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Suppressive Effect of Darkness on the Development of Powdery Mildews

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Abstract: The effect of darkness on powdery mildew development was evaluated in the present study. *Blumeria graminis* f. sp. *tritici*, *Erysiphe pisi* and *Sphaerotheca cucurbitae* were incubated under various light conditions. The formation of haustoria and appressoria on hyphae and the elongation of hyphae were suppressed drastically by incubation in the continuous dark condition. Development of the powdery mildews was delayed by incubation in the continuous light condition. These suppressive effects of light conditions were consistent among the three powdery mildews investigated. *B. graminis* incubated in the continuous dark condition formed only primary haustoria that were larger in size than those formed in regular light conditions (12 h light/12 h dark), while *E. pisi* and *S. cucurbitae* formed secondary haustoria in the continuous dark condition. Re-irradiation of the powdery mildews incubated in the continuous dark condition led to recovery of development of the powdery mildews. Treatment of host plants with glucose and sucrose reversed the suppressive effect of darkness and promoted development of the powdery mildews. These results suggest that the reduced growth of powdery mildews under continuous dark or light condition might be due to loss of nutrients, such as carbohydrates, from host cells under these conditions. On red, green, yellow and blue light re-irradiation following incubation in the continuous dark condition, the formation of secondary haustoria by *B. graminis* was observed, although the number of haustoria per colony was significantly smaller than that by white light re-irradiation. Black blue light (310 to 410 nm) did not induce the formation of secondary haustoria. Taken together, this study demonstrated that light conditions affect powdery mildew development, suggesting that light conditions are indispensable for the infection of host plants by powdery mildew.

Key words: Powdery mildew, darkness, light, haustoria

INTRODUCTION

Plant protection against powdery mildew that infects over thousands of plants all over the world is accomplished by treatment with conventional fungicides, salts, silicones, detergents and biological control agents (Bush *et al*., 2006; Fauteux *et al*., 2006; Hukkanen *et al*., 2007; Schuerger and Hammer, 2003; Shishkoff and McGrath, 2002; Suzuki *et al*., 2006). Fungicides, in particular, have been used widely to protect plants against powdery mildew because they have high protective efficiency and are labor- and cost-effective due to ease of application. However, there are certain problems associated with the application of fungicides, one being environmental pollution, which has been the cause of apprehension among the public in the past decade. The control of environmental pollution by residual of fungicides has become a critical subject in relation to the maintenance of food and environmental safety in the future. Another problem is the spontaneous generation of isolates that show resistance to fungicides (Bernhard *et al*., 2002; Délye *et al*., 1997). Isolates of the grape powdery mildew fungus, *Uncinula necator*, which are resistant to sterol demethylation-inhibiting fungicides (DMIs), have a single mutation at one codon of the gene encoding eburicol 14 alpha-demethylase, the target of DMIs (Délye *et al*., 1997). The generation of fungicide-resistant powdery mildew isolates appears to occur at a higher frequency than that of other fungal pathogens because powdery mildew generates progenies rapidly and forms a large number of new conidia in a day.

Many researchers have investigated the effects of environmental factors, especially light conditions (light intensity, light spectrum and photoperiod), on the growth of powdery mildew, in efforts to suppress the generation of powdery mildew (Kenyon *et al*., 2002; Schuerger and Brown, 1997; Willocquet *et al*., 1996). Nishiyama *et al*. (1966) were the first to demonstrate the formation of secondary haustoria, not primary ones, on cultivation in the dark, suggesting that there might be a unique rhythm

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for the formation of haustoria and a specific mechanism that regulates haustorium formation in the light/dark cycle. However, there remain a lot of uncertainties concerning the interaction between light conditions and the formation of haustoria.

