

THE EFFECTS OF VARIOUS WAVELENGTHS OF LIGHT  
ON CONIDIAL DISCHARGE IN ENTOMOPHTHORA GRYLLI PRESENIUS

by

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## INTRODUCTION

The genus Entomophthora is found in the Entomophthorales amid the commonly called "algal fungi" or "Phycomycetes." It is a relatively small genus containing some 104 species (Thaxter, 1888), but only 15 have been reported from the Western Hemisphere (Hutchinson, 1963). These fungi have long been known and have been extensively studied. Thaxter (1888) in a classic work monographed the order and made many observations on the biology of these fungi.

All of the species of Entomophthora are parasitic on insects, attacking immature and/or adult stages of some 20 families of insects. However, according to Thaxter (1888), those of the order Diptera are the greatest sufferers and epizootics among insects are fairly common (MacLeod, 1963).

Among the 6 genera of the Entomophthorales, only Entomophthora has the unique feature of discharging its conidia forcibly from the conidiophores. Conidia may be expelled 8-10 mm from the conidiophores. In an earlier study by Pady et al. (1969), discharge of the conidia was shown to be correlated with light and under conditions of alternating light and dark a definite diurnal (circadian) pattern of sporulation was evident.

The purpose of this study was to explore the effects of various light wavelengths on the diurnal rhythm of spore discharge.

## REVIEW OF LITERATURE

The genus Entomophthora was originally described by Cohn in 1855 as Empusa for a fungus parasite of the house fly based on Empusa muscae Cohn, the type species. Fresenius (1856) recognized that the name Empusa had already been pre-empted by a genus of orchids and proposed the name Entomophthora for the genus. This has been followed by the somewhat indiscriminate use of both names; we are following the nomenclature used by Hutchinson (1963).

Species of Entomophthora are parasitic on a relatively large number of insects (Thaxter, 1888). However, Diptera and Hemiptera appear to be the 2 orders of insects that these fungi most frequently infect, and from which the greatest number of species have been isolated. It is apparent that there is some specificity of hosts for each species of Entomophthora (Thaxter, 1888; Steinhaus, 1949). This specificity, however, is by no means certain or uniform since some species of Entomophthora infect a wide range of hosts, including insects of different orders.

The typical mode of infection among these forms is through contact rather than through ingestion (MacLeod, 1963). However, a number of factors such as the nature of the outer integument may influence the degree of infectivity by the various species of Entomophthora (Thaxter, 1888). It is suspected that the thin body wall of some insects, particularly flies, is readily penetrated at almost any site on the body, thus accounting for the prevalence of these insects as hosts of Entomophthora.

Once inside, the fungus continues to grow by a peculiar

budding process in which hyphal bodies are produced until the body cavity is almost filled (Fitzpatrick, 1930; Steinhaus, 1949). Shortly after the death of the insect, conidiophores develop from the hyphal bodies and emerge through the less resistant portion of the exoskeleton of the host (Steinhaus, 1949). A single conidium is then produced and forcibly discharged.

Although species of Entomophthora have received considerable attention and study, little has been done with them in regard to daily periodicities of spore discharge. Only 3 reports are known dealing with this matter. In a study of the air spora using a sampler located in an arable field near London, England, Hamilton (1959) found conidia to be present in the air with peaks at 5 A.M. and 1 P.M.

Pady et al. (1969) studied the effects of light and dark on the daily patterns under controlled environmental conditions in the laboratory and found that discharge was stimulated by light. Peaks occurred 2-3 hr after initial stimulation. This was followed by a gradual decline in sporulation until the light period on the second and third days which produced peaks of decreasing magnitude. On the fourth day, the fungal colony was exhausted and spore discharge did not occur.

Although there have been no previous studies on the effects of various spectrum wavelengths upon the pattern of spore discharge in Entomophthora, work has been done on other fungi with similar mechanisms of spore discharge.

In an analysis of spore discharge of Sordaria (Ingold and Dring, 1957; Ingold, 1958; Walkey and Harvey, 1967), it was

concluded that blue rays are the most effective in stimulating spore discharge, with yellow rays stimulating to a much lesser extent and hardly any discharge of spores at all with green or red.

In a study of the light reaction of Pilobolus, Allen and Jolivette (1914) found that sporangia were discharged very accurately toward white and blue light, much less accurately toward yellow light, and very inaccurately at red light.

Four years later, Parr (1918) carried out spectrum studies on Pilobolus with great care and precision. He found that Pilobolus responds heliotropically to the light of all the regions of the visible spectrum, from red to violet. The minimum response is in red and the maximum in blue with no intermediate maxima or minima existing.

## MATERIALS AND METHODS

In the fall of 1966 numerous collections of decaying wood with fungi of various sorts were brought into the greenhouse. They were usually cut into sections approximately 10 inches long and placed on peat moss in plastic trays (Fig. 1). The trays of wood were placed in a wooden frame chamber covered with clear plastic (Fig. 2). The trays were sprayed with water once or twice each day depending upon the rate of drying. In addition, to maintain high humidity a cool mist vaporizer was situated outside the chamber and provided with a large plastic tube through which moisture was blown into the chamber (Fig. 2). The vaporizer, which was connected to a timer, discharged water vapor into the chamber for 3 min at 15 min intervals.

Temperatures in the greenhouse were usually near 21 C at night with a high humidity, at or near the saturation point. However, on bright sunny days the temperatures often exceeded 32 C. These conditions were favorable for the development of a great variety of fungi used in spore discharge studies. They were also favorable for the development and maintenance of a rather large population of the black winged fungus gnat Bradysia and its fungal parasite, Entomophthora grylli Fres.,<sup>(1)</sup> which was brought into the greenhouse inadvertently along with the wood collections. We have been successful in maintaining both the gnat and the fungus for over 2 years in the mist chambers.

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(1) Identification of the fungus was verified by J. Hutchinson (Personal Correspondence, 1963).

Fig. 1. Section of decaying wood on peat moss in a plastic tray. Infected larvae of Bradysia may be seen as small white bodies on the surface of the wood.



Fig. 1

Fig. 2. Wooden frame mist chamber with vaporizer and plastic trays containing sections of wood in which the larvae of Bradysia and E. grylli were developing.



Fig. 2

The larvae of Bradysia that developed in the decaying wood (Fig. 1) became infected by feeding on or coming into contact with conidia in the substratum. Once initial infection was established, the disease apparently developed rapidly until the insect body was almost filled with hyphal bodies. Shortly before death, larvae became sluggish and moved to the surface of the wood where they expired. This usually occurred during the night.

The infected larvae were white in color and somewhat mealy in appearance due to the conidiophores of E. grylli that covered the outer surface of the larvae. Many of the larvae were able to escape infection and reproduce to maintain the population that provided a daily source of fresh material.

Two different sampling techniques were used in the following experiments. One was the Kramer-Collins (K-C) intermittent spore sampler (Kramer and Pady, 1966) while the other was a continuous type sampler (K-C A-type continuous spore sampler) described below.

The Kramer-Collins A-type spore sampler is constructed of plastic and consists of a rack on which a 1 x 3 inch glass microscope slide is pulled at a constant rate over a slit 3 x 20 mm in the base of the rack. A single infected larva was placed on peat moss in a petri dish. The sampler was then placed on the petri dish so that the larva was situated lengthwise in the slit of the sampler and approximately 2 mm from the slide. Conidia were discharged upward and impinged on the bottom of the silicone coated slide.

The slides were pulled over the slit at a rate of 6 mm per

hour by means of a plastic clip and thread attached to a spool on the hour hand shaft of a clock motor (Fig. 3). In practice the slides were read at 3 mm intervals, i.e. every  $\frac{1}{2}$  hr. The first reading was at 3 mm, the next at 6 mm, etc.

