THE EFFECT OF ULTRAVIOLET RADIATION ON DISCHARGED PYCNIDIOSPORES OF SEPTORIA TRITICI

By

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CHAPTER I

INTRODUCTION

Lethal effects of sunlight upon microorganisms was first noted about the time that pure culture technique came into wide use (13). In nature, most fungi are exposed during a part of their life cycle to solar originated ultraviolet (UV) radiation. When UV radiation is in the shorter wave lengths (below 300 nm), biological activity is commonly retarded (26).

Sensitivity of fungal spores to UV radiation is contingent upon several factors, some of which remain imperfectly understood. Hyaline spores are generally considered to be more sensitive than pigmented ones (18). Generalizations relative to UV sensitivity of spores may lead to imperfect conclusions as a result of such confounding factors as tolerance to dessication and temperature. However, knowledge of the sensitivity of progagules of plant pathogenic fungi to UV radiation is a prerequisite to understanding the spread and development of diseases caused by them.

Septoria tritici Rob. ex Desm. (the imperfect stage of Mycosphaerella graminicola (Fuckel) Sand.) causes Septoria leaf blotch of wheat (11). The conidia of S. tritici ooze out from pycnidia in infected wheat leaves in gelatinous cirrhi when the pycnidia are wet from rain or dew and when the relative humidity approaches 100%. Expelled cirrhi may remain on the leaf surfaces until dissolved by moisture or dispersed by splashing and wind-borne rain. Also, it is suspected that cirrhi may

be dislodged by wind or wind-induced leaf movements and dispersed by air movements. Periods during which conidia in cirrhi may be exposed to UV radiation range from a few minutes to several days.

This study was conducted to determine the effects of UV radiation on viability of discharged conidia of S. tritici.

CHAPTER II

LITERATURE REVIEW

The region of the spectrum now designated as ultraviolet was discovered in 1801 by John Wilhelm Ritter who found that radiant energy below that which is visually perceptible would blacken silver salts. The UV region can be divided into three equal wavelength bands: vacuum UV, from 100-200 nm, far-UV from 200-300 nm, and near-UV from 300-400 nm (13).

In nature, most fungi are exposed during a portion of their life cycle to some far-UV radiation (mainly 290-300 nm), and to considerable near-UV (300-380 nm) and visible (380-750 nm) radiation (18). Ultraviolet radiation, particularly in the wavelength range of about 260 nm, may produce mutation or death in fungi (2). Prior to the Silurian era the earth's surface was exposed to mutagenic and lethal wavelengths of UV radiation of less than 290 nm. Much diversity of form and physiology of fungi may derive from a reservoir of mutagenic changes originating during this early era (18).

Effects of far-UV on survival of fungi depends on many factors. Spores, or conidia, for example, are much more resistant to lethal effects of UV than are vegetative mycelia. Sensitivity of spores is frequently related to color. Pigmented spores often survive longer exposures to far-UV than colorless spores; and thickness of spore wall may be involved in tolerance of fungi to radiation. Age also may influence sen-

sitivity of spores (19). Old spores of Aspergillus melleus are more tolerant to far-UV than are young spores. Exposure of dry spores to light usually has no effect on their subsequent germination (18). Spores in nature are often protected from rapid loss of water by a gelatinous matrix (7, 20), which also may protect them against UV radiation. According to Uspenskaya and Reshetnikova (27), conidia of fungi in the genera, Ascochyta and Phoma, maintained viability at higher UV doses much better when immersed in pycnidial slime. Stevens (24) found that germination of Glomerella cingulata ascospores was reduced by a five second exposure to direct radiation at 21 cm, and killed (or germination stopped) by a fifteen second exposure. However, more than ninety seconds of exposure was required to kill all spores when they were covered by 1.5 mm of corn meal agar. Excessive dosages of radiation, particularly at the shorter wavelengths (237.8-366.6 nm) inhibited sporulation of Alternaria chrysanthemi (17). Arsenijevic (3) reported that S. tritici exposed to UV radiation for three minutes failed to produce colonies.

