolet plus fluorescent plus incandescent lighting (uv-fl-in) on conidiation. **b)** The effect of varying photoperiods of polychromatic irradiation from fluorescent plus near-ultraviolet, and fluorescent plus near-ultraviolet plus incandescent lamps on conidial production. **c)** The effect of hydrogen-ion concentration on conidial production. **d)** Comparison of twelve carbohydrate sources on conidiation: left to right, the sources are: fructose (fr); galactose (ga); glucose (gl); xylose (xy); rhamnose (rh); lactose (la); maltose (ma); sucrose (su); trehalose (tr); dextrin (de); soluble starch (st); and potato-broth extract (pe). **e)** The effect of cyclic incandescent lighting when utilized to supplement the first 4 hr of the 14-hr photoperiod of fluorescent and near-ultraviolet irradiation from 1 to 7 days, progressing with 4-hr intervals, after which four replicate cultures of each experimental series were removed to fluorescent and near-ultraviolet light for the remaining time. The 4 to 28 hr represent total hr of cumulative light. **f)** Comparison of 4 hr of cyclic to noncyclic lighting when utilized to supplement the 14-hr photoperiod of fluorescent and near-ultraviolet irradiation at three different times of application for a 7-day period. The time periods in which 4 hr of cyclic versus noncyclic lighting was applied to: (1) the first 4 hr of the 14-hr light period; (2) the middle 4 hr of this light period; or (3) to the last 4 hr of this light period.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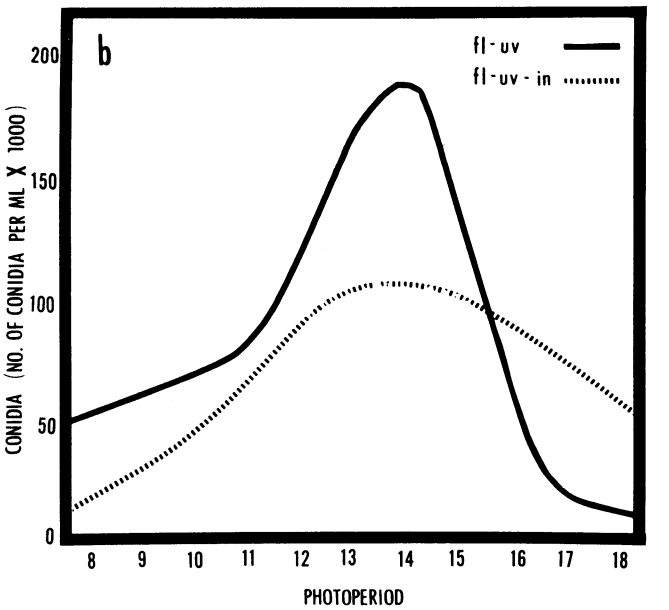
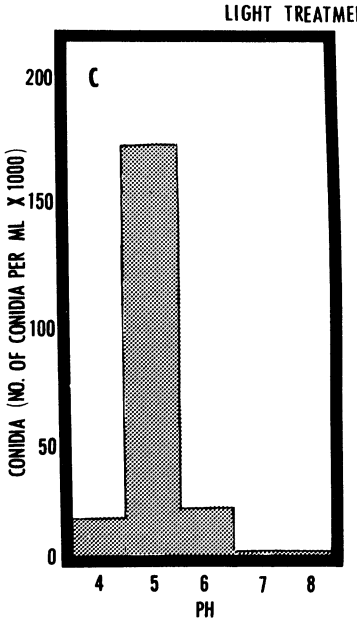
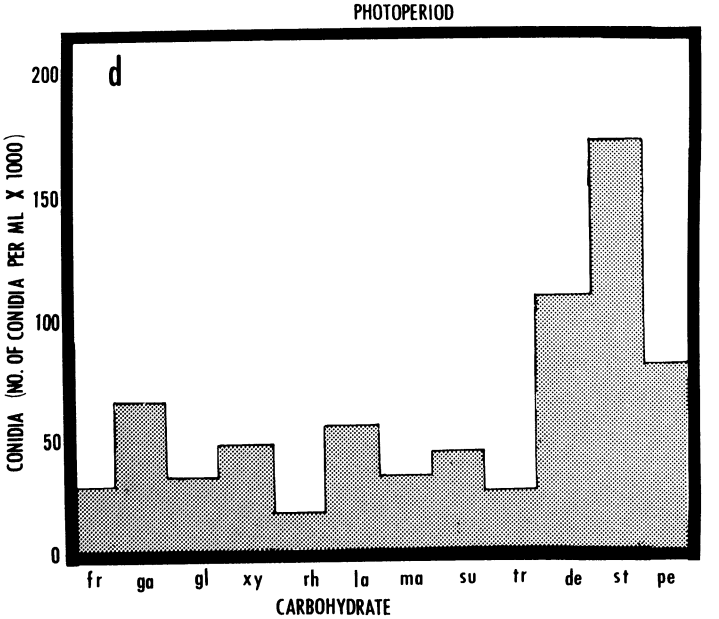
150
100
50
0
dk in fl fl-in uv uv-fl uv-fl-in
LIGHT TREATMENT