In the studies using the K-C intermittent sampler, infected larvae were collected from trays of wood in the mist chamber between 7:30 and 9:30 A.M. daily. Four or five larvae were placed on damp peat moss in a 150 ml beaker and covered with aluminum foil. The beaker was then placed in the environmental chamber to condition the larvae in complete darkness for 24 hr. This conditioning was done to prevent any stimulatory effect induced by exposure to the light before or during collection of the larvae. After this period the beaker was placed on the intermittent sampler with the inlet  $\frac{1}{4}$  inch above the larvae as shown in Fig. 4. The results obtained using the intermittent sampler represent the second day of sporulation, whereas results obtained with the continuous sampling technique represent the first day of sporulation.

The sampler inlet was modified by the addition of a terminal glass tube so as not to interfere with transmission of the filtered light being used. The sampler motor and pump were located outside the environmental chamber with connections to the sampler being made through wall ports (Fig. 4). The sampler was equipped with cams to operate for  $2\frac{1}{2}$  min periods at 15 min intervals for a total of 10 min sampling time each hour. The 4 samples taken each hour were superimposed on single hourly bands. Slides were changed daily (at 12 noon) at the beginning of the 12 hr light period. In this way spore deposits were collected in distinct hourly bands

Fig. 3. Kramer-Collins A-type continuous spore sampler,  
as set up to study spore discharge in E. grylli.

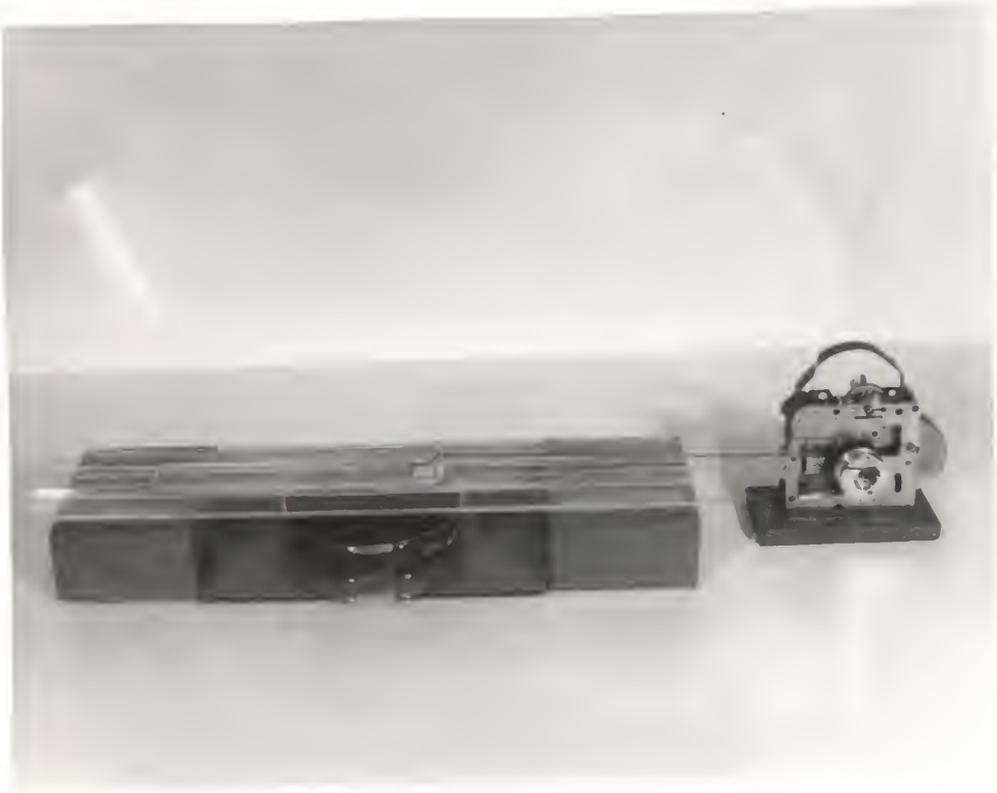


Fig. 3

Fig. 4. Kramer-Collins intermittent spore sampler setup (upper shelf) to study spore discharge in Entomophthora grylli in an Isco Environmental Chamber. The vacuum pump is shown on the stand at the side of the chamber.

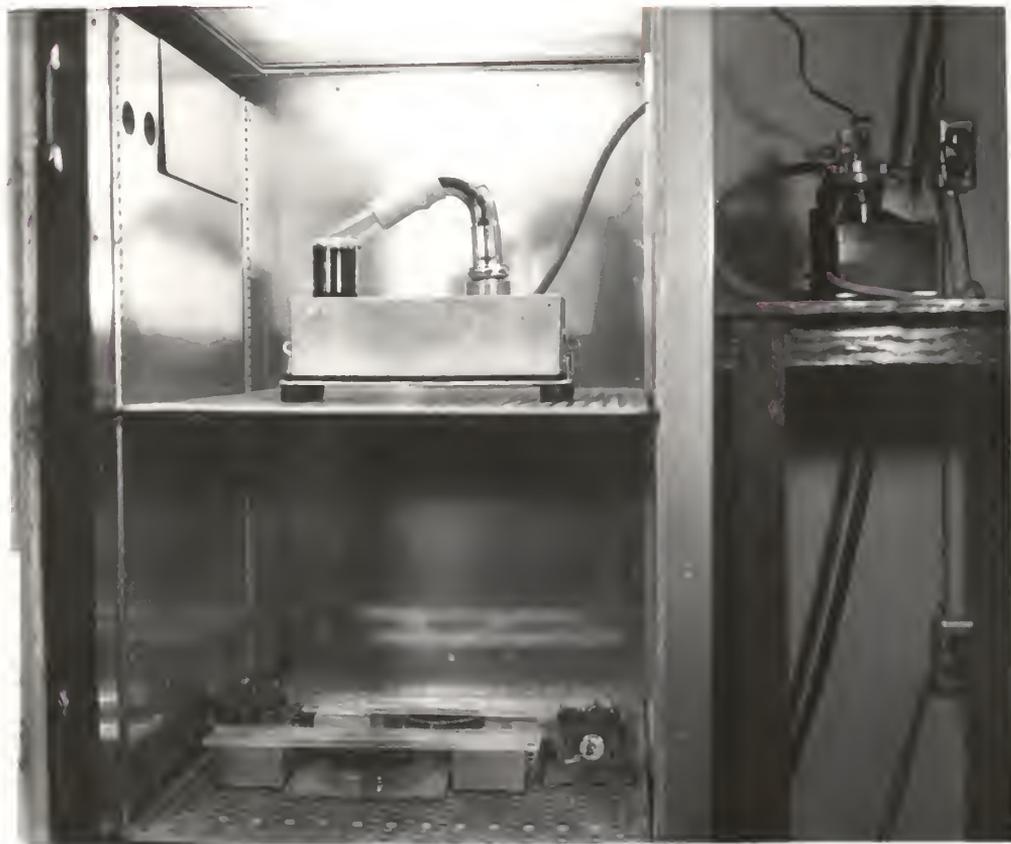


Fig. 4

over a 24 hr period.

In studies using the continuous type of sampler, infected larvae were collected from trays of wood from which all dead larvae were removed the previous afternoon and then covered with aluminum foil. Dead infected larvae collected the following morning were those that had crawled to the surface and expired while the trays were covered and thus were not exposed to light. The trays were uncovered in a dark room at noon the following day and the larvae collected using only a flashlight covered with the same filter being used in the experiment. Caution was taken to prevent exposure to light prior to continuous sampling.

The studies were conducted in an environmental chamber (Isco Model E-1; Instrument Specialties Co.; Lincoln, Neb.)(Fig. 5) in which the relative humidity, temperature, and photoperiod could be standardized and maintained at a constant level.