Near-UV is very effective in stimulating diverse species of imperfect fungi to sporulate (18, 16). According to Leach (18), Ascochyta pisi, Helminthosporium dematioideum, Stemphylium botryosum and Alternaria chrysanthemi are all induced to sporulate by wavelengths of monochromatic UV from 230-360 nm, but not by longer wavelengths. Leach (16) and Cooke and Jones (8) used near-UV to stimulate sporulation of S. tritici and S. nodorum. Negative phototropism (growth away from light source) was also induced by wavelengths shorter than 350 nm and by those somewhere between 350 and 510 nm (5).

Full daylight has been reported to reduce germination, growth, or

sporulation of most fungal plant pathogens (1). This may have an effect on disease development. According to Schall et al. (22), maize anthracnose symptoms are expressed most on cloudy days, i.e., when solar radiation is low. High light intensity and longer photoperiods have been shown to decrease lesion size and/or numbers in infections due to Phytopthora infestans and Alternaria solani on potato leaves, Phytopthora drechsleri on safflowers and Helminthosporium turcicum on corn. Reports on higher light intensity were said to have caused an apparent decrease in disease severity on corn infected by Colletotrichum graminicola (10). By contrast, Fellows (9) found that high daylight intensities during the incubation period enhanced infection by S. tritici of the wheat cultivar Westar. The most lesions per leaf and the percent of leaves infected increased as the light intensity was increased from 0 to 1300 ft cd. Benedict (4) demonstrated a differential effect of light intensity on the number of pycnidia produced in four cultivars. Using three light intensities (2,000; 8,000; and 12,000 lx), the number of pycnidia per lesion varied from fewer than 25 for the cultivar 'Capelle Desprez' at all intensities to about 400 in the cultivar 'Joss Cambier' at 2,000 lx. Intermediate numbers of about 150 and 250 pycnidia per lesion occurred in cultivars 'Maris Ranger' and 'Kolibri,' respectively. Except for 'Capelle Desprez,' more pycnidia were produced at 2,000 lx than at higher intensities.

The UV intensity in early morning and late afternoon is very low when compared with that in the middle of the day. Absorption in the atmosphere is greater for shorter wavelengths than for the longer wavelengths. The UV wavelengths of 320 nm and less doubles in intensity between 9:00 a.m. and 12:00 noon. At all wavelengths, intensity is

maximum at noon and lower at morning and evening, but variation is much greater for the shorter than for longer wavelengths. Seasonal variation is greatest in June and least in December. This seasonal change is greatest for shorter wavelengths. While intensity of the 340-380 nm band only increases by a factor of about two between December and June, the 300 nm band increases a hundredfold. Accordingly, total energy measurements can be very misleading regarding erythemal or biological effects of sunlight. Solar radiation varies from place to place and is influenced by a number of factors: altitude, time of day, season, latitude, and atmospheric conditions. In the solar spectrum, the UV intensity is only one millionth of that of 314.3 nm for the sun at its zenith in midlatitude (14).

Capacity of short wavelengths, including near-UV (300-380 nm), to kill cells has been known for a long time. Doses in the near-UV region required to induce lethality are of the order of 1000 times those needed with far-UV (12).

Short wavelengths are absorbed specifically by nucleic acids (260 nm) and proteins (280 nm). Long wavelengths as well as visible and infrared light is selectivily absorbed by pigment systems and produces changes in the electron population at electronic and vibrational levels (23). The short wavelength side of the UV region covers that energy range where excitation rather than ionization is predominant (22). The action spectrum for many mutational changes corresponds with the absorption spectrum of deoxyribonucleic acid (DNA) with 260 nm radiation being the most effective. In Chaetomium globosum, however, 280 nm radiation is most effective. The action spectra for killing or causing mutation in spores of Trichophyton metagrophytes are similar to the absorption

spectrum for DNA (12). Although lethal effects of UV are generally attributed to wavelengths in the 200-300 nm range, evidence exists that near-UV and visible light can also be lethal, at least for the bacterium, Escherichia coli. This has not been proven for fungi (18).

