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# Influence of phototropic response of spore germ tubes on infection process in *Colletotrichum lagenarium* and *Bipolaris oryzae*

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**The germ tubes of *Colletotrichum lagenarium* showed negative phototropism to UV-blue (300-520 nm) and far-red (>700 nm) regions with maximum in the near ultraviolet (NUV) region, while monochromatic radiations of 575-700 nm (yellow-red region) induced positive phototropism with maximum in the red region. Green light (520-575 nm) was ineffective. Negative phototropism-inducing wavelength regions inhibited germ tube growth and positive phototropism-inducing wavelength regions promoted it significantly. *Bipolaris oryzae* did not show any phototropic response and light did not affect the germ tube growth. These results indicate that the lens effect, in combination with the light growth reaction and light growth inhibition, is the mechanism of the phototropism of germ tubes of *C. lagenarium*. NUV radiation, which induced negative phototropism of *C. lagenarium*, promoted appressorium formation, while red light, which induced positive phototropism, suppressed it significantly. In the case of *B. oryzae*, light did not affect the infection structure formation. These results indicate that negative phototropism of germ tubes of *C. lagenarium* favors the infection process by facilitating the contact of the tips of germ tubes with the host surface, while positive phototropism has the opposite effect.**

Key Words——*Bipolaris oryzae*; *Colletotrichum lagenarium*; germ tube growth; infection structure; phototropism.

Light is one of the most important environmental factors that may play a role in plant disease development (Colhoun, 1973). It affects fungal organisms in different ways that can be both stimulatory or inhibitory on many processes of their growth, development, reproduction and other behavior (Carlile, 1965; Emmett and Parbery, 1975; Tan, 1978; Manachère, 1985; Koch and Hoppe, 1987; Honda and Miyawaki, 1989; Honda et al., 1992). Phototropic reactions (positive or negative) are particularly significant in relation to spore dispersal, spore germination and plant infection (Koch and Hoppe, 1987; Honda et al., 1992).

Several authors have reported that close contact or adhesion of germ tubes to host surfaces is essential for infection structure initiation (Dey, 1933; Staples and Macko, 1980; Nicholson, 1984). Negative phototropism may improve the contact of the tips of the germ tubes with host surfaces, resulting in the promotion of infection structure formation and supposedly favoring penetration of the germ tubes into the host tissue, thus increasing the frequency of infection (Yarwood, 1932; Banbury, 1959; Koch and Hoppe, 1987). So far, attempts to prove the possibility that negative phototropism favors the penetration of the germ tubes into the host tissue have been inconclusive. Honda et al. (1992) have confirmed the ecological significance of negative phototropism of spore germ tubes of *Septoria obesa* Sydow in the plant infection process in both laboratory and greenhouse experiments.

The involvement of negative phototropism of spore germ tubes in the host infection process is significant, though information on phototropism of plant pathogenic fungi is inadequate and almost all research has concentrated on *Phycomyces* and indirect host-penetrating, i.e., stomatal penetrating fungi (Fromme, 1915; Banbury, 1959; Welty and Christensen, 1965; Koga et al., 1984; Koch and Hoppe, 1987; Honda and Miyawaki, 1989; Honda et al., 1992). This prompted us to investigate the phototropic response of germ tubes of direct host-penetrating fungi and to confirm the ecological significance of negative phototropism of spore germ tubes in the host infection process.

## Materials and Methods

**Culturing of fungi** *Colletotrichum lagenarium* (Pass.) Ell. et Halst. was cultured on YpSs medium (1.5% starch, 0.4% yeast extract, 0.1% $K_2HPO_4$, 0.05% $MgSO_4 \cdot 7H_2O$, 2% agar) at 26℃ in an incubator furnished with two 10 W daylight-type fluorescent lamps (FL10 D, Toshiba, Tokyo) suspended 30 cm above the culture plates with the light fluence rate of 435 $\mu W/cm^2$ at the plate surface. Abundant salmon-colored spores were formed within 7-8 d of incubation.