In this study, to elucidate the effect of darkness on powdery mildew development, host plants were inoculated with three different genera of powdery mildews, wheat powdery mildew fungus *Blumeria graminis* f. sp. *tritici*, pea powdery mildew fungus, *Erysiphe pisi* and cucumber powdery mildew fungus, *Sphaerotheca cucurbitae* and incubated under various light conditions. Consequently, we demonstrated that incubation of the powdery mildews in the continuous dark condition suppressed development of the powdery mildews and that this suppressive effect was recovered by re-irradiation with light and treatment with carbohydrates.

MATERIALS AND METHODS

Test fungi: *Blumeria graminis* (Syn. *Erysiphe graminis*) f. sp. *tritici* and *Sphaerotheca cucurbitae* were collected from fields in Akita Prefecture in 2002-2003. *Erysiphe pisi* de Cansole race 1 was a gift from Dr. H. Kunoh of the Faculty of Bioresources, Mie University. These fungi were maintained on seedlings of wheat (*Triticum aestivum* L. cv. Gogatsukomugi), pea (*Pisum sativum* L. cv. Megurousui) and cucumber (*Cucumis sativum* L. cv. Shinhokusei 1), respectively. Wheat was grown in a growth chamber at 25°C and 60% relative humidity under light (150 $\mu mol^{-2}\ s^{-1}\ m^{-2}/\mu A$, 12 h light day^{-1}). Pea and cucumber were grown in a greenhouse at 25°C.

Inoculation and incubation of powdery mildews: Leaf fragments were excised from the first leaves of wheat. Leaf disks of pea and cucumber were prepared from cotyledons. Using a paintbrush, the abaxial surface of the leaves was inoculated with freshly grown conidia of powdery mildews on host plants. Inoculation was performed at 9 AM, 3 h later from the lighting-up time (6 AM) in the regular light condition (12 h light/12 h dark). Incubation was performed at 25°C under various light conditions. After incubation for the indicated times, the leaf fragments and disks were fixed and destained with FAA solution (equal volumes of formaldehyde, ethanol and acetic acid). The whitened samples were stained with saturated cotton blue solution to visualize the morphological characteristics of the powdery mildews.

Light conditions: To determine the effect of darkness on powdery mildew development, fungi were incubated under the following light conditions.

- **Regular light condition:** Leaf fragments and disks inoculated with the powdery mildews were incubated under white light condition (150 $\mu mol^{-2}\ s^{-1}\ m^{-2}/\mu A$, 12 h light day^{-1}). This condition was termed 12L/12D in this study.
- **Continuous dark:** Powdery mildews were incubated in the continuous dark condition during the incubation period. This condition was termed 24D in this study.
- **Continuous light:** Powdery mildews were incubated under white light condition (150 $\mu mol^{-2}\ s^{-1}\ m^{-2}/\mu A$, 24 h light day^{-1}) during the incubation period. This condition was termed 24L in this study.
- **Re-irradiation with light:** To determine the effect of light re-irradiation on the development of powdery mildews incubated in the continuous dark condition, fungi were incubated initially in 24D for 72 h and then in 12L/12D for the indicated times. This condition was termed 24D-12L/12D in this study.

Treatment with carbohydrates: Leaf fragments and disks inoculated with the powdery mildews were incubated in 24D on filter paper wetted with 1, 10 and 100 mM glucose or sucrose. H_2O was used as control. As another experimental control, leaf fragments and disks inoculated with the powdery mildews were incubated in 12L/12D without carbohydrates. Development of the powdery mildews was observed 72 h post inoculation.

Induction of haustorium formation by irradiation with various colored lights: To identify which colored light induces the formation of secondary haustoria by *B. graminis*, *B. graminis* was incubated for 72 h in the continuous dark condition and transferred into an incubator with exposure to various colored lights (12 h light day^{-1}), followed by further incubation for 72 h. The colored lights used were red light (610-700 nm, max 660 nm; FL20S R-F, National), green light (490-590 nm, max 530 nm; FL20S G-F, National), yellow light (500-700 nm, max 580 nm; FL20S Y-F, National), blue light (380-540 nm, max 440 nm; FL20S B-F, National) and black blue light (310-410 nm, max 350 nm; FL20S BL-B, National). As control, *B. graminis* was incubated in 12L/12D with regular white light or in 24D after incubation for 72 h in 24D. The number of haustoria per colony was counted 72 h post irradiation of colored lights.