CHAPTER III

MATERIALS AND METHODS

UV Radiation Measurements

Radiation measurements were limited to the germicidal wavelength of 254 nm. Measurements (mW/cm^2) were obtained with a spectroline, model DM-254N, shortwave (254 nm) UV photometer (manufactured by Spectronics Corporation, Westbury, NY 11590). In this thesis, radiation intensity is used in the same sense as radiant flux which is defined as radiant energy which crosses unit area in unit time (25). In the laboratory the UV sensor was held horizontally and as directly beneath the UV source as spatial conditions of experiments would permit. Outdoor measurements (unless otherwise indicated) were made with the sensor directly facing the sun. This resulted in higher intensity readings than those obtained when the sensor was horizontal.

Source of Cirrhi

Leaves with lesions containing pycnidia of S. tritici were harvested from nearly mature greenhouse grown plants of the wheat (Triticum aestivum) variety 'Chinese Spring' which had been inoculated with S. tritici (designated St-22) isolated from wheat grown near Stillwater, Oklahoma. The plants had been in growth stages eight to nine at time of inoculation. Harvested leaves were taped flat to paper towels and stored at 4°C until needed.

Pycnidia were stimulated to discharge conidia in tendril or globe-shaped cirrhi by clamping 3-4 cm lesion bearing leaf segments to microscope slides with paper clips and then placing each unit on glass rods on wet paper in polystyrene petri dishes (Kimble, 100x15 mm). Prior to attaching them to glass slides, leaf segments were dipped in 10% alcohol for about thirty seconds and then rinsed with distilled water. This process greatly reduced the quantity of Alternaria sp. and Helminthosporium sp. conidiophores and conidia that sometimes developed in the lesions. Abundant cirrhi were expelled from pycnidia after forty-eight hours.

Effect of UV Radiation on Conidia in Cirrhi at Different RH Values

Leaf segments bearing exuded cirrhi were removed from the petri dish moist chamber and cut in half. (Later, one half of each lesion served as an untreated check and one half was exposed to UV radiation.) Each half then was clipped to a microscope slide and placed on glass rods in a polystyrene petri dish containing 10 ml of deionized distilled water or a molal solution of either NaCl and NaOH with water activity (a_w) values near 0.98, 0.95, 0.90, 0.85, 0.80, 0.75, 0.70, 0.65, 0.60, 0.55, and 0.50. In this thesis, a_w values are often changed to relative humidity (RH) by multiplying by 100. NaCl was used only to obtain the a_w value of 0.98. NaOH was used to obtain all values less than 0.98. The amount of NaCl and NaOH used to prepare the solutions (Appendix) were obtained from tables published by Lang (15) and Robinson and Stokes (21), respectively. After placing the lesions bearing pycnidia with expelled cirrhi over the solutions, petri dish covers were sealed in place with

parafilm "M" (American Can Co., Greenwich, CT 06830) and stored in darkness at a constant 25±0.1°C for five days in a low temperature incubator (Precision Scientific Group, GCA Corp., 3737 West Cortland St., Chicago, IL 60647).

Undisturbed expelled cirrhi held over the water and salt solutions were exposed while sealed in the petri dishes for varying lengths of time between zero and twenty-four hours to far-UV radiation. Exposures were made inside a three-sided rectangular wood box (40 cm high x 40 cm deep x 80 cm long) with black interior walls. The fourth side of the box (40 x 80 cm) was closed with a black drop cloth-shield to permit easy access. A 7 cm x 60 cm slot was centered in the top of the box and the light source placed on the slot. A slide warmer (Type CSE manufactured by Clinical Scientific Equipment Co., Melrose Park, IL) was placed inside the box to assure that a more or less constant temperature was maintained at the bottom of the petri dishes during exposure. (This precaution proved unnecessary because room temperature was maintained at 22°C by a fixed thermostat control and the temperature inside the box was about 28°C when the light source was operating.) A G.E. germicidal lamp "A" (254 nm) manufactured by General Electric Co. (Nela Park, Cleveland, OH 44112) was used as the radiation source.