Except for studies using continuous illumination or continuous dark, a photoperiod of 12 hr (LD 12:12) was used beginning at 12 noon with a temperature of 70 F (21 C) and 90% relative humidity. Studies were conducted in a series with each wavelength (color) used for approximately a 4-6 day period with fresh infected larvae sampled and changed every 24 hr.

Cinemoid color filters were used to obtain the various spectrum wavelengths used in these studies. The basic wavelengths used were 400 mu (violet), 450 mu (violet/blue), 500 mu (green), 600 mu (orange), 650 mu (orange/red), 700 mu (red), (Table 1).

Fig. 5. Isco Environmental Chamber.

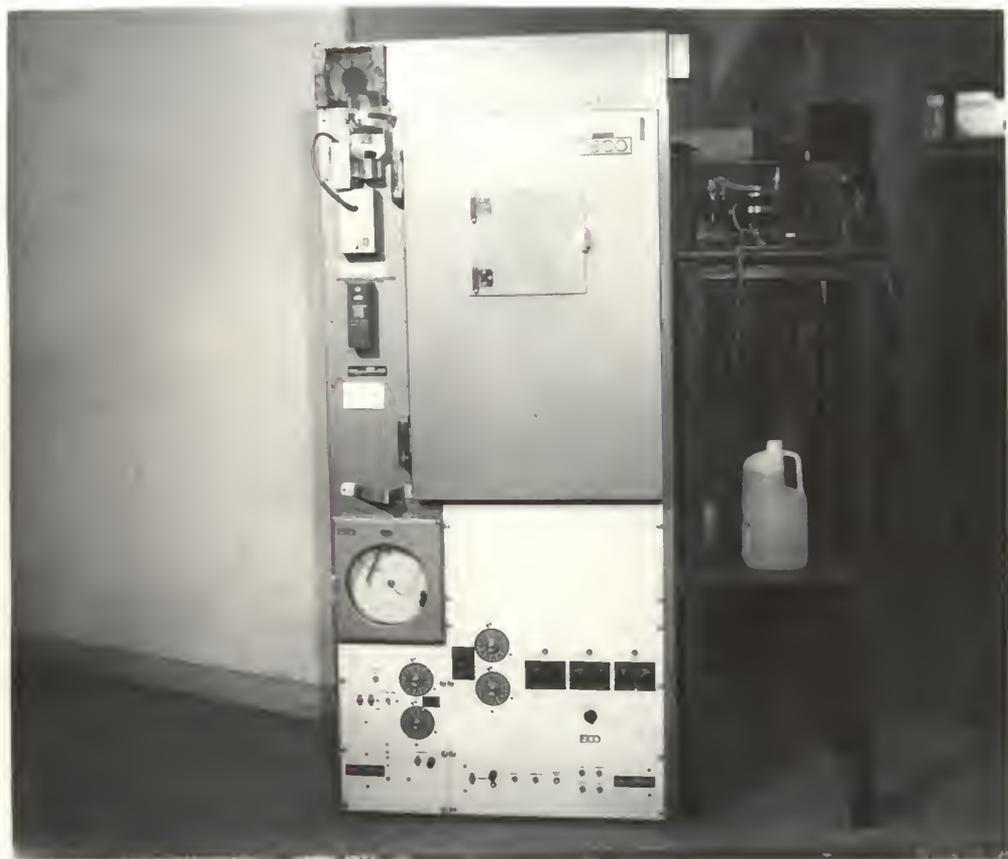


Fig. 5

TABLE 1. Cinemoid Filters

Filter Number	Range of Light Transmission in $\mu$	Maximum Transmission in $\mu$	Light Intensity in $\text{ergs/cm}^2/\text{sec}$
25 & 32	400-450; 650-700	400	2000
20	400-525	450	2000
24	450-580	500	2500
5	500-700	600	6000
6	560-700	650	2500
25 & 5	650-700	700	2000

Standard sheet size of the filters was 20 x 24 inches. The filters were taped in place on the window at the top of the Isco chamber, which is located directly below the lamps. All ports and possible entries through which other light might enter the chamber were closed by taping with black cloth tape. Slides and fresh infected larvae were changed at the same time after the light period came on at 12 noon, thus eliminating the need of another light source by which to work and keeping the opening of the chamber door at a minimum.

## RESULTS

Under white light (all the wavelengths of the spectrum) using a continuous sampler, Entomophthora began to discharge its spores upon light stimulation (Fig. 6) and reached its maximum peak of sporulation within 1-3 hr with a gradual decline in the spore discharge pattern the remainder of the sampling period. Pady et al. (1969) used an intermittent sampler and under white light obtained a similar pattern.

Although two different types of samplers were used, the vacuum operated K-C intermittent sampler and the K-C A-type continuous sampler, similar patterns of spore discharge occurred. It was felt that the vacuum operated intermittent sampler might alter the micro-environment sufficiently to affect the pattern of spore discharge. The A-type continuous sampler which is designed to collect spores as they are self impinged directly from the conidiophores was used as a check against this possibility.

Using cinemoid filters no. 25 and no. 32 with a transmission of 400 mu (violet) and a continuous sampler, sporulation began immediately upon light stimulation (Fig. 7). The maximum peak in sporulation was reached in approximately 2 hr followed by a rapid decline the next hour and a gradual decline the remainder of the sampling period. Sampling with an intermittent sampler under the same conditions, a corresponding spore discharge pattern to that recorded by the continuous sampler was observed following the initial stimulation. However, with the intermittent sampler there was a slightly faster decline in the spore discharge pattern

Fig. 6. Spore discharge of Entomophthora grylli under white light. Arrow indicates the beginning of the sampling period in light.