Observation of powdery mildew development: Observations were performed with a light microscope, focusing on the following infection processes of powdery mildews: a) The formation of haustoria and appressoria on hyphae. The number of haustoria or appressoria on hyphae per colony was counted. b) The elongation of

hyphae. The total length of hyphae per colony was measured with a micrometer under a light microscope. c) The size of primary haustoria. To determine the effect of darkness on the size of primary haustoria formed by *B. graminis*, the width from tips of digitate processes at one side to that at the other side was measured periodically with a micrometer under a light microscope.

Statistics: Results are presented as means±standard errors. Student's t-test was used for statistical analysis.

RESULTS

Effect of darkness on formation of haustoria: Three powdery mildews, *B. graminis*, *E. pisi* and *S. cucurbitae*, were incubated in continuous dark (24D) and regular light (12L/12D) conditions. The number of haustoria or appressoria on hyphae formed by one colony was counted and compared between the two light conditions. The continuous dark condition, 24D, suppressed the formation of haustoria regardless of the genus of powdery mildew (Fig. 1). The number of haustoria formed by one colony of *B. graminis* and *S. cucurbitae* incubated in 24D was significantly smaller than that in 12L/12D from 72 h post inoculation (Fig. 1A and C). Haustoria formed by *E. pisi* could not be counted exactly because primitive haustoria were too small to be seen. Therefore, the number of appressoria formed on hyphae per colony was counted for *E. pisi*. The formation of appressoria by *E. pisi* was also suppressed by incubation in 24D throughout the incubation period (Fig. 1B). While *E. pisi* and *S. cucurbitae* formed multiple haustoria in one colony, *B. graminis* never formed secondary haustoria throughout the incubation period (Fig. 1A). Primary haustoria formed by *B. graminis* incubated in 24D were larger than those formed by the same fungus incubated in 12L/12D (Fig. 2). The size difference was observed from 36 h post inoculation. In the case of *E. pisi* and *S. cucurbitae*, no difference could be seen between the sizes of primary haustoria in 24D and in 12L/12D (data not shown). The germination of primary germ tubes (only for *B. graminis*) and appressorial germ tubes, the maturation of appressoria and the formation of primary haustoria and secondary hyphae were not affected by incubation in the continuous dark condition (data not shown). These results suggest that light condition is an essential environmental factor for the formation of haustoria by the powdery mildews and that darkness suppresses the formation of haustoria by the powdery mildews.

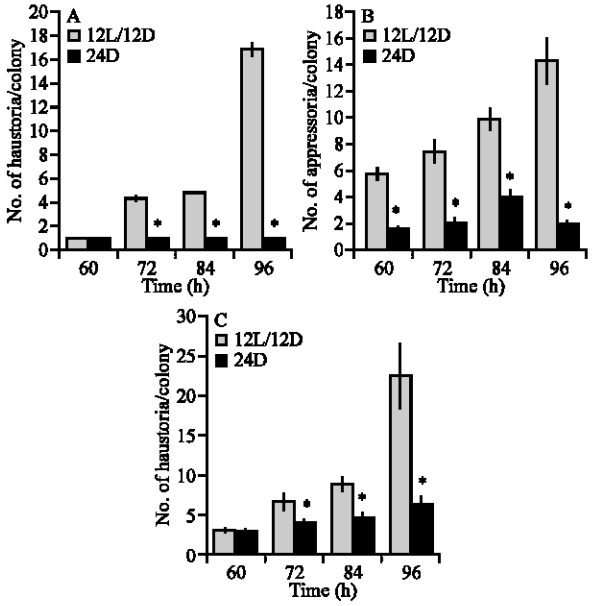

Fig. 1: Suppressive effect of darkness on the formation of haustoria. *B. graminis* (A), *E. pisi* (B) and *S. cucurbitae* (C) were incubated in 12L/12D or 24D for the indicated times. The number of haustoria per colony of *B. graminis* and *S. cucurbitae* and the number of appressoria on hyphae per colony of *E. pisi* were counted periodically. Bar, standard error (n = 20). *p<0.01, compared with 12L/12D