Distance from the lamp to the leaf segments was 30±1 cm. The 1 cm variation derived from the impossibility of placing all lesions directly below the lamp when more than one lesion was being exposed at the same time. Intensity of radiation at lesion sites was 0.11 ± 0.2 mW/cm^2. This intensity was between 65% and 70% of intensity at the same sites when petri dish lids were not above the photometer sensor.

Effect of radiation on spore viability was determined by direct ob-

servation. Cirrhi from three to five pycnidia, in each irradiated and non-irradiated lesion half, were transferred to drops of sterile yeast extract-malt extract liquid medium (2g of yeast extract [Difco Laboratories, Detroit, MI 48232] and 5g of malt extract [U. S. Biological Corp., Cleveland, OH 44128] in one liter of distilled water) in double-depression concavity microscope slides. Cover slips were placed over depressions and sealed with petroleum jelly. Double-depression slides were used to facilitate pairing of spores from irradiated and corresponding nonirradiated lesion segments during incubation. After forty-eight hours at room temperature, drops of the spore containing medium were transferred to microscope slides and examined through a compound microscope for evidence of reduced germination. All combinations of RH values and UV exposure times used in the experiment were repeated four times, and in some instances five and six times.

Effect of UV Radiation on Washed Conidia

Petri dishes containing a yeast extract-malt extract agar medium (0.5g of yeast extract, 2g of malt extract, and 4g of agar in one liter of distilled water) were flooded with 1-2 ml of liquid medium containing budding conidia and incubated at room temperature (20-22°C). After seven days the agar surface was covered with a light pink mass of conidia in a gelatinous matrix. Approximately 0.25-0.50 cc of spores and matrix were removed with a rubber policeman and smeared on a millipore filter. One liter of deionized distilled water was poured over the conidia and drawn through the filter. The conidia were then scraped from the filter paper and plated in 0.3 ml of deionized distilled water in concavity microscope slides and exposed for forty-eight hours to 0.11

mW/cm^2 of 254 nm wavelength. Unwashed conidia from the petri dish culture were similarly exposed. After exposure to UV radiation, samples of conidia were transferred to yeast extract-malt extract medium and observed for evidence of viability.

Tolerance of S. tritici conidia in cirrhi and in matrix from cultures grown on agar to far-UV (254 nm) irradiation was compared with that of conidia from three genera of fungi--Fusarium sp., Gloeosporium sp., and Cryptococcus sp. (a yeast); and cells of three bacteria--Bacillus licheniformis, Xanthamonas malvacearum, and an unidentified yellow isolate. The Fusarium sp. culture, obtained from Dr. L. L. Singleton, had been isolated from roots of wheat. The Gloeosporium sp. culture was obtained from Dr. K. Conway. The culture of X. malvacearum was obtained from Dr. W. M. Johnson. B. licheniformis was isolated from soil, and Cryptococcus and the yellow bacterium were washed from surface of wheat leaves.

Conidia or cells of each organism were placed in three drops of deionized distilled water in each depression on concavity slides and exposed to 254 nm UV radiation with an intensity of 1.21 mW/cm^2 at a distance of 8.0±1.0 cm from the source and at a temperature of 30°C. Exposure ranged from one to ninety-six hours without interruption. At the end of each treatment, irradiated and non-irradiated (control) conidia or cells of each organism were placed in malt-yeast extract agar medium and checked for viability after twenty-four to forty-eight hours, depending upon growth rate of the organism. All treatments were repeated at least four times.

CHAPTER IV

RESULTS

There were no discernible lethal effects or reductions in viability of S. tritici conidia at twelve discrete RH levels after continuous exposure for twenty-four hours at radiation intensity of 0.11±0.02 mW/cm^2 of 254 nm wavelength. Conidia evinced their viability by budding and formation of germ tubes in liquid yeast extract-malt extract medium within four days after UV exposure. Further, transfer of exposed conidia to yeast extract-malt extract agar produced colonies in all cases. The intensity of 0.11 mW/cm^2 was approximately 78% of the mean intensity (0.14± 0.02 mW/cm^2) at noon on five clear days in January at Stillwater, Oklahoma, and 53% of the mean intensity (0.208± mW/cm^2) at noon on five clear days in April, May, and June. Also, this intensity was essentially the same as a noon measurement of about 0.11 mW/cm^2 on a horizontal plane reported for wavelengths of 313 nm and shorter at noon on a "very clear" day, 11 April 1943, at Washington, D.C. (6).