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*Bipolaris oryzae* (Breda de Haan) Shoemaker was cultured on V-8 juice agar medium (20% V-8 juice, 0.2% $CaCO_3$, 1.7% agar) at 25℃. After 5-6 d of incubation the aerial hyphae were removed by washing with a soft brush and sterilized water. The culture surfaces were then allowed to dry for 30 min, then incubation was resumed at the same temperature under continuous near ultraviolet (NUV) radiation (FL15 BLB, National, Japan) with the light fluence rate of 360 $\mu W/cm^2$ for 7 h followed by incubation in a dark box for 24 h to promote spore formation.

**Preparation of spore suspension** Spores were harvested by adding sterilized water to each plate and gently scraping loose the spore masses. After centrifugation (2,000 rpm for 10 min) the collected spores were resuspended in sterilized and deionized water and their concentration was adjusted to $1.5\text{-}2 \times 10^5$ conidia/ml using a hemacytometer.

**Phototropic response of germ tubes** Spore suspensions (0.2 ml) were introduced onto water-agar plates (agar 16 g, water 1,000 ml; 10 ml/6 cm diam Pyrex Petri dish) by use of a micropipette. The inoculated suspensions were dispersed over the whole surface by jerking the plates gently, then dried up by exposure for 10-15 min to air flow on a clean bench. Inoculated plates were incubated at 25℃ under different wavelengths of light from fluorescent lamps (FL 20SSD/18, Mitsubishi, 550 $\mu W/cm^2$; FL 20S·BLB, Toshiba, 450 $\mu W/cm^2$; FL 20S·B-F, National, 261 $\mu W/cm^2$; FL 20S·G-F, National, 204 $\mu W/cm^2$; FL 20S·Y-F, National, 360 $\mu W/cm^2$; FL 20S·R-F, National, 287 $\mu W/cm^2$; FL 20S·FR-74, Toshiba, 328 $\mu W/cm^2$) suspended 20 cm above the plates. The fluence rates of the radiations were measured using a thermopile with a quartz window (MIR-100Q; Mitsubishi Yuka, Yokkaichi, Japan) coupled with a digital multimeter (TR6846; Advantest, Tokyo). Control plates in light-tight boxes were placed near the test plates under the same conditions. After a fixed period of irradiation (10 h for *C. lagenarium* and 2 h for *B. oryzae*) inoculated plates were observed under a light microscope to determine the phototropic response of germ tubes. The germ tubes with tips growing away from the light source into the agar surface were considered to be negatively phototropic, and those growing upward from the agar surface toward the light source positively phototropic. The germ tubes showing no phototropic response were considered to be neutral. Percentages of conidium germination and phototropic response of germ tubes were determined by examining 200 spores and 200 germ tubes, respectively, in 3-4 randomly selected areas of each plate for each replication. For germ tube growth, 60 germ tubes were measured randomly per replication. Each experiment was repeated three times and data obtained were averaged and analyzed statistically.

**Observation of infection structure formation under different wavelengths of light from fluorescent lamps by onion epidermal strip method** The third and fourth scales of an onion bulb were used in this experiment. The epidermis stripped from the inner side of a scale was cut into small sections (1.5 cm × 1.5 cm) and washed thoroughly 4-5 times with sterilized water. The washed strips were then put surface-up on sterilized glass slides in Pyrex Petri dishes lined with sterilized moist blotting paper. Drops (50 $\mu l$) of conidial suspension were dropped on the epidermal strips with a micropipette and incubated under light of different wavelengths at 25℃. Infection structures were observed under a light microscope after 15 h and 6 h of incubation for *C. lagenarium* and *B. oryzae*, respectively. Germ tubes with and without infection hyphae were counted as infection hyphae and germ tubes, respectively. For each replication, 180-200 germ tubes were evaluated, and each experiment was repeated thrice. Data obtained were averaged. To facilitate observation, fungal structures were stained with a solution consisting of 0.2% trypan blue, 20% v/v melted phenol, 20% v/v lactic acid, 40% v/v glycerol and 20% water (Xiao et al., 1994).