Effect of darkness on elongation of hyphae: To analyze the effect of darkness on the elongation of hyphae in the

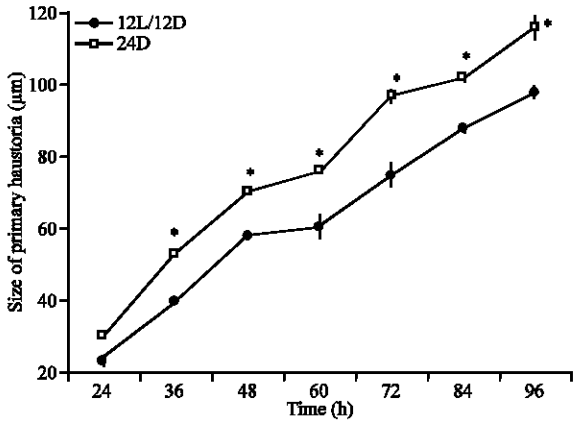

Fig. 2: Size of primary haustoria formed by *B. graminis* incubated under different light conditions. *B. graminis* was incubated in 12L/12D or 24D for the indicated times. The size of primary haustoria was measured periodically as described in Materials and Methods. Bar, standard error (n = 30). *p<0.01, compared with 12L/12D

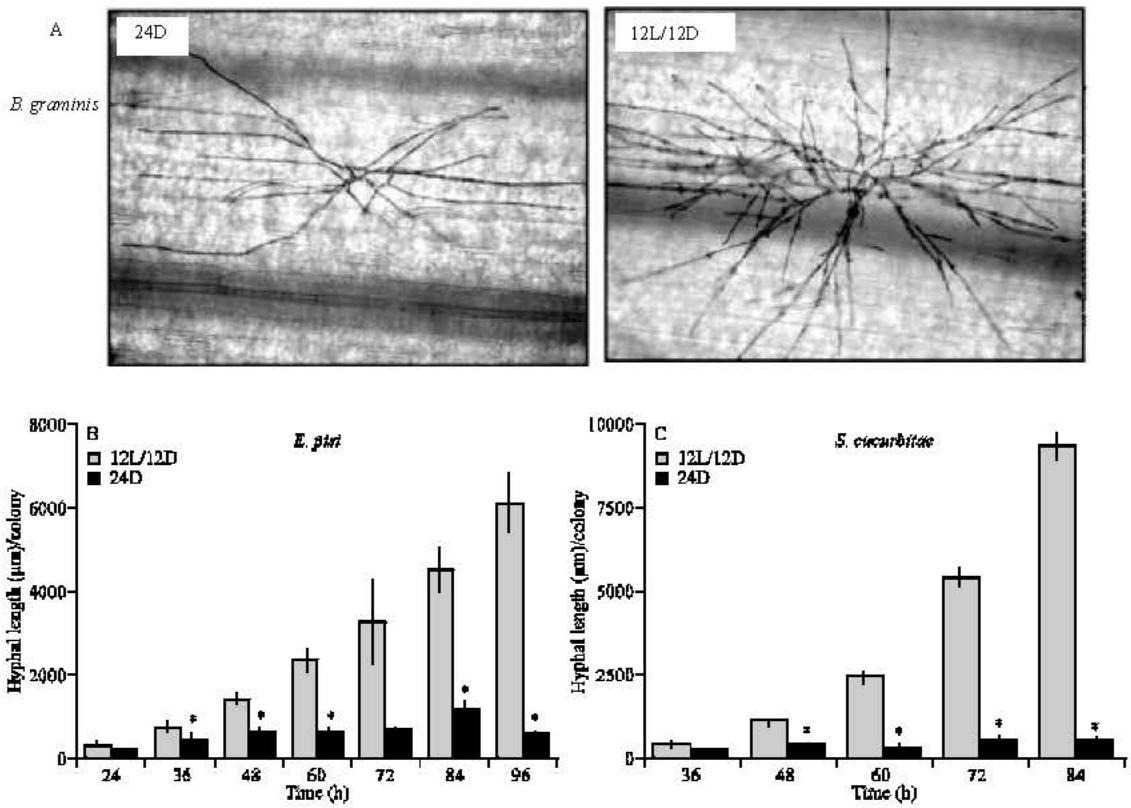

Fig. 3: Suppressive effect of darkness on the elongation of hyphae. Powdery mildews were incubated in 12L/12D or 24D for the indicated times. (A) Colonies of *B. graminis* incubated for 96 h in 12L/12D or 24D. The elongation and branching of hyphae in a single colony formed in 24D were less than that in 12/12D. (B and C) Total length of hyphae formed by *E. pisi* (B) and *S. cucurbitae* (C) was measured periodically using a micrometer. Bar, standard error (n = 20). *p<0.01, compared with 12L/12D

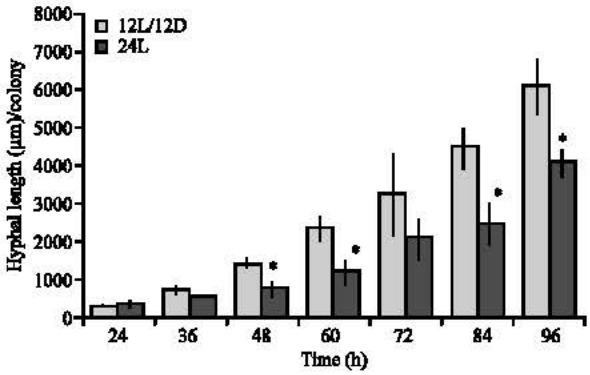

Fig. 4: Suppressive effect of continuous light irradiation on the elongation of hyphae. *E. pisi* was incubated in 12L/12D or 24L for the indicated times. Total length of hyphae per colony was measured periodically using a micrometer. Bar, standard error (n = 20). *p<0.01, compared with 12L/12D