b
fl-uv
fl-uv-in
CONIDIA (NO. OF CONIDIA PER ML X 1000)
200
150
100
50
0
8 9 10 11 12 13 14 15 16 17 18
PHOTOPERIOD


c
CONIDIA (NO. OF CONIDIA PER ML X 1000)
200
150
100
50
0
4 5 6 7 8
PH


d
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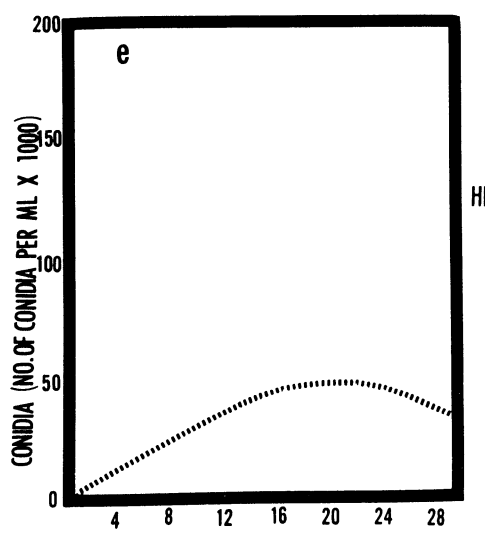
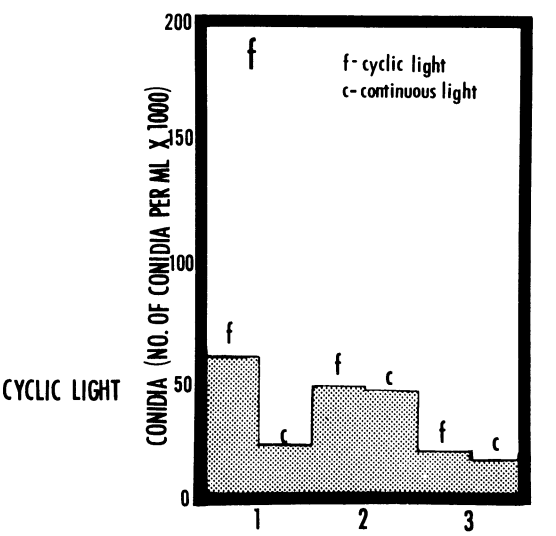
200
150
100
50
0
fr ga gl xy rh la ma su tr de st pe
CARBOHYDRATE


e
CONIDIA (NO. OF CONIDIA PER ML X 1000)
200
150
100
50
0
4 8 12 16 20 24 28
HRS - CYCLIC LIGHT


f
f-cyclic light
c-continuous light
CONIDIA (NO. OF CONIDIA PER ML X 1000)
200
150
100
50
0
f
c
f
c
f
c
1 2 3
CYCLIC LIGHT

carbohydrate treatments (four replicates each) were exposed simultaneously to near-UV and fluorescent irradiation for 14-hr photoperiods for 7 days.