## Results

**Effect of light on conidium germination** Figure 1 shows the effect of light quality on conidium germination of *C. lagenarium*. Monochromatic radiation of both NUV and far-red wavelengths showed significant inhibitory effect on conidium germination. Blue light, green light, yellow light and red light did not affect the germination consistently. White light was slightly inhibitory compared with

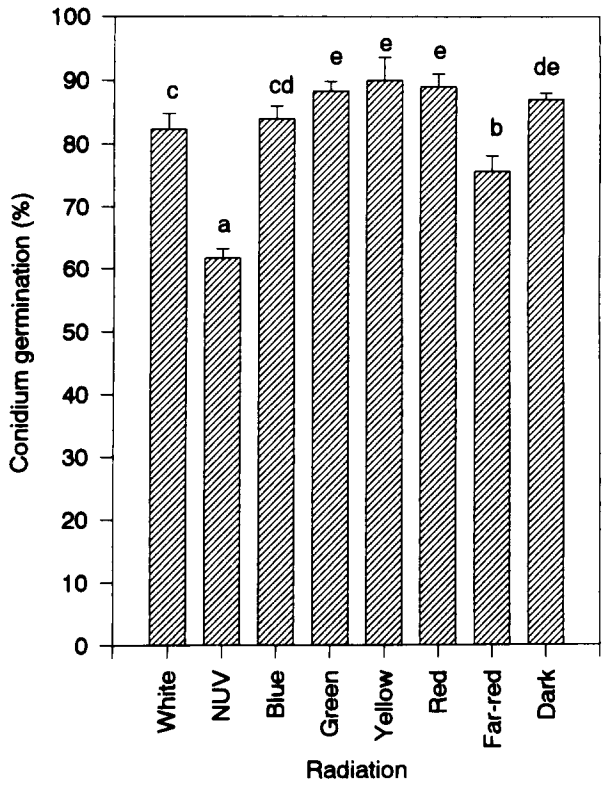


Fig. 1. Effect of radiation of different wavelengths on conidium germination of *Colletotrichum lagenarium*.
Bars in the columns show the standard errors. Values followed by the same letter are not significantly different at $P<0.05$.

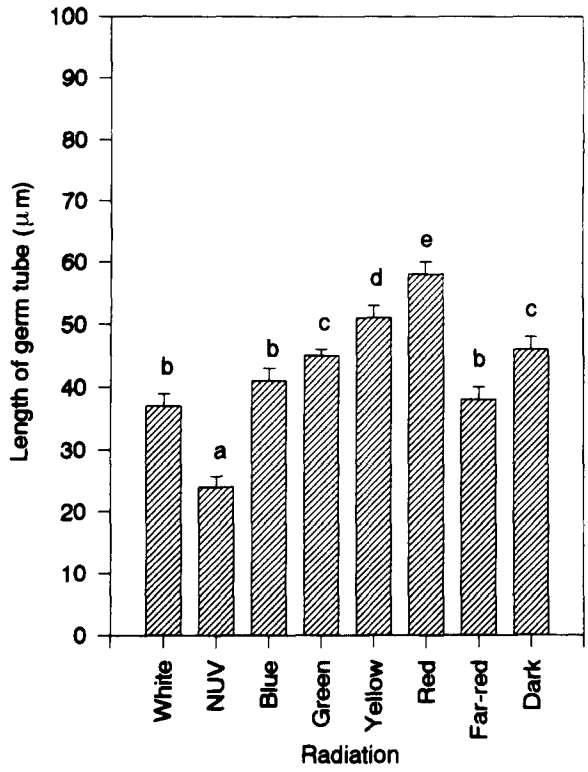


Fig. 2. Effect of radiation of different wavelengths on germ tube growth of *Colletotrichum lagenarium*.
Germ tubes were measured after 10 h of irradiation. Bars in the columns show the standard errors. Values followed by the same letter are not significantly different at $P<0.05$.