powdery mildews, the total length of hyphae elongating from one colony was measured. In the case of *B. graminis*, the total length of hyphae could not be measured because a few hyphae overlapped with the margin of wheat epidermal cells (Fig. 3A). However, it was obvious that the elongation and branching of hyphae in 24D were less than those in 12L/12D (Fig. 3A). The total length of hyphae formed by *E. pisi* and *S. cucurbitae* incubated in 24D was less than that formed by the same fungi incubated in 12L/12D (Fig. 3B and C). Both fungi showed little hyphal elongation in 24D during the entire incubation period. There was no sporulation by the three powdery mildews incubated in 24D during the entire incubation period (data not shown). These results suggest that darkness suppresses the elongation and branching of hyphae and the colonization of the powdery mildews.

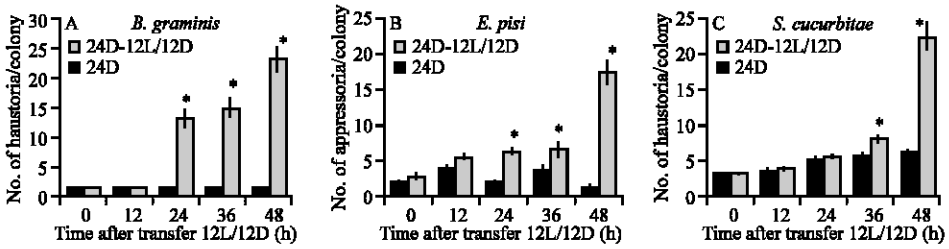

Fig. 5: Recovery of powdery mildew development by light re-irradiation. Powdery mildews were incubated in 24D for 72 h, followed by transfer and incubation in 12L/12D (24D-12L/12D). As control, after incubation in 24D for 72 h, powdery mildews were continuously incubated in 24D. The number of haustoria per colony of *B. graminis* (A) and *S. cucurbitae* (C) and the number of appressoria on hyphae per colony of *E. pisi* (B) were counted periodically. Bar, standard error (n = 20). *p<0.01, compared with 24D