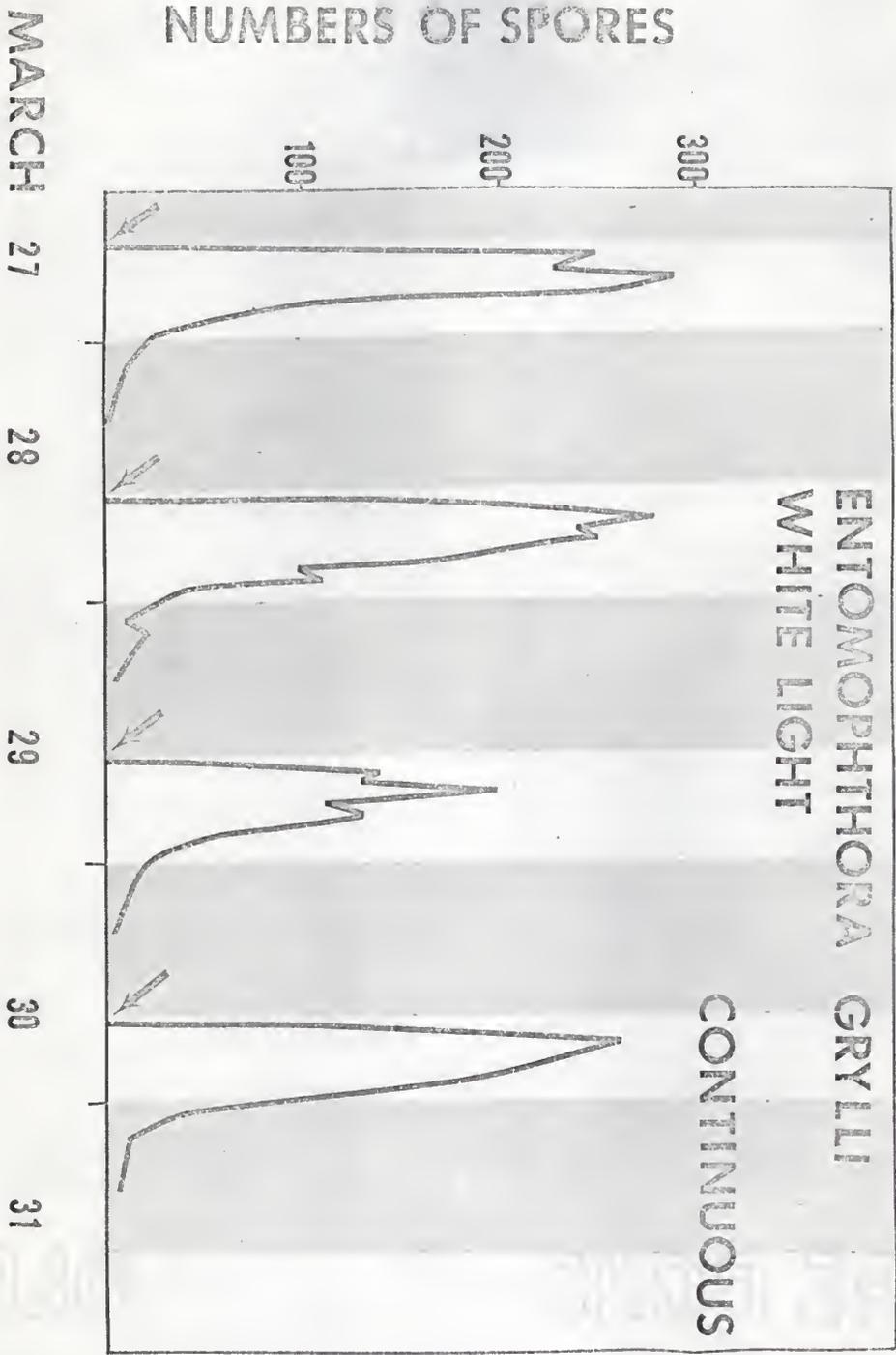


Fig. 6

Fig. 7. Spore discharge of Entomophthora grylli  
under 400 mu (violet light). Arrow  
indicates the beginning of the sampling  
period in light.

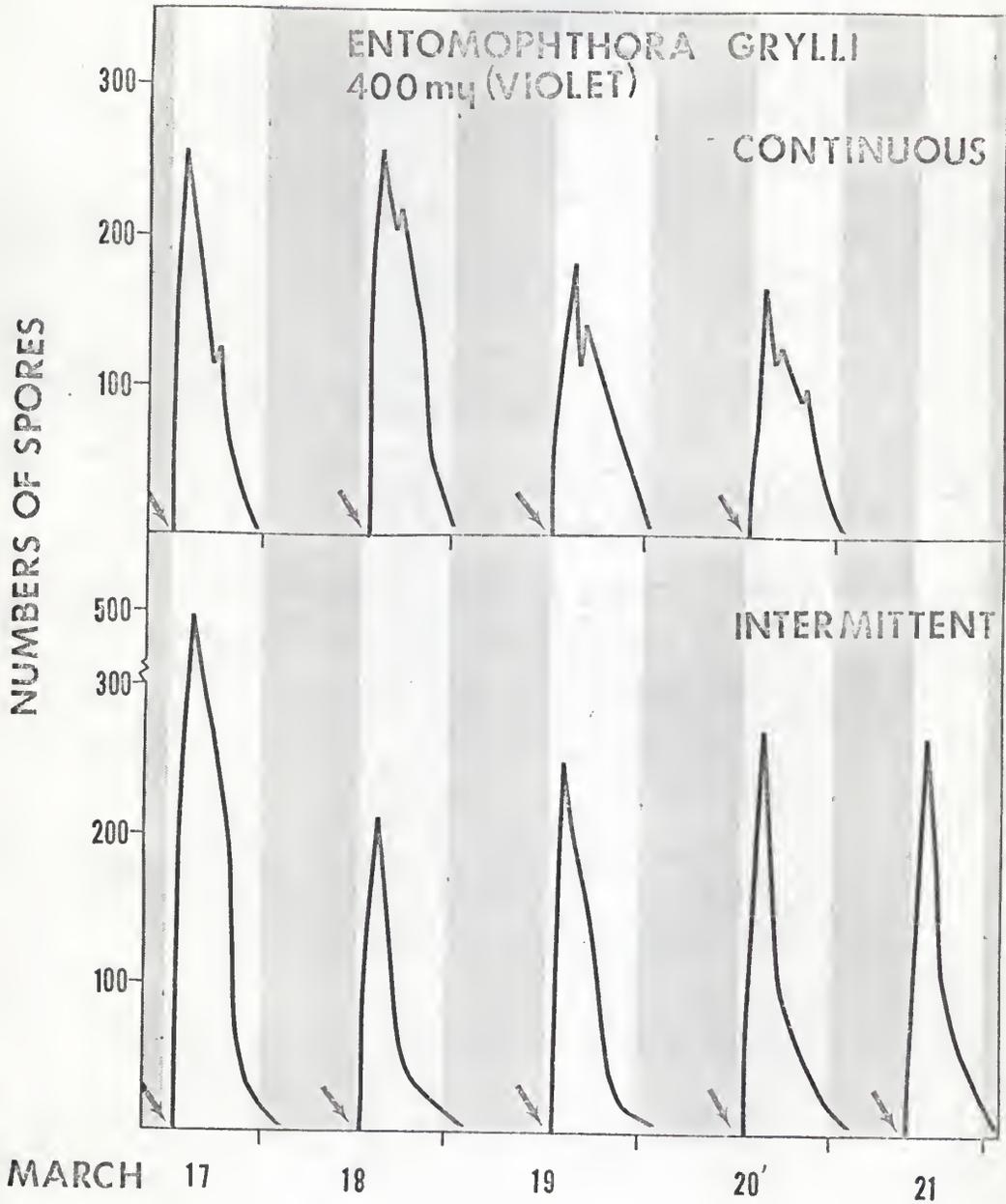


Fig. 7

after the maximum peak was obtained (Fig. 7).

Entomophthora, sampled with a continuous sampler under 700 mu (red) using cinemoid filters no. 25 and no. 5, produced a spore pattern with a relatively high initial response with the spore discharge near the maximum for 2-4 hr followed by a gradual decline in sporulation the remainder of the sampling period (Fig. 8). Intermittent sampling of Entomophthora under 700 mu consistently reached a maximum peak of sporulation in 3 hr, followed by a rapid drop in spore discharge within an hour after the maximum peak was obtained (Fig. 8). This rapid decline in spore discharge was succeeded by a more gradual decline in sporulation, starting 5-6 hr after the initial stimulation, until the end of the experiment. Eleven to twelve hours after initial stimulation, the spore discharge pattern reached its minimum. This could possibly mean that Entomophthora may not be stimulated for as long a duration under 700 mu as normally found under very short wavelengths of light.

The spore discharge pattern obtained with each sampler under 450 mu (violet/blue) light wavelengths was found to reach a maximum peak in 1-3 hr followed by a slow decline the remainder of the sampling period (Fig. 9). Similar spore patterns were obtained using 500 mu light wavelengths with the maximum peak reached in 1-4 hr, again followed by a gradual decline in the spore discharge pattern (Fig. 10). With the 600 mu and 650 mu light wavelength filters, both samplers obtained spore discharge patterns that reached a maximum in 1-3 hr succeeded by a gradual decline in sporulation the remainder of the sampling period (Fig. 11, 12).

Fig. 8. Spore discharge of Entomophthora grylli under 700 mu (red light). Arrow indicates the beginning of the sampling period in light.