Inasmuch as radiation dosage is the product of radiant flux times length of exposure, a continuous exposure from an artificial source for a given time can be converted to equivalency of solar exposure units (hours, day, etc.) using curves of solar radiation over time. Hourly measurements of radiation intensity were not made for any daylight period during April and May when Septoria leaf blotch develops most rapidly in Oklahoma. However, intensity of wavelengths in the biological detri-

mental ranges of 313 nm and shorter were monitored hourly between 6:00 a.m. and 6:00 p.m., 11 April 1943, by Coblentz and Stair (6). By measuring (with a Lambda area meter), areas under the twelve hour radiation curves plotted by Coblentz and Stair (6), and under a continous twenty-four exposure plotted to the same scale, I determined that twenty-four hours of continuous exposure to 313 nm and shorter wavelengths to be equivalent to 7.56 days with twelve hours of sunlight. Since energy reaching the earth's surface decreases with decreasing wavelength, it can be reasonably assumed that intensity of the 254 nm wavelength used in this experiment was equivalent to more than eight days in April.

Conidia produced in artificial culture and washed free of visually discernible matrix evinced no apparent detrimental effect from forty-eight hours of continuous exposure to 0.11 mW/cm^2 of 254 nm wavelength.

Conidia of S. tritici, in cirrhi from leaf-borne pycnidia and in matrix from agar culture, transferred to drops of deionized distilled water in microscopic depression slides survived ninety-six hours of continuous exposure to 254 nm wavelength at an intensity of 1.21 mW/cm^2 (Table I). The experiment was terminated after ninety-six hours. Consequently, full capacity of S. tritici conidia to survive in the 254 nm band were not determined. They were, however, much more tolerant to radiation than other tested soil and phylloplane fungi and bacteria. Cryptococcus sp. spores and the unidentified yellow bacterium were killed between twenty-four and thirty-six hours of exposure; Fusarium conidia were killed between twelve and eighteen hours; Pythium sp. (mycelium) only), B. licheniformis and X. malvacearum were killed between six and twelve hours; and the Gloeosporium conidia were killed in less than three hours.

TABLE I

VIABILITY OF SPORES AND CELLS OF ORGANISMS IRRADIATED WITH 254 nm AT AN INTENSITY OF 1.21mW/cm^2[a]

Organism	Time in Hours 0	3	6	12	14	18	24	36	48	60	72	84	96
Gloeosporium sp	+[b]	+											
Pythium sp	+	+	+	+									
Bacillus licheniformis	+	+	+	+									
Xanthamonas malvacearum	+	+	+	+									
Fusarium sp	+	+	+	+	+								
Cryptococcus sp	+	+	+	+	+	+	+	+					
Yellow bacterium	+	+	+	+	+	+	+	+					
Septoria tritici	+	+	+	+	+	+	+	+	+	+	+	+	+

[a]Spores and cells of the organisms in concavity microscope slides were irradiated with UV at 30°C at a distance of 8 cm ± 1 from the light source.

[b]+ = viable

CHAPTER V

DISCUSSION

Conidia of S. tritici in the matrix of cirrhi from leaf-borne pycnidia, in slime of actively budding cultures on artificial medium, or after being washed free of any visible matrix are very tolerant to UV radiation in the 254 nm wavelength. Tolerance of conidia in cirrhi was equally manifested in twelve discrete RH conditions ranging from 50-100% under radiation intensity of 0.11 mW/cm^2. These results are in partial accord with those from experiments of Uspenskaya and Reshetnikova (27) which showed that conidia of Ascochyta and Phoma maintained viability at high UV doses when immersed in pycnidial slime.