Effect of continuous light irradiation on powdery mildew development: Continuous white light irradiation delayed the development of powdery mildews, but did not completely stop the development. For example, the total length of hyphae formed by *E. pisi* in 24L was less than that formed by the same fungus in 12L/12D from 48 h post inoculation (Fig. 4). The elongation of hyphae in 24L was not stopped; rather, it showed a gradual increase. *B. graminis* and *S. cucurbitae* also showed elongated hyphae in 24L, although the total length of hyphae in 24D was less than that in 12L/12D (data not shown). Sporulation by the three powdery mildews incubated in 24L was observed at the end of the incubation period (data not shown).

Recovery of powdery mildew development from suppressive effects of darkness by re-irradiation with light: Incubation of the powdery mildews in the continuous dark condition suppressed the formation of haustoria and the elongation of hyphae (Fig. 1 and 3). To determine whether this suppressive effect could be recovered by re-irradiation with light, the powdery mildews were incubated in 24D for 72 h, followed by incubation in 12L/12D for the indicated times. The formation of haustoria by *B. graminis* and *S. cucurbitae* was recovered 24 and 36 h post transfer from 24D to 12L/12D, respectively (Fig. 5A and C). The formation of appressoria on hyphae of *E. pisi* was also recovered 24 h post transfer. Hyphal growth of the three powdery mildews incubated in 24D was also recovered by re-irradiation with light (data not shown). These results suggest that light re-irradiation after incubation in the continuous dark condition reversed the suppressive effect of darkness and recovered development of the powdery mildews.

Induction of powdery mildew development in continuous dark condition by treatment with carbohydrates: Leaf fragments and disks inoculated with powdery mildews

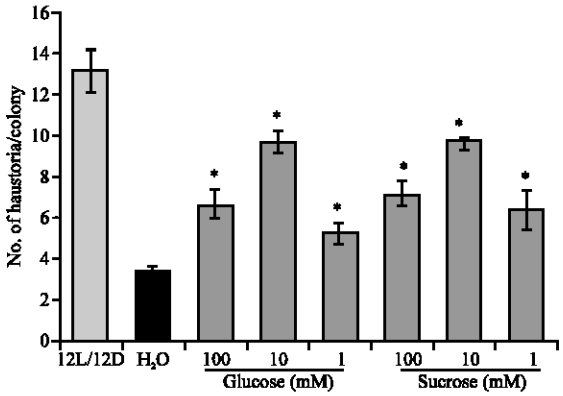

Fig. 6: Induction of powdery mildew development by treatment with carbohydrates. *S. cucurbitae* was incubated in 24D with various concentrations of glucose or sucrose. As controls, *S. cucurbitae* was incubated in 12L/12D or 24D without carbohydrates. The number of haustoria per colony was counted 72 h post inoculation. Bar, standard error (n = 20). *p<0.01, compared with 24D

were incubated in 24D with glucose or sucrose. Figure 6 shows that the treatment with glucose and sucrose increased the number of haustoria per colony of *S. cucurbitae* compared with that in 24D without carbohydrates (Fig. 6), although the number was smaller than that in 12L/12D without carbohydrates (Fig. 6, 12L/12D). The elongation of hyphae in *S. cucurbitae*, the formation of haustoria and the elongation of hyphae in *B. graminis* and the formation of appressoria and the elongation of hyphae in *E. pisi* were also promoted in 24D by treatment with carbohydrates (data not shown).