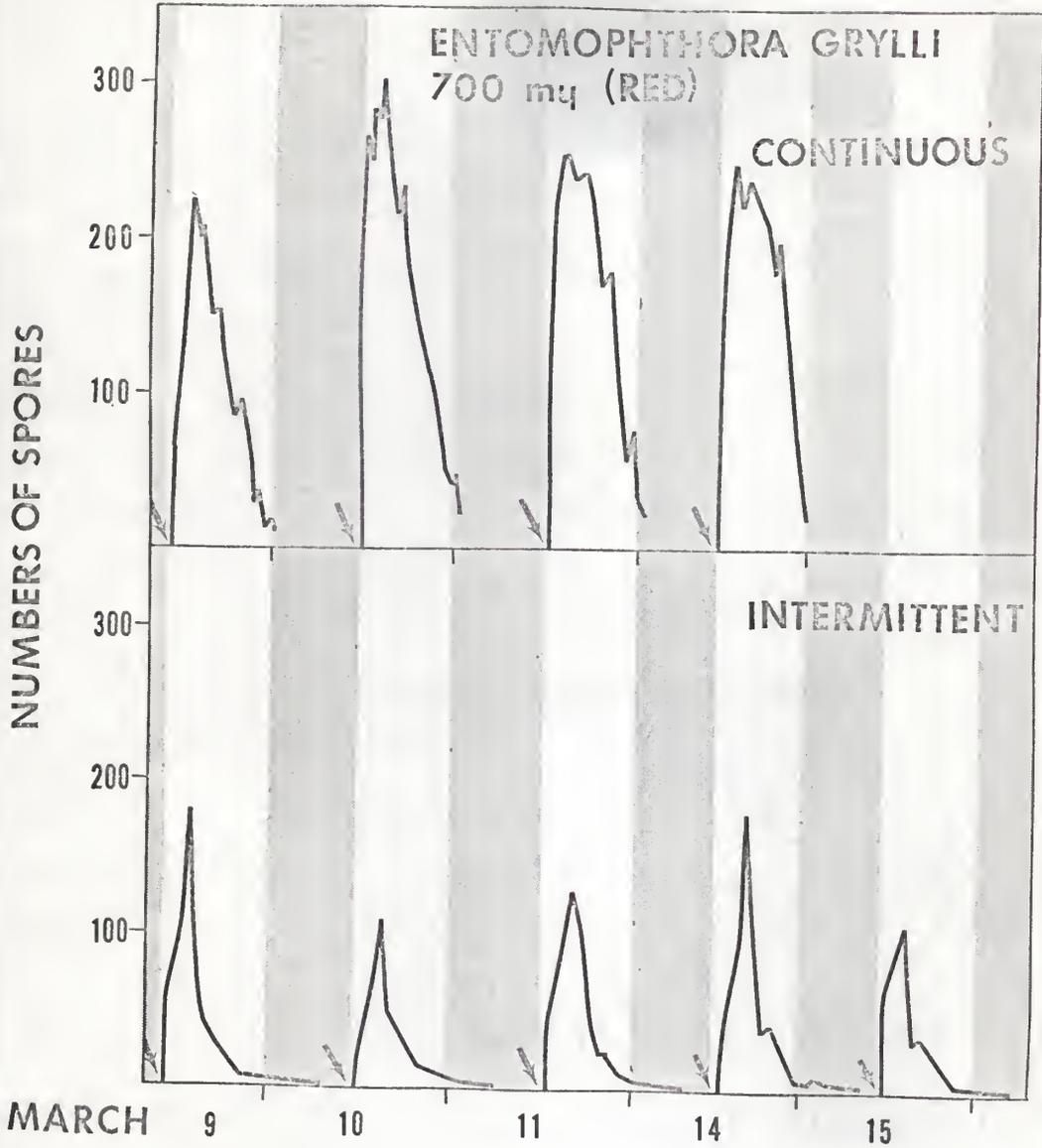


Fig. 8

Fig. 9. Spore discharge of Entomophthora grylli  
under 450 mu (blue light). Arrow indicates  
the beginning of the sampling period in  
light.

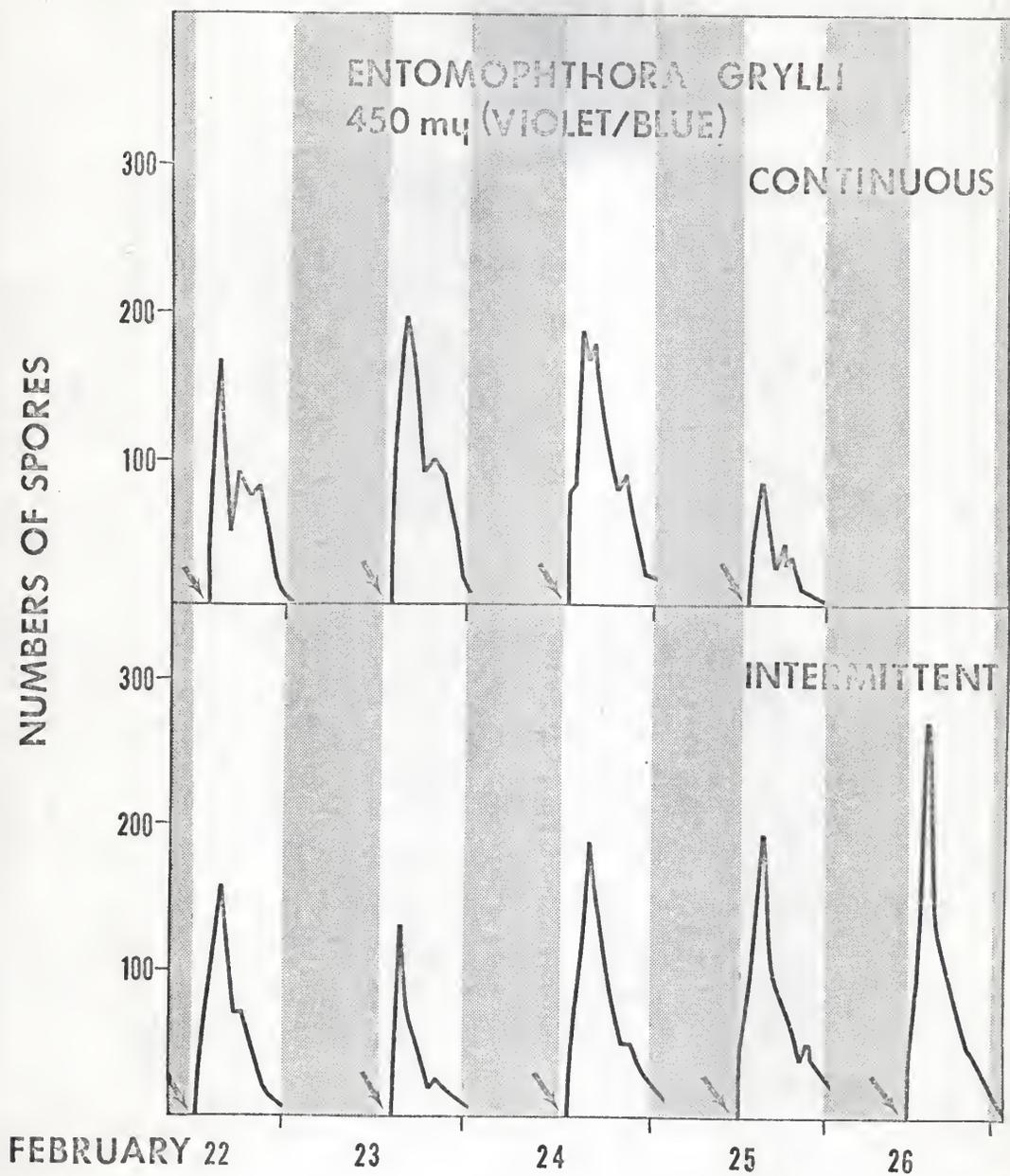


Fig. 9

Fig. 10. Spore discharge of Entomophthora grylli under 500 mu (green light). Arrow indicates the beginning of the sampling period in light.