Hydrogen-ion concentration.—Conidiation was studied at 5 pH levels with a 14-hr photoperiod using a combination of near-UV and fluorescent lamps at a distance of 45 cm for 7 days. The pH of the media was adjusted with a citrate-phosphate buffer (stock solution of 0.1 M solution of citric acid and 0.2 M of dibasic sodium phosphate) for pH 4.0 to 6.0 and a phosphate buffer (stock solution of 0.2 M solution of monobasic sodium phosphate and 0.2 M of dibasic sodium phosphate) for pH 7 and 8 (four replicates each). The pH was adjusted before autoclaving to the desired value with a Beckman Zeromatic pH meter. Change in the pH was determined with pHydrion paper after 11 days in culture.

Conidiation from mature sclerotia and apothecial fundaments.—Fifty sclerotial colonies were grown for 21 days in the dark on PDA to permit full development of the sclerotia. The colonies were then incubated for 30 days under a 12-hr fluorescent light photoperiod before transfer to darkness at 9 C. The apothecial initials were produced in culture as described previously (2) and, upon reaching a height of 1 to 2 mm above the sclerotium, 25 colonies were transferred to the combination of near-UV and fluorescent light and the remaining 25 colonies were transferred to the combination of fluorescent and incandescent light.

Determination of propagule numbers.—The number of conidia produced was determined by flooding the colonies with 5 ml of distilled water, pouring the conidial suspension into a beaker, agitating on a vortex mixer, and counting the conidia at a magnification of 100 X in a hemacytometer. Ten replicate counts were made and the average number of conidia per ml of conidial suspension was determined for each experiment.

Pathogenicity tests.—Pathogenicity tests were conducted after exposure of the cultures to irradiation. A water suspension of ca. 1,000 conidia/ml was atomized on 75-day-old onion plants of the cultivar Elite (Harris Seed Co.). The inoculated plants were maintained at high humidity in a growth chamber for 6 days at 18 C under fluorescent and incandescent irradiation at a 12-hr photoperiod. The disease reaction was recorded after 6 days.

RESULTS.—*Polychromatic light, photoperiod, and cyclic lighting.*—Conidiation on juvenile mycelium of isolate A-9 did not occur in complete darkness or under incandescent, fluorescent, or a combination of fluorescent and incandescent irradiation with 14-hr photoperiods (Fig. 1-a), whereas mutant A-64 conidiated under all these conditions. The following results pertain to wild-type isolate A-9. Conidiophores without conidia and abundant aerial hyphae formed on cultures exposed to the fluorescent lamps. Only sclerotia and aerial hyphae formed under continuous fluorescent irradiation or continuous darkness. Few conidia were produced when the cultures were exposed to only near-UV irradiation. Near-UV had the effect of suppressing aerial hyphal development while enhancing the production of sclerotia and conidiophores. There was an inverse relationship between the amount of aerial mycelium and conidiation. The mycelium tended to overgrow the vegetative colony and suppress further conidiation. Exposing the cultures to more than 4 days of darkness induced excessive development of sclerotia and subsequent failure of conidiation from the mycelium. The maximum number of conidia produced with near-UV and fluorescent irradiation was ca. 12 times that produced with near-UV irradiation, and ca. 2 times that produced with near-UV plus fluorescent and incandescent irradiation.

The maximum number of conidia were produced at the 14-hr photoperiod with near-UV and fluorescent irradiation (Fig. 1-b). There was some stimulation of conidiation by 8- and 18-hr photoperiods, but much less than by 13- to 15-hr photoperiods. A twofold increase occurred when near-UV and fluorescent irradiation was applied rather than a near-UV, fluorescent and incandescent combination. Exposure to the latter treatment beyond a 14-hr photoperiod induced development of abnormal conidia, oblong to fusiform in shape, and not produced in the typical *Botrytis*-cluster. When exposed to continuous fluorescent and near-UV irradiation at 18 C, a significant reduction in conidiation occurred as compared to the 14-hr photoperiod.