Induction of haustorium formation by irradiation with colored light: *B. graminis* incubated in the continuous dark condition formed only primary haustoria even at

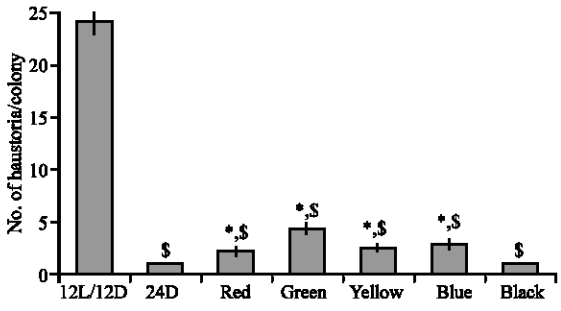

Fig. 7: Induction of haustorium formation by irradiation with various colored lights. *B. graminis* was incubated in 24D for 72 h, followed by incubation for 72 h under various colored lights or under regular white light as control (12L/12D). As another control, *B. graminis* was incubated in 24D for 144 h (24D). The number of haustoria per colony was counted 72 h post irradiation with colored lights. Bar, standard error (n = 10). *p<0.01, compared with 24D. $ p<0.01, compared with 12L/12D

96 h post inoculation (Fig. 1). Whether the formation of secondary haustoria by *B. graminis* incubated in the continuous dark condition was induced by a specific light spectrum was investigated with various colored lights. After incubation in 24D for 72 h, *B. graminis* was further incubated with exposure to various colored lights (12 h light day^{-1}) for 72 h. Irradiation with red, green, yellow or blue light induced the formation of secondary haustoria by *B. graminis* (Fig. 7). However, the number of haustoria formed per colony was significantly smaller than that by white light re-irradiation (Fig. 7). Irradiation with black blue light did not induce the formation of secondary haustoria.

DISCUSSION

Powdery mildew is any of the obligate biotrophic fungal parasites that don't kill infected host cells and appear to absorb nutrients from the host cells through haustoria. According to these unique characteristics, the formation of haustoria has become a target to protect host plants from powdery mildew. Actually, cultivars resistant to powdery mildew induce hypersensitive cell death (Koga *et al*., 1988; Vanacker *et al*., 2000) and papilla formation (Aist *et al*., 1979; Bushnell and Berqquist, 1975; Gold *et al*., 1986) to block the formation of haustoria in host cells. However, at this time, the regulation of haustorium formation and the function of haustoria are not completely understood. In the present study, to understand the regulation of haustorium formation by environmental conditions, we evaluated the effect of light conditions on powdery mildew development, particularly the formation of haustoria, with three different genera of powdery mildews.

Incubation of *B. graminis*, *E. pisi* and *S. cucurbitae* in the continuous dark condition suppressed the formation of haustoria or appressoria on hyphae and the elongation of hyphae compared with incubation in the regular light condition (Fig. 1 and 3). Many researchers have demonstrated the effects of photoperiod and light intensity on the infection process of powdery mildew (Aust *et al*., 1977; Carver and Phillips, 1982; Carver and Williams, 1980; Edwards, 1993). Aust *et al*. (1977) evaluated the effect of light on the formation of haustoria by *B. graminis* f. sp. *hordei* and demonstrated that low light intensity retarded fungal growth. Their result supports our finding that the incubation of *B. graminis* f. sp. *tritici* in the continuous dark condition suppressed the formation of haustoria and the elongation of hyphae. Meanwhile, Carver and Phillips (1982) investigated the effects of photoperiod on the formation of haustoria by *B. graminis* f. sp. *hordei* and demonstrated that *B. graminis* under short photoperiod (6 h light day^{-1}) formed more haustoria than that under long photoperiod (18 h light day^{-1}). Taken together, darkness may exert diverse regulatory effects on powdery mildew development: on the one hand, the formation of haustoria is promoted by darkness, as described by Nishiyama *et al*. (1966) and Carver and Phillips (1982); on the other hand, low light and continuous darkness reduce or suppress powdery mildew development, as suggested by Aust *et al*. (1977) and the present study. Since light re-irradiation, which might lead to recovery of the photosynthetic process in host plants, might also lead to recovery of powdery mildew development (Fig. 5), it is plausible that reduced growth of the powdery mildews under low light or the continuous dark condition might result in loss of nutrients, such as carbohydrates, from host cells under these light conditions, as discussed by Carver and Phillips (1982). In fact, treatment with glucose and sucrose induced the formation of haustoria by the powdery mildews even if they were incubated in the continuous dark condition (Fig. 6). These results may explain why darkness suppresses the formation of haustoria by the powdery mildews. It is known that glucose is transported from host plant to powdery mildew (Mendgen and Nass, 1988; Sutton *et al*. 1999). Sucrose also might be transported from host plant to powdery mildew after it is metabolized in the host plant (Mendgen and Nass, 1988). Thus, the suppressive effects of darkness on powdery mildew development might result in