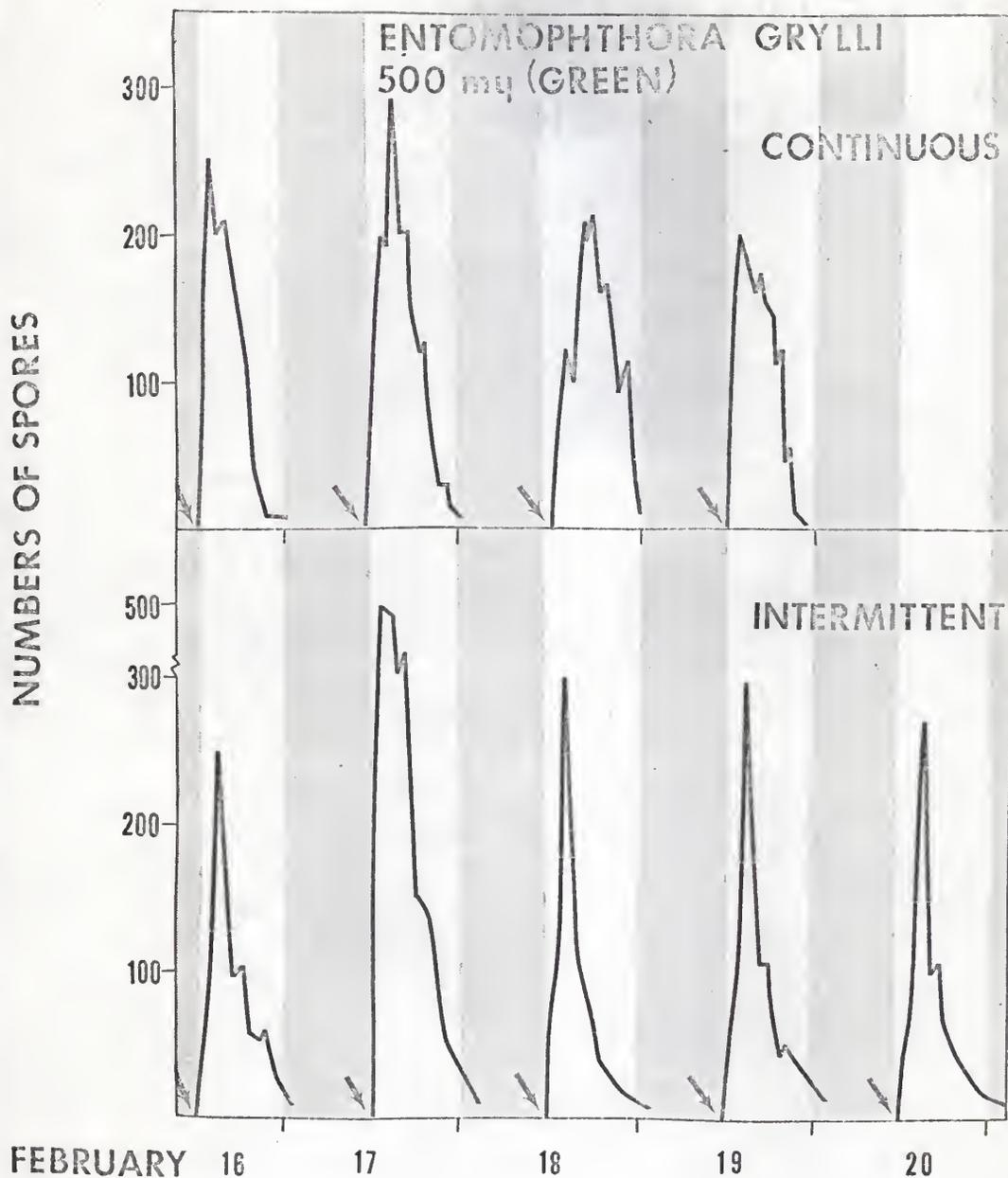


Fig. 10

Fig. 11. Spore discharge of Entomophthora grylli under 600 mu (orange light). Arrow indicates the beginning of the sampling period in light.

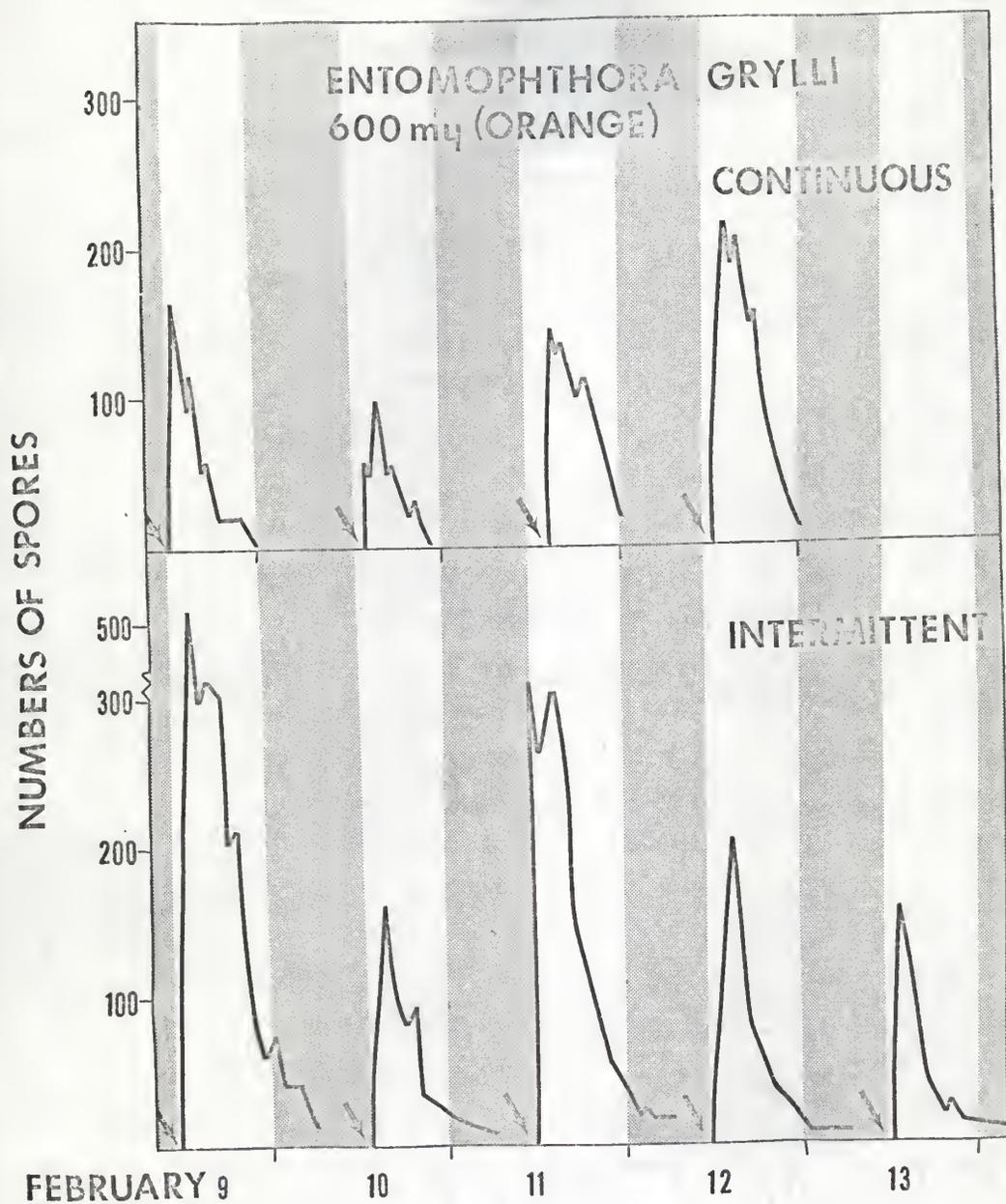


Fig. 11



Fig. 12. Spore discharge of Entomophthora grylli under 650 mμ (orange/red light). Arrow indicates the beginning of the sampling period in light.