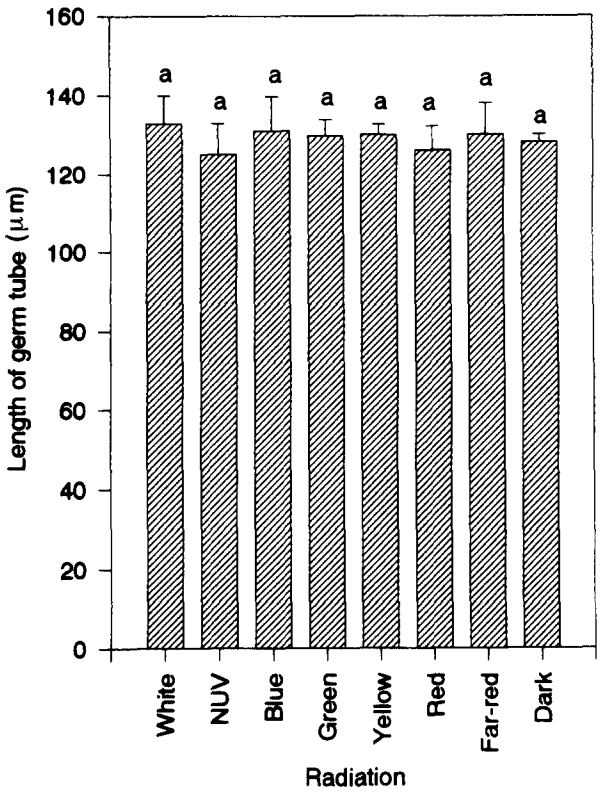


Fig. 3. Effect of radiation of different wavelengths on germ tube growth of *Bipolaris oryzae*.
Germ tubes were measured after 2 h of irradiation. Bars in the columns show the standard errors. Values followed by the same letter are not significantly different at $P<0.05$.

the dark control.

**Effect of light on germ tube growth** Figure 2 shows the average length of germ tubes of *C. lagenarium* for each light treatment. NUV, white, blue and far-red radiation inhibited germ tube growth significantly with the maximum inhibition in the NUV range. Statistically, there was no significant difference between white, blue and far-red radiation. In contrast, red light and yellow light promoted the germ tube growth significantly. Green light neither promoted nor inhibited germ tube growth. This result indicates that the UV-blue (300-520 nm) and far-red (>700 nm) regions are inhibitory to fungal growth, and the yellow-red region (575-700 nm) favors fungal growth. The green region (520-575 nm) is neutral. In the case of *B. oryzae*, light of different wavelengths did not affect the germ tube growth significantly (Fig. 3).

**Phototropic response of germ tubes** Figure 4 shows the phototropic response of germ tubes of *C. lagenarium*. NUV, white, blue, and far-red radiation induced a negative phototropic response, with the maximum effect in the NUV region, where 64% of germ tubes showed a negative phototropic response. On the other hand, red light and yellow light induced a significant positive phototropic response, with the maximum in the red region, where 67% of germ tubes were positively phototropic. This result showed that UV-blue (300-520 nm) and far-red (>700 nm) regions induced a negative phototropic response, and yellow and red (575-700 nm) regions induced a positive response of conidium germ tubes of *C. lagenarium*. The green (520-575 nm) region was neutral.

Under NUV radiation, 64% of germ tubes were negatively phototropic and 33% positively phototropic, but under red light 32% of germ tubes were negatively and 67% positively phototropic. Under simultaneous NUV and red irradiation, the germ tubes showed both positive (46%) and negative (43%) phototropic responses to almost the same level, and statistically there was no significant difference from the dark control. Similarly, under simultaneous red and far-red irradiation, the difference between negative and positive phototropic responses of germ tubes decreased significantly compared with those under red or far-red radiation alone. The results indicate the possibility of an antagonistic relationship between NUV and red radiation, and between red and far-red radiation, on the phototropic response of germ tubes of *C. lagenarium*.

In the case of *B. oryzae*, germ tubes showed the same phototropic response as the dark control to the radiation of different wavelengths, and no statistically significant differences were found between treatments (Fig. 5).