Cyclic incandescent lighting applied to the first 4 hr of the photoperiod of near-UV plus fluorescent light for 1 to 7 days (4 to 28 cumulative hour cyclic incandescent light exposure) improved conidiation (Fig. 1-e). Cyclic light when applied to the first 4 hr of the 14-hr photoperiod resulted in a significant increase in sporulation over applications at the middle or end of the photoperiod compared to continuous incandescent light (Fig. 1-f). The latter enhanced aerial hyphal growth from the juvenile mycelium while retarding sclerotial development. Cyclic lighting, however, permitted good sclerotial development while reducing the amount of aerial hyphae formed over the mycelium. The minimum amount of cyclic light necessary for improved conidiation in the 14-hr photoperiod was about 4 hr. Extending cyclic light beyond 4 hr caused excessive development of aerial hyphae over the colony and interfered with normal sclerotial development.

No differences were observed in the level of conidiation with a 14-hr photoperiod of fluorescent and near-UV irradiation when a system of alternating night and day temperatures of 18 and 23 C was compared to a constant temperature of 18 C.

Carbohydrates.—The use of polysaccharides and potato-extract broth in place of the mono- and disaccharides resulted in greater numbers of conidia (Fig. 1-d). The aged soluble starch stimulated maximum conidiation, whereas dextrin was less effective. Fresh soluble starch produced fewer conidia than dextrin or potato extract. No differences in conidial production occurred when the mono- and