the loss of energy from host plant, suggesting that the uptake of nutrients from host plant is necessary for powdery mildew to form haustoria in host cells. However, the direct effect of darkness on powdery mildew cannot be dismissed and further studies are needed to evaluate the suppressive effect of darkness on powdery mildew development.

Continuous light irradiation delayed powdery mildew development, although the suppressive effect is weaker than that in the continuous dark condition (Fig. 4). Carver and Williams (1980) showed similar results that the number of haustoria formed in one colony of *B. graminis* f. sp. *hordei* under continuous light irradiation was smallest among the photoperiods they investigated. Carver and Carr (1978) also showed that *B. graminis* f. sp. *avenae* formed less haustoria under continuous light irradiation than under the dark/light condition. Although continuous light irradiation might alter host and/or fungal metabolism, it is difficult to determine whether the irradiation affects directly host, fungi, or both.

Interestingly, *B. graminis* formed only primary haustoria in the continuous dark condition even at 4 days post inoculation (Fig. 1A). In contrast, powdery mildews belonging to other genera, *E. pisi* and *S. cucurbitae*, formed multiple haustoria even in the continuous dark condition (Fig. 1B and C). The primary haustoria formed by *B. graminis* in the continuous dark condition were larger than those formed in the regular light condition (Fig. 2). It is plausible that *B. graminis* incubated in the continuous dark condition generates larger primary haustoria to collect more nutrients from host cells because no secondary haustoria were formed in the continuous dark condition. While *B. graminis* formed large haustoria having digitate processes, haustoria formed by *E. pisi* and *S. cucurbitae* were small and round. This morphological difference among the powdery mildews might explain why only *B. graminis* did not form secondary haustoria in the continuous dark condition. Further investigations are necessary to clarify the morphological and functional differences among haustoria from various genera of powdery mildews.

Light spectrum is an important factor for germination, mycelial growth, sporulation and colonization of powdery mildew (Elad, 1997; Schuerger and Brown, 1997; Willocquet *et al*., 1996). Similar to white light re-irradiation, colored light irradiation led to recovery of the development of *B. graminis* incubated in the continuous dark condition, although the extent of recovery was less than that by white light re-irradiation (Fig. 7, 12L/12D). The observation that the broad light spectrum induced the formation of secondary haustoria led us speculate that the broad light spectrum is necessary for *B. graminis* to form haustoria in host cells, although whether colored light affects directly host, fungi, or both is uncertain. Ultraviolet A (350 to 550 nm) inhibited the colonization of cucumber powdery mildew (Schuerger and Brown, 1997), while ultraviolet B (280 to 320 nm) decreased the germination rate and mycelial growth of grape powdery mildew (Willocquet *et al*., 1996). The finding that black blue light (310 nm to 410 nm) did not induce the formation of secondary haustoria (Fig. 7) suggests that black blue light might be utilized as one component of plant management against *B. graminis*.

In the present study, responses to various light conditions were similar among the three genera of powdery mildews, suggesting that light conditions are indispensable for the powdery mildews to establish infection on host plants. Further studies should be conducted to determine various photoperiods, light intensities and/or light spectra that would affect not the growth of plants but powdery mildew development.

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