**Effect of light on infection structure formation** NUV

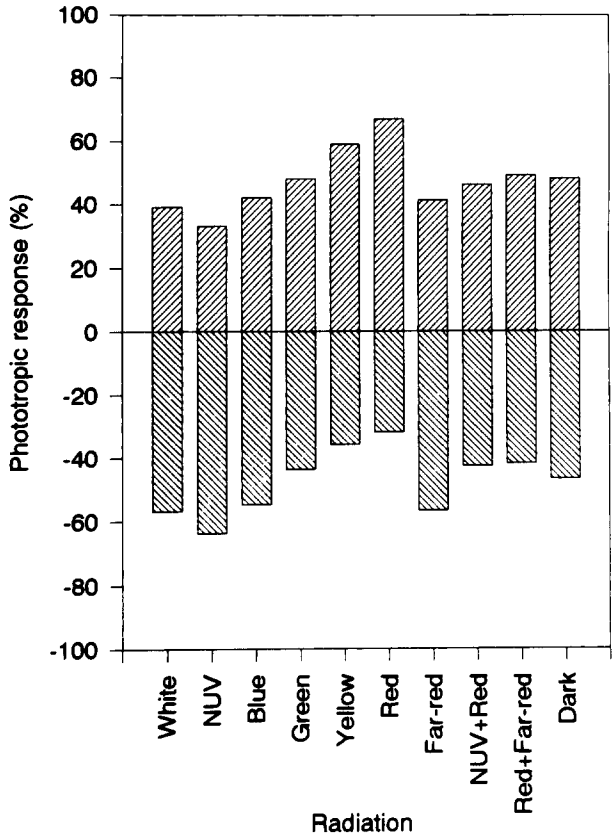


Fig. 4. Phototropic response of germ tubes of *Colletotrichum lagenarium*.
Germ tubes were evaluated after 10 h of irradiation.

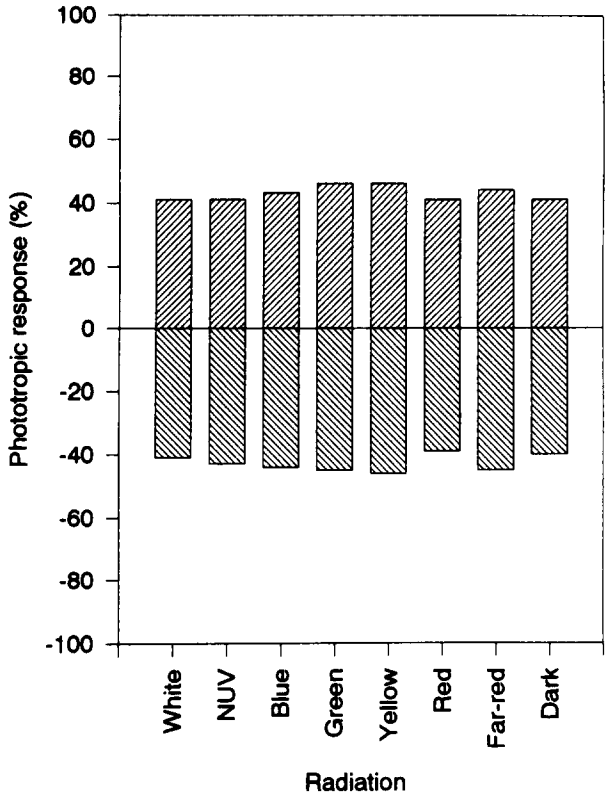


Fig. 5. Phototropic response of germ tubes of *Bipolaris oryzae*.
Germ tubes were evaluated after 2 h of irradiation.

radiation, which induced a strong negative phototropic response of germ tubes of *C. lagenarium*, promoted appressorium formation significantly: 79% of germinated conidia produced appressoria. In contrast, red light, which induced a strong positive phototropic response, inhibited appressorium formation (34%) significantly and increased the proportion of germ tubes without appressoria (66%) over that in the dark control (Fig. 6).

In the case of *B. oryzae*, neither NUV nor red radiation showed any significant effect on infection hypha formation compared with the dark control, and no statistically significant differences were found between them (Fig. 7).