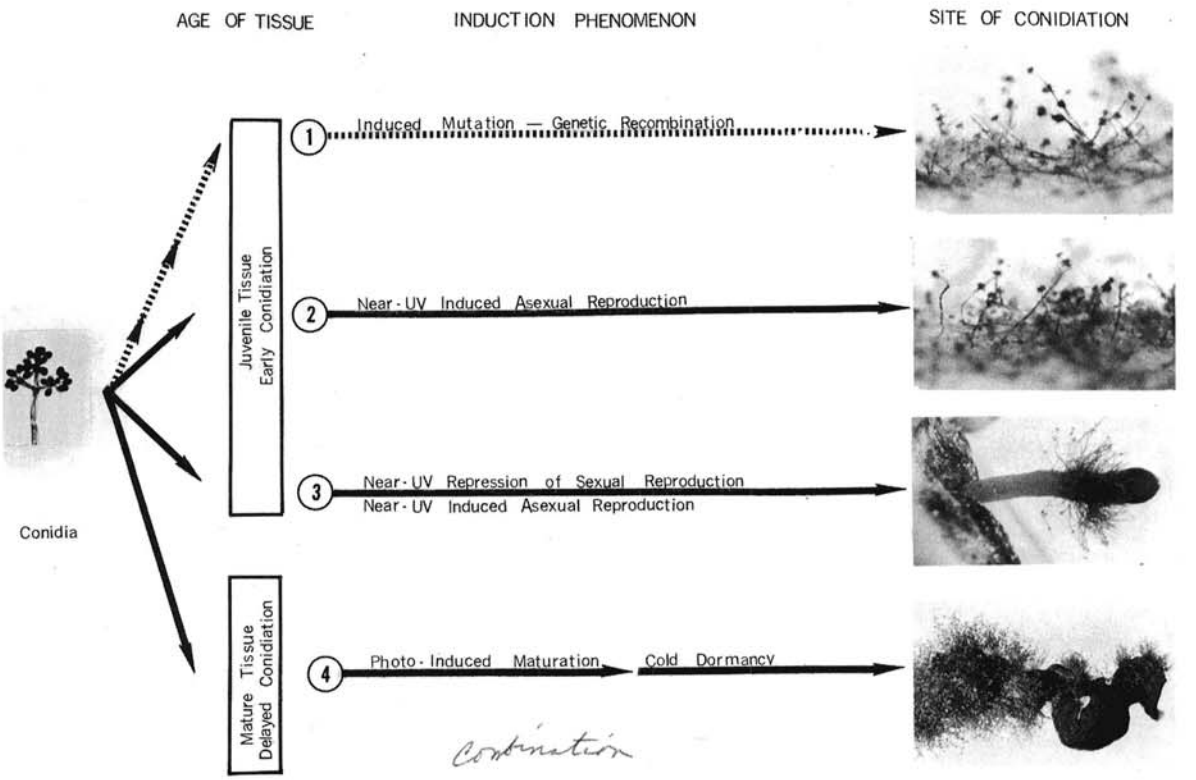


Fig. 2. Conidiation of *Botryotinia squamosa* in vitro in relation to age of the fungal tissue, induction phenomenon, and site of conidiation (vegetative mycelium, apothecial initial, and sclerotium). Juvenile mycelium is considered to be 1 week old or less while mature mycelium is older. **1)** Mutant segregate A-64 sporulated in darkness in 7 to 11 days from an actively growing colony. **2)** Wild type isolates were stimulated to sporulate in 7 to 11 days from actively growing vegetative mycelium when exposed to simultaneous irradiation of near-ultraviolet (near-UV) plus fluorescent light. **3)** Sclerotial cultures with apothecial initials aborted when exposed to near-ultraviolet plus fluorescent irradiation and then commenced asexual sporulation in 7 to 14 days from the stipe tissue. **4)** The sclerotial cultures first were grown on potato-dextrose agar in darkness for 21 days at 18 C, after which time the cultures were exposed to fluorescent irradiation which constitutes "photo-induced maturation" for 30 days at 18 to 21 C followed by "cold dormancy" in darkness for 30 to 60 days at 9 C. During cold dormancy, the sclerotia commenced asexual sporulation.

disaccharide sugars were compared. Fructose, xylose, maltose, and sucrose produced abnormally oblong to fusiform spores, whereas the remaining sugars tended to produce more elliptical-shaped botryose-spores. Aged soluble starch and potato-extract broth supported the best growth for sclerotial production, whereas the mono- and disaccharides produced more aerial hyphal development.

Hydrogen-ion concentration.—The most favorable hydrogen-ion concentration for conidiation was pH 5.0; some conidiation occurred at pH 4 and 6 (Fig. 1-c). More aerial hyphae developed at pH 4 than at 5 or 6. No noticeable growth occurred at pH 7 or 8. Concentric zones were formed as alternating rings of sparse and dense areas of conidiation that corresponded to the regions of the mycelium that were exposed to darkness and 14-hr irradiation at pH 6.

Phenomenon of conidiation.—When cultures of different ages and stages in the life cycle of *B. squamosa* were exposed to a 14-hr photoperiod of near-UV irradiation, conidiophores were produced on: (i) the sclerotia; (ii) the vegetative mycelium of an actively growing colony; or (iii) from apothecial fundaments. Irradiation of sclerotia for 1 month by fluorescent bulbs at 18 to 21 C with a 14-hr photoperiod followed by cold-dormancy at 6 to 9 C induced sporulation from the sclerotium in 1 to 2 months, whereas near-UV and fluorescent irradiation of mycelium at 18 to 21 C (14-hr photoperiod) stimulated the juvenile mycelium to sporulate in ca. 7 days. Spore morphology was not altered by conditions which favored sporulation. The juvenile mycelium was rather sensitive to irradiation for conidiation, whereas the older mycelium was virtually insensitive. Conidiation on apothecial initials occurred when cultures with apothecial initials were placed under near-UV and fluorescent irradiation (14-hr photoperiod). The apothecial initials aborted and asexual reproduction commenced in 7 to 14 days (Fig. 2). The conidiophores arose only from a midpoint region on the apothecial initial.

