Differential Spore Production by *Botrytis cinerea* on Agar Medium and Plant Tissue Under Near-Ultraviolet Light-Absorbing Polyethylene Film

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ABSTRACT

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Plastic films containing additives that alter their transmission of the light spectrum may be useful tools for the control of aerial plant pathogens of greenhouse crops. Several samples of polyethylene films containing additives that absorb near ultraviolet (nUV) light in the range 280 to 380 nm were compared for their ability to affect spore germination, mycelial growth, and sporulation of *Botrytis cinerea* on agar medium. One film was selected and further evaluated. The kinetics of spore production by the pathogen was similar on agar medium and on tomato stem tissue, and whether incubation took place under the nUV-absorbing film or under a control film. However, spore production on both types of substrates under the nUV film remained at less than 0.05% that of the control for several weeks after inoculation, demonstrating that the nUV film inhibited rather than delayed sporulation. A sharp reduction of spore production was also observed on other plant tissues. However, the efficiency of the nUV film appeared different for different plants, and it was lower on flowers and cotyledons than on stem tissue. Two of the five strains of *B. cinerea* tested on tomato stem tissue were less sensitive to sporulation inhibition by the nUV film. To clarify the potential of nUV films for the control of gray mold on greenhouse crops, the epidemiological significance of these results needs to be further examined in light of the abundance of such strains in the environment.

Gray mold, caused by *Botrytis cinerea* Pers.:Fr., is among the most important diseases on sheltered crops. It is particularly damaging on tomatoes grown in plastic-covered tunnels, as microclimatic conditions are often highly conducive to disease development (9). No *Botrytis*-resistant commercial varieties are available, and chemical control of gray mold has become increasingly difficult due to resistance to fungicides (4).

Control of this disease may be enhanced by complementing existing methods with measures that hinder disease development. One such measure may consist in covering shelters with plastic films containing additives that alter their transmission of the light spectrum. Vakalounakis (19) demonstrated that films absorbing long-wave infrared radiation increased night temperatures and decreased relative humidity, resulting in a climate less conducive to the development of several fungal diseases. Films absorbing near-ultraviolet (nUV) radiation (lower limits of transmission between 345 and 390 nm, depending on the studies) have been shown to reduce spore production in vitro for several pathogens of vegetable crops, including *Alternaria dauci* (Kühn) Groves & Skolko, *Alternaria porri* (Ellis) Cif., *Alternaria brassicae* (Berk.) Sacc., *Botrytis squamosa* J.C. Walker, *Stemphylium botryosum* Wallr. (12), *B. cinerea* (6,10), and *Alternaria solani* Sorauer (12,18). In greenhouse experiments, the nUV films provided a reduction in the incidence of disease caused by some of those pathogens, as compared to control films (6,10,12,18). Although spore counts on diseased tissue or in the air of the greenhouses were not reported in these studies, one would suspect that the observed reduction in disease incidence under the nUV film may have resulted from an inhibition of spore production by the pathogens on plant tissue.

However, the situation may be somewhat more complex, as several factors have been shown to interfere with the effect of light on the development of a fungus (1). Some fungi that require induction by light for sporulation on agar media do not need such induction in the presence of plant tissue or plant extracts (7,11). Furthermore, it has been reported for *A. solani* (2) and *Stemphylium* sp. (13) that oxidizing agents such as hydrogen peroxide, and hormones such as ergosterols, may act as substitutes for the light requirements in the regulation of spore production. For *B. cinerea*, results from several studies suggest that a nutritional control of spore production might also interfere with the effect of light, and that strains of this fungus may differ in their requirement for light induction of sporulation. For example, little or no sporulation was observed in the dark on potato-dextrose agar (PDA) or malt extract agar (MA) by several researchers (5,6,10), while Tan and Epton (16) reported that sporulation in the dark amounted to nearly 20% of that of the lighted control when the fungus was grown on MA medium. Furthermore, some isolates of *B. cinerea* have been shown to sporulate abundantly in the dark on MA (6,14), on PDA (17), and on an unspecified enriched medium (5). Sporulation in the dark was also reported in vivo on cabbage in cold storage (3) and on geranium (8).

In a preliminary study, we tested samples of polyethylene films that differed in their transmittance of light, for their ability