## Discussion

In a study of phototropism in fungi, Carlile (1965) concluded that positive phototropism occurs in fungi and is seen in both unicellular and multicellular organs. Negative phototropism is rare in nature compared with the wide distribution of positive phototropism. Negative phototropism of spore germ tubes of plant-pathogenic fungi is important in the plant infection process. A few plant-pathogenic fungi have been reported to show negative phototropism, including *Septoria obesa* H. et P. Sydow (Honda and Miyawaki, 1989), *Phakopsora pachyrhizi* Syd. (Koch and Hoppe, 1987), *Puccinia rhamni* (Persoon) Wettstein (Fromme, 1915), *Puccinia coronata* Corda, *Puccinia graminis* Persoon f. sp. *avenae* Eriksson et E. Henning, *Puccinia graminis* Persoon f. sp. *tritici* Eriksson et E. Henning and *Puccinia triticina* Eriksson (Forbes, 1939). The sporangiophore of a piloboloid mutant, genotype *pil*, of *Phycomyces* was reported to be negatively phototropic (Koga et al., 1984). Negative phototropism has also been observed in hyphae of *Septoria nodorum* Berkeley (Calpouzos and Lapis, 1970) and of *Aspergillus restrictus* G. Smith (Welty and Christensen, 1965).

In this study, germ tubes of *C. lagenarium* under unilateral irradiation in the NUV, blue, white, and far-red regions showed a negative phototropic response, with the maximum under NUV radiation. However, germ tubes also exhibited positive phototropism under monochromatic irradiation with yellow light and red light. This result indicates that the phototropic response of germ tubes of *C. lagenarium* depends on wavelength of the radiation. UV-blue (300-520 nm) and far-red (>700 nm) regions induced negative phototropism, and wavelengths of 575-700 nm (yellow and red regions) induced positive phototropism. Radiation of 520-575 nm (green region) was neutral. Under NUV radiation, 64% of germ tubes were negatively phototropic, while 42% of germ tubes showed negative phototropism in blue light (Fig. 4). This suggests that the probable cause of negative phototropism is the effect of NUV radiation. These

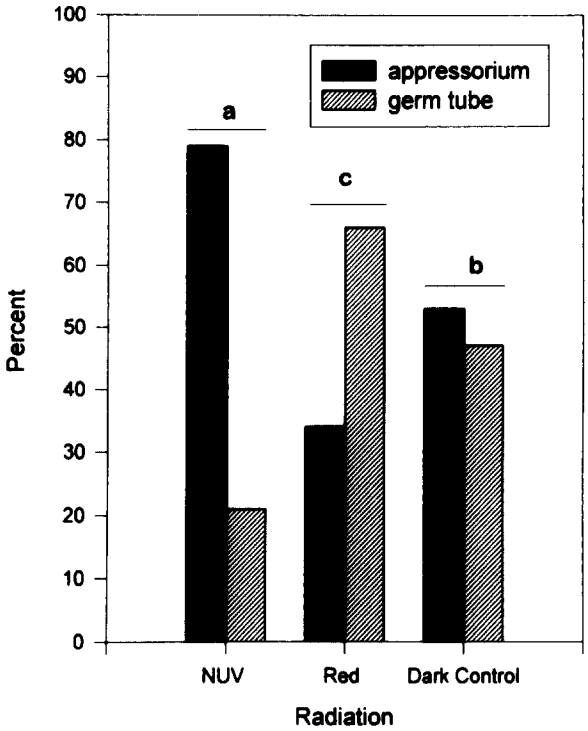


Fig. 6. Effect of NUV and red radiation on appressorium formation of *Colletotrichum lagenarium* after 15 h of irradiation.
Differences between appressorium and germ tube formation were analyzed statistically; columns not followed by the same letter are significantly different at $P<0.05$.