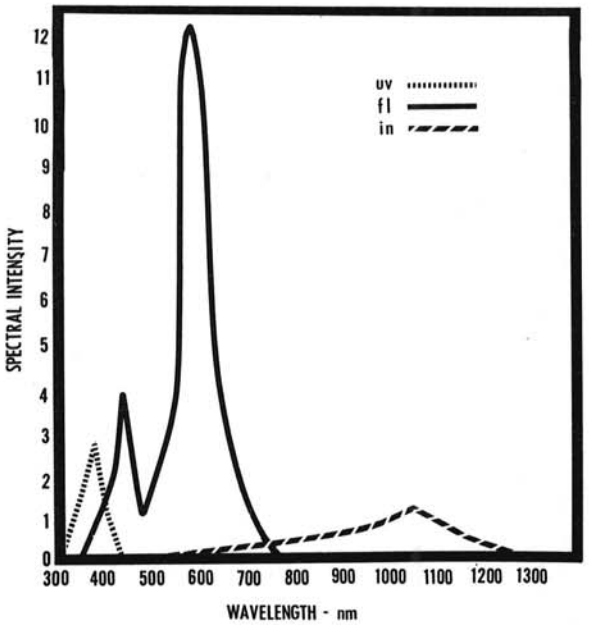


Fig. 3. Spectral distribution of three light sources: 40-w Sylvania fluorescent BLB black light lamp (uv); 40-w Sylvania incandescent bulb (in); and 40-w Sylvania fluorescent cool-white lamp (fl). Spectral intensity was measured in μw per cm^2 per mm with a spectroradiometer.

Apothecial initials exposed to fluorescent plus incandescent light continued normal sexual development.

Pathogenicity tests.—Pathogenicity was not altered by conditions which favored conidiation. Six days after inoculation of onion with isolate A-9 conidia (produced under near-UV irradiation) leaf spotting occurred, followed by blighting of the foliage during the next 4 days.

DISCUSSION.—Sexual and asexual reproduction in many fungi is stimulated by light. The blue to near-UV range is recognized as the portion of the spectrum stimulating conidiation (4, 14). Maximum conidiation of *B. squamosa* from juvenile mycelium in these studies was achieved by irradiation with a combination of BLB near-UV and fluorescent lamps, suggesting that both near-UV and portions of the visible spectrum (particularly in the blue & violet ranges) are necessary for the total process of conidiophore production and conidiation. Near-UV light appears to regulate conidiophore formation. The near-UV lamp utilized in this study emits some blue and violet light, which may have induced the minimal production of conidia observed when only the near-UV lamp was used. Formation of maximum numbers of conidia of *B. squamosa* appears to be stimulated by portions of light of the visible spectrum. Leach (9) suggested that because natural sunlight is comprised of near-UV, and since fluorescent lamps emit a small but significant amount of near-UV, much of the literature reporting successful reproduction in visible light actually may have resulted from stimulation by near-UV radiation. The literature frequently is not clear on the distinction between near-UV and violet light. Jagger (7) indicates the visible light spectrum as 380 to 780 nm, with the limits determined by average human visual sensitivity and the near-UV range as 300 to 380 nm. Other authors list different ranges (8, 15). Studies with monochromatic light of the visible and near-UV regions are needed to quantify the action spectra for production of conidiophores and conidia of *B. squamosa*. Such studies also should include short and long periods of exposure of both juvenile mycelium and sclerotia.

Cyclic lighting is used widely in commercial floriculture (16), but its use has received little attention by workers investigating fungi. The reasons for increased conidiation of *B. squamosa* in the present study when cyclic lighting was applied during the first 4 hr of a 14-hr photoperiod are not known and should receive additional attention. The role of infrared light, particularly that emitted from the incandescent lamp, on conidiation of *B. squamosa* requires further study. Inclusion of infrared light with different combinations of near-UV and fluorescent lamps also should be studied. The differences in the triggering mechanisms for conidiation from juvenile mycelium and sclerotia are attributed to physiological differences between the two fungal tissues. Exposure for 30 days to fluorescent light, followed by cold incubation in darkness for 1 to 2 months, stimulated the sclerotium to conidiate. Continuous exposure to darkness did not trigger conidiation. Small amounts of irradiation from the near-UV region of the spectrum over a long period of exposure to fluorescent lamps before the cold treatment in the dark may have stimulated conidiation from the sclerotia.