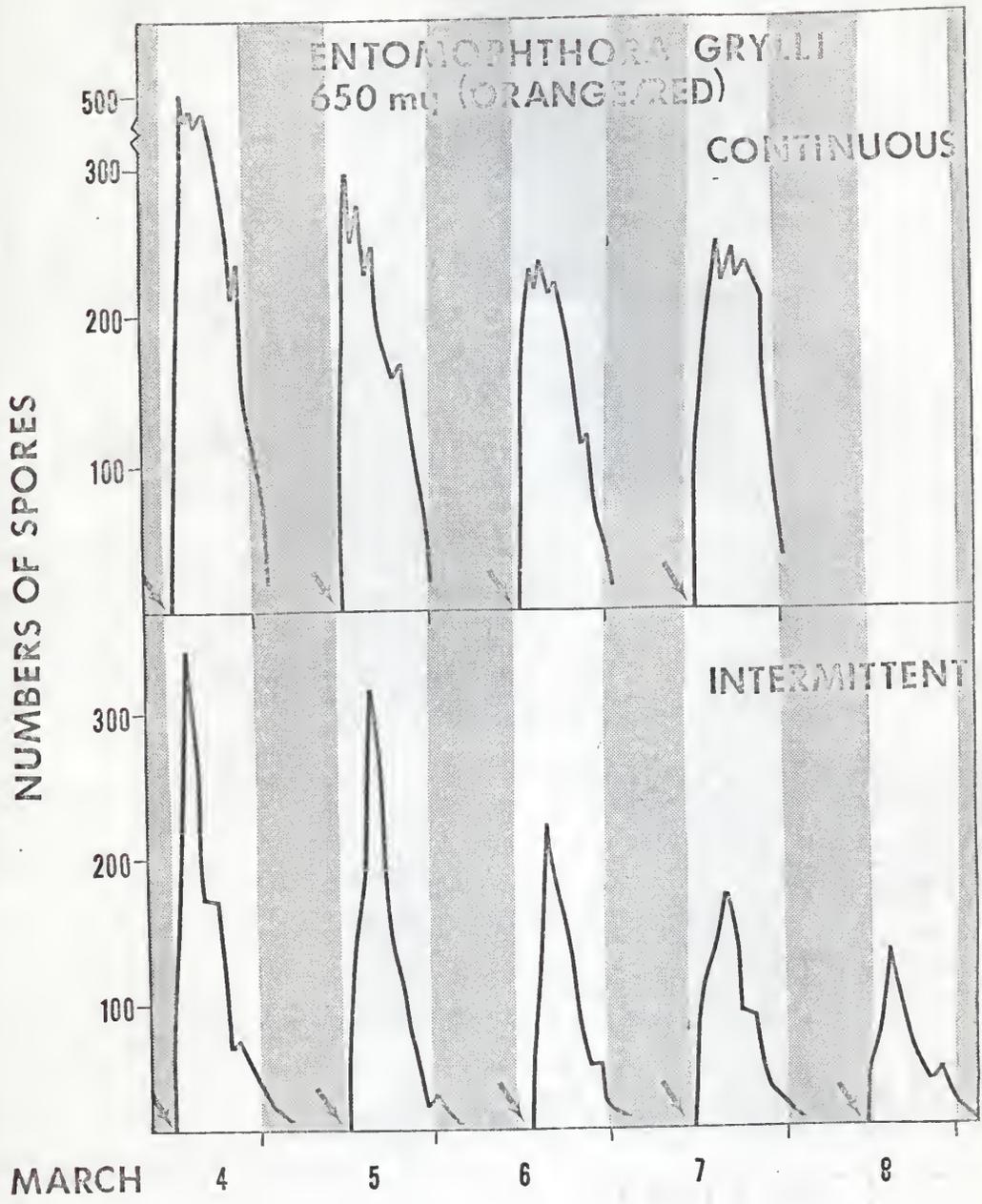


Fig. 12

Studies using these various intermediate wavelengths (450-650 mu) demonstrated a similar spore pattern to those observed under 700 mu and 400 mu. In both sampling techniques, stimulation of spore discharge was immediate with peaks in sporulation being reached in 1-4 hr, with a rapid drop in spore discharge following the maximum peak and a gradual decline in discharge the remainder of the sampling period.

The sensitive response of Entomophthora to various wavelengths indicated that an exposure of short duration might be adequate to stimulate spore discharge. Entomophthora sampled with a continuous sampler under wavelengths of 700 mu and 400 mu have the same discharge pattern following 1 min of light stimulus (Fig. 13). Four hours after sampling began in the dark, the fungus was exposed to 1 min of light and the spore discharge pattern, which was on gradual decline, temporarily levelled off for 1-2 hr. Although the 1 min exposure was insufficient to cause an increase in spore discharge, a stimulatory effect was evident. Using the same technique and exposing the Entomophthora to 400 mu (violet) for 6½ min, an immediate rise in the spore discharge pattern occurred (Fig. 13). This indicates that the physiological response necessary to affect spore discharge is somewhat accumulative in Entomophthora. It took more than 1 min but less than 6½ min of exposure to affect the maximum discharge of spores, indicating there is an intermediate exposure time necessary for maximum spore discharge. Approximately 5 hr after the initial 6½ min stimulation the fungus was exposed to continuous light for the remainder of the sampling period, and a second peak of approximately the same magnitude was produced. (Fig. 13).

Fig. 13. Spore discharge pattern of Entomobrythora grylli following 1 min and 6½ min of light stimulus.