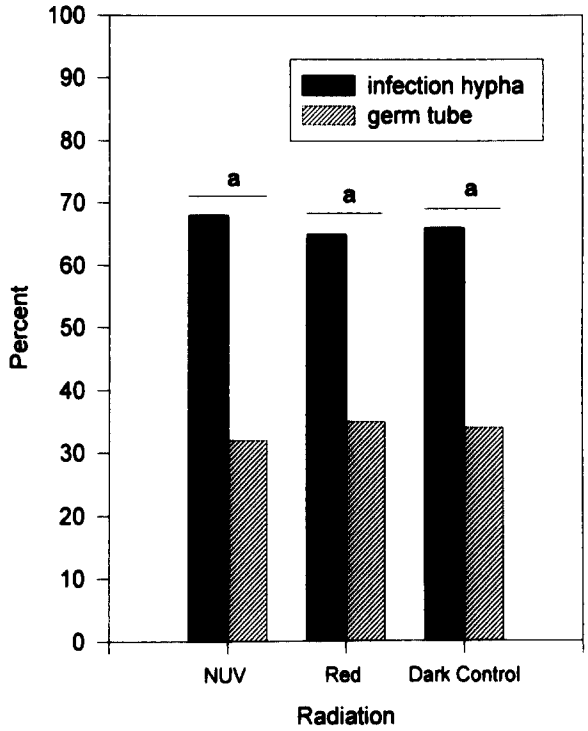


Fig. 7. Effects of NUV and red radiation on infection hypha formation of *Bipolaris oryzae* after 6 h of irradiation.
Differences between infection hypha and germ tube formation were analyzed statistically; columns not followed by the same letter are significantly different at $P<0.05$.

results are in general agreement with Curry and Gruen (1957), who reported that negative phototropism of sporangiophores of *Phycomyces* was induced by UV radiation; and with Honda and Miyawaki (1989), who found that monochromatic radiations of 580–700 nm (red region) induced positive phototropism of *S. obesa*. The negative phototropic response of germ tubes under white light may be due to the greater amount of negative phototropism-inducing light components.

NUV radiation induced strong negative phototropism of germ tubes of *C. lagenarium* and red light induced strong positive phototropism. When both NUV and red radiations were applied simultaneously, the percentages of both negative and positive phototropic responses of germ tubes decreased sharply. These results suggest an antagonistic relationship between the negative phototropism-inducing NUV radiation and positive phototropism-inducing red light. When these two radiations are applied at the same time, the effect of each negates the other, resulting in a phototropic response like that of the dark control. Similar results were found on simultaneous use of red and far-red radiations. These results are supported by the previous findings on the phototropic response of germ tubes of *S. obesa* (Honda and Miyawaki, 1989), that an antagonistic relationship exists between the negative phototropism-inducing UV-blue region and the positive-phototropism inducing red region.

Effective wavelengths for inducing positive phototropism in *Phycomyces* sporangiophores have been repeatedly confirmed since Castle (1961) revealed that the short wavelengths of the visible spectrum were most effective. A detailed action spectrum for positive phototropism was determined by Curry and Gruen (1959), which demonstrated a maximum of effectiveness at 445 nm, a shoulder at 470 nm with an abrupt fall-off on the long wavelength side, and a secondary maximum near 370 nm, although detailed action spectra for the negative phototropism of germ tubes or hyphae have not yet been determined. Koch and Hoppe (1987) studied the dose-response curves for negative phototropism of uredospore germ tubes of *P. pachyrhizi* at several wavelengths ranging from 372 nm to 600 nm and concluded that negative phototropism of germ tubes was a blue-light effect, and that wavelengths longer than 600 nm (red light) were ineffective in phototropism. Honda and Miyawaki (1989) showed that, in *S. obesa*, negative phototropism of germ tubes was induced by radiation between 300 nm and 520 nm, with maxima at 380 nm in the near ultraviolet region and 460 nm in the blue region, and that radiations of 580–700 nm induced positive phototropism. Senger and Schmidt (1986) summarized more than 16 action spectra, but none of these includes activity at wavelengths longer than 580 nm. However, wavelengths longer than 580 nm induced positive phototropism in germ tubes of *C. lagenarium*; moreover, the orientation of this effect is opposite to that of NUV radiation.

Blaauw (1914) coined the term "light growth reaction" for the response of growth acceleration in *Phycomyces* sporangiophores induced by irradiation, and postulated that the "cylindrical lens action" of a sporangiophore is responsible for the fluence rate being higher on the distal side of the sporangiophore than proximal side. In this mechanism, the growing zone acts as a convergence lens, and thus the distal side of the sporangiophore receives a more intense light stimulus than the proximal side, resulting in positive phototropism of the sporangiophore and greater growth on the distal than proximal side. This hypothesis was supported by the finding that when a sporangiophore is immersed in a medium of higher refractive index than air, e.g., liquid paraffin, the cell becomes a diverging lens and phototropic bending is reversed (Buder, 1918). Tsuru et al. (1988) elaborated the theory by taking into consideration intracellular light scattering and attenuation, the length of light path (cell diam), and so on. The increased intracellular scattering and attenuation caused the maximal fluence rate of light to be lower on the distal than on the proximal side of the sporangiophore cell. Koga et al. (1984) reported that when the cell diam exceeds 210 $\mu$m, the phototropism in *Phycomyces* sporangiophores is reversed due to a loss of the convergent lens effect of the cell.