In nature, fungi are exposed to diurnal solar irradiation. Under a simulated diurnal cycle of 14 hr, concentric zones were formed as alternating rings of sparse and dense areas of conidiation at pH 6. These rings corresponded to the regions of the mycelium that were exposed to either the dark or light conditions. Under all other conditions with the standard substrate, conidiation occurred over the entire plate with no evidence of rhythmic growth when the fungus was exposed to a diurnal cycle. Esser (5) demonstrated that rhythmic growth in *Podospora anserina* depends on the pH of the medium for its fullest expression. These investigations of *B. squamosa* support his observations that increasing hydrogen-ion concentration may enhance rhythmic growth when fungi are exposed to a diurnal light cycle. Conidiation occurred under both continuous irradiation and a simulated 8- to 18-hr diurnal cycle. The 13- to 15-hr photoperiods were more efficient for inducing maximum conidiation than was continuous irradiation in vitro. Such conditions would be expected to occur in nature during midsummer when this fungus is active in New York.

Soluble starch as a carbohydrate source in a mineral salts medium provides a suitable substrate for the induction of asexual sporulation by near-UV

irradiation of *B. squamosa* (3). When both old and new sources of soluble starch were compared, maximum induction of conidiation occurred with the former when cultures were exposed to near-UV light. Whether sporulation was stimulated by contaminants which occurred in the aged soluble starch or by compound(s) resulting from structural change(s) during aging or a specific plant source is not known.

In pure culture, conidiophores arose either from the juvenile vegetative mycelium or from the mature sclerotium, but not simultaneously from both. Leach (9) reported that the age of the mycelium of *Ascochyta pisi* affects its sensitivity to irradiation. A scheme showing the relationships between light and conidiation from the sclerotium, vegetative mycelium, and apothecial initials in *B. squamosa* is summarized in Fig. 2. With the cold treatment, conidiation occurs abundantly on the surface of the sclerotium, but never from the mature vegetative mycelium of the same colony. This sequence compares favorably to that expected in nature. Mutant segregate A-64 sporulated in the dark in 7 to 10 days at 18 C from an actively growing colony (2). Sporogenic substances (18) may be produced in the absence of light in mutant A-64, whereas they are produced via a photo-stimulated pathway in wild type isolates of the fungus. Leach (10, 11) and Leach & Trione (12) reported that sexual reproduction in *Pleospora herbarum* is triggered by either near-UV irradiation (photo-induction) or low temperatures (cold induction). In *B. squamosa*, a similar system appears to be operative for asexual reproduction. Two control mechanisms are hypothesized for conidiation depending on whether conidiophores arose from the sclerotium or from the juvenile mycelium. The temperature and light requirements for the two sites of conidiation (juvenile or mature tissue) are distinct. The sclerotium was not stimulated to conidiate until given a cold treatment. No conidiation and little growth occurred from juvenile tissue when it was exposed to lower temperature. These data suggest that the triggering mechanism for conidiation from the sclerotium (cold treatment) is different from that of the juvenile mycelium (light treatment).

The phenomenon of near-UV repression of sexual reproduction coupled with near-UV induced asexual reproduction suggests that the apothecial stage of *B. squamosa* is not likely to occur in nature during conditions of high near-UV light intensities. However, the conidial stage may be more likely to occur in nature when near-UV light is most intense. These findings suggest that a photo-stimulated pathway is operative in the two reproductive processes of *B. squamosa*. The light-activated pathway in the sexual process of reproduction is quite distinct from that occurring in the asexual reproductive process. Thus, the pattern of different light requirements in *B. squamosa* has a profound effect on dictating when a particular reproductive process will occur in nature.

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