NUMBERS OF SPORES

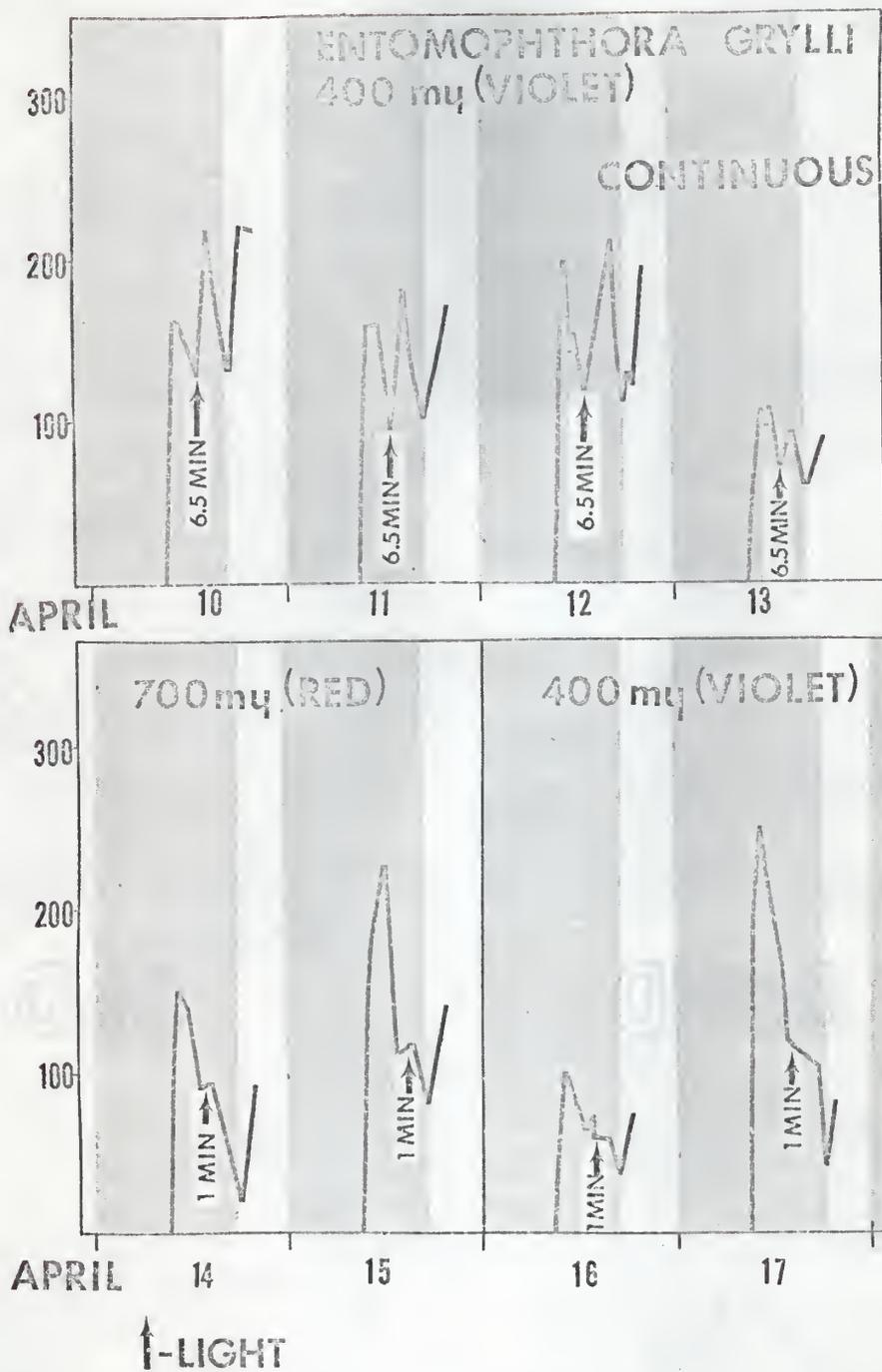


Fig. 13

## DISCUSSION

Exposure to all colors of the visible spectrum has a pronounced effect on the discharge of conidia in Entomophthora grylli. The maximum peak of spore discharge occurred 2-3 hr after exposure to white light. Pady et al. (1969), studying the diurnal periodicity of spore discharge of this same species, obtained similar results after exposure to white light. However, when light sources of different wavelengths were used the responses varied slightly, indicating that the quality of light had some effect on the discharge of spores.

In an analysis of spore discharge of Sordaria, Ingold and Dring (1957), Ingold (1958), and Walkey and Harvey (1967), concluded that blue rays were most effective in stimulating spore discharge with green and yellow rays stimulating to a much lesser extent and hardly any discharge of spores when exposed to red light. The more rapid rise of sporulation to the maximum peak indicates that blue light stimulated spore discharge of Entomophthora more effectively than did other wavelengths.

The rate of spore discharge in Entomophthora following stimulation by the various intermediate wavelengths is very similar. However, under 700 mu (red) the rate of spore discharge is slower and the spore discharge pattern reaches a minimum earlier than when stimulated by 400 mu (violet). It took 2 hr before the maximum peak of spore discharge was reached under 400 mu compared with 3 hr to reach a maximum under 700 mu. This indicates that stimulation is slower and lasts for a shorter duration under high wave-

lengths. There seemed to be no effect on the number of spores developed, as peaks of similar magnitude were reached with all of the various wavelengths.

In Entomophthora the quantity of light seems to be of some significance and could be of more importance than the quality of light used. In studies of Sordaria fimicola Ingold and Marshall (1963) found the same time interval between initial stimulation and maximum response, provided the amount of light supplied was sufficient. In Entomophthora the presentation time does not vary with the wavelengths but a minimum amount of presentation time is found to be necessary for maximum stimulation of spore discharge to take place. An exposure of 1 min to light temporarily halts a decline in sporulation in Entomophthora and an exposure of 6½ min is enough to obtain maximum sporulation.

Walkey and Harvey (1967) did similar work on Sordaria where they investigated the effect of brief light exposure on subsequent spore discharge. They found that a time exposure as short as 1 min in duration produces a high spore discharge response but the response is delayed for 1-2 hr. Ingold and Marshall (1963), working with Sordaria, studied the effect of brief exposure of a high light intensity on subsequent discharge in darkness. They concluded that a time exposure of 50-200 sec was necessary for maximum discharge. In the studies of Entomophthora it was found that there is no delayed stimulatory effect to light but discharge of spores occurs immediately upon being exposed to light. Whatever the mechanism for the perception of light, it is very efficient.

Ingold (1958) pointed out in his studies with Sordaria that

the visible pigment or pigment complex was concerned with photo-reception in connection with the stimulation of spore discharge by light. However, in Entomophthora the conidia and conidiophores are hyaline and rarely colored. If pigment and pigment complexes are concerned with the responses to various wavelengths in Entomophthora it is those pigment complexes that are not visible to the naked eye. If a completely albino mutant could be produced, the significance of pigment in light-stimulated spore discharge could be put conclusively to the test (Ingold, 1956).

## SUMMARY

Studies on the effects of various light wavelengths on the diurnal rhythm of spore discharge in Entomophthora grylli Fres. have been undertaken. The fungus regularly infected the larvae of Bradysia, black winged fungus gnat, which inhabited trays of wood being maintained in a mist chamber in a greenhouse. The host and the fungus have been maintained and have furnished fresh material daily for over 2 years. All studies were done in an E-1 Isco Environmental Chamber using 2 different sampling techniques.

From this study it was found that Entomophthora is stimulated to discharge its spores in a distinctive spore pattern in response to the light of all regions of the visible spectrum. Stimulation is immediate with no delayed response. The maximum peak of spore discharge is reached in approximately 1-3 hr under the various light wavelengths. Similar results were obtained with both the vacuum operated Kramer-Collins (K-C) intermittent spore sampler and the K-C A-type continuous spore sampler.

Although no major variation occurred in the spore discharge pattern under the different wavelengths, the maximum peak in spore discharge is reached approximately 1 hr slower under 700 mu (red) than under 400 mu (violet). Also, the decline following the maximum peak is slightly more rapid with the minimum in the spore discharge pattern reached 1-2 hr earlier under 700 mu than under 400 mu.

The presentation time required to produce maximum stimulation does not vary with the different wavelengths of the visible spec-

trum, but in all regions of the spectrum a minimum presentation time of the light stimulus is needed for subsequent maximum sporulation.

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Studies on the effects of various light wavelengths on the diurnal rhythm of spore discharge in Entomophthora grylli Fres. have been undertaken. The fungus regularly infected the larvae of Bradysia, black winged fungus gnat, which inhabited trays of wood being maintained in a mist chamber in a greenhouse. All studies were conducted in an E-1 Isco Environmental Chamber in which all environmental conditions were standardized.

It was found that Entomophthora is stimulated to discharge its spores in response to the light of all regions of the visible spectrum. The maximum peak in sporulation is reached in approximately 1-3 hr under all the various light wavelengths. Stimulation is immediate with no delayed response. Similar results were obtained with both the vacuum operated Kramer-Collins (K-C) intermittent sampler and the K-C A-type continuous sampler.

No major variation occurred in the spore discharge pattern under the different wavelengths, although the maximum peak in spore discharge is reached approximately 1 hr slower and the minimum 1-2 hr earlier under 700 mu than under 400 mu.

The presentation time required to produce maximum stimulation does not vary with the different wavelengths of the visible spectrum, but in all regions of the spectrum a minimum presentation time of the light stimulus is needed for subsequent maximum sporulation.