Wavelengths of 580–700 nm promoted the germ tube growth of *C. lagenarium* and concentrated radiation of these wavelengths with a higher fluence rate on the distal side resulted in positive phototropism. On the contrary, irradiation of short wavelengths (320–500 nm) and of 700–780 nm induced negative phototropism and inhibited germ tube growth. These results are in general agreement with the previous findings of Honda and Miyawaki (1989) that radiations that induced negative phototropism of germ tubes inhibited germ tube growth and those that induced positive phototropism promoted germ tube growth. *Bipolaris oryzae* did not show a phototropic response and light did not significantly affect the germ tube growth (Figs. 3, 5). These results indicate that the lens effect in combination with the light growth reaction and light growth inhibition is the mechanism of the phototropism of germ tubes in *C. lagenarium*.

Negative phototropism-inducing radiations promoted infection structure formation significantly in *C. lagenarium*. On the other hand, the radiations that induced positive phototropism reduced it significantly (Fig. 6). This result demonstrates the ecological significance of phototropism in the plant infection process. Several investigators have reported that close contact or adhesion of fungal conidium germ tubes to the host surface is essential for infection structure initiation (Dey, 1933; Staples and Macko, 1980; Nicholson, 1984). In a study of phototropism of the germ tubes of clover powdery mildew, Yarwood (1932) reported that appressoria are produced by the germ tubes due to contact stimuli and their formation is dependent to certain extent on the vigor of the phototropism. Fromme (1915) was the first to state that a continuous turning away from light may serve to bring the germ tube into contact with the surface of the host and be chiefly responsible for its entrance into the stomatal opening. Later, many researchers followed Fromme's suggestions (Gäumann, 1946; Gettkandt, 1954; Banbury, 1959; Koch and Hoppe, 1987). However, attempts to prove the possibility that negative phototropism favors penetration of the germ tubes into host tissue have so far been inconclusive. Honda et al. (1992) proved the ecological significance of negative phototropism in the plant infection process in both laboratory and greenhouse experiments. They showed that elimination by use of an ultraviolet absorbing (UVA) vinyl film of UV wavelengths shorter than 390 nm, which induced negative phototropism of conidium germ tubes of *S. obesa*, significantly reduced the invasion of germ tubes through the stomata by reducing the negative phototropic response of germ tubes. They also showed that, in greenhouse experiments, the number of brown spot lesions on chrysanthemum seedlings in the UVA vinyl film greenhouse was significantly lower than that in the common agricultural (CA) vinyl film greenhouse, indicating the effect of light on the initial invasion process of germ tubes. Thus, brown spot disease of cultivated chrysanthemum caused by *S. obesa* can be controlled successfully by manipulating the negative phototropic response of germ tubes.

Here, however, instead of host plants we used onion epidermal strips as a preliminary measure to prove the ecological significance of phototropism in plant infection. According to Homma et al. (1983), this method does not affect fungal growth, and the fungus can develop through all growth stages of its life cycle, i.e., conidial germination, appressorial formation and penetration. No inhibitory effect on growth of the studied fungi was observed in our preliminary experiments. *Bipolaris oryzae* showed no significant phototropic response, and light did not affect the formation of infection structures (Fig. 7), though within 5–6 h of inoculation it produced very clear and distinct infection hyphae. This result is in accordance with the findings of Benedict and Palmerley (1979). In contrast, *C. lagenarium* showed negative and positive phototropism in response to radiations of certain wavelengths. Negative phototropism-inducing radiation promoted the infection structure formation and radiation that induced positive phototropism reduced it significantly, indicating the importance of negative phototropism in the initial host infection process of germ tubes of *C. lagenarium*.

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