Webb (28) studied effect of light (wavelengths of 280-320 nm, 340-450 nm, and 520-580 nm) and RH on viability of air-borne cells of the bacterium Serratia marcescens. Numbers of cell deaths per unit of time decreased as the wavelength increased. At different RH levels, 55-65% was always the critical level above which cells were stable and below which they were extremely susceptible to radiation. In earlier studies (29), he suggested that inositol protected cells from desiccation by replacing "bound" water in the cells which is removed at around 60% RH. Since RH affected sensitivity to light, he reasoned that presence of inositol should prevent damage to cells held at 30% RH (28). This was found to be true both for UV in the 280-320 nm range and for white light. The fact that conidia of S. tritici were tolerant to UV radia-

tion when washed free of visible matrix, suggests that the tolerance probably derives from a chemical presence which may be either intracellular or bonded in or on the conidium wall. It seems reasonable to assume that such a protective chemical may also exist exogenously in the matrix.

Results of this study also indicate that S. tritici conidia are resistant to prolonged exposures of germicidal UV relative to the reactions of seven other microorganisms. Septoria tritici conidia remained viable after ninety-six hours of continuous exposure to an intensity of 1.21 mW/cm^2 of 254 nm wavelength. Conidia of Gloeosporium, the most sensitive of the organisms tested, were killed in less than three hours. An earlier report (24) indicated that Gloeosporium conidia could be killed by a fifteen second exposure to UV radiation from a lamp. Like those of S. tritici, conidia of Gloeosporium are embedded in slime, yet sensitivity of the two organisms to far-UV radiation differ greatly. Conidia of the Fusarium culture were inactivated between twelve and eighteen hours of exposure. The limited scope of this study precluded the collection of data which would indicate why these three hyaline-spored fungi, commonly found as pathogens of aerial parts of plants, should differ so widely in their sensitivity to UV radiation. Possibly the one, two, and one to three nucleate conidia of Gloeosporium, Fusarium, and S. tritici, respectively, may confer a disparity of tolerance by presenting unequal probabilities for radiation "hits" on vital DNA sites per unit time.

The bacteria, X. malvacearum and B. licheniformis, and the fungus, Pythium, tolerated between six and twelve hours of radiation; while the yeast, Cryptococcus, and the unidentified yellow bacterium withstood more than twenty-four hours. Inasmuch as S. tritici, Cryptococcus, and

the yellow bacterium are natural inhabitants of leaf surfaces, it is logical to assume that these organisms have either evolved protective mechanisms against lethal rays of sunlight, or they have evolved as foliar inhabitants as a result of such mechanisms.

Based on this study, it may be concluded that any natural inhibition to development of Septoria leaf blotch is derived from factors other than lethal effects of UV rays from the sun.

CHAPTER VI

SUMMARY

S. tritici pycnidiospores were extremely tolerant to UV radiation with 254 nm wavelength. They survived without any discernible damage under the following conditions and radiation intensities: (a) in cirrhi at relative humidities of 50, 55, 60, 65, 70, 75, 80, 85, 90, 95, 98 and 100%, under continuous exposure for twenty-four hours at an intensity of 0.11 mW/cm^2; (b) after being washed with 1000 ml of deionized distilled water and exposed for ninety-six hours at an intensity of 1.21 mW/cm^2; and (c) transferred in cirrhi to a water droplet and exposed for ninety-six hours at an intensity of 1.21 mW/cm^2. By contrast, spores or cells of *Gloeosporium* sp., *Bacillus licheniformis*, *Xanthamonas malvacearum*, *Fusarium* sp., *Cryptococcus* sp., and an unidentified yellow bacterium survived an intensity of 1.21 mW/cm^2 for 3, 12, 12, 14, 36, and 36 hr respectively.

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APPENDIX

WATER ACTIVITY OF SATURATED SOLUTIONS AT 25°

%	Gm Wt of NaOH, NaCl dissolved in 100 ml of deionized distilled water
100	Deionized distilled water only
98	2.92 g NaCl
95	5.86 g NaOH
90	10.90 g NaOH
85	15.36 g NaOH
80	19.19 g NaOH
75	22.84 g NaOH
70	26.26 g NaOH
65	29.54 g NaOH
60	32.73 g NaOH
55	35.90 g NaOH
50	39.17 g NaOH

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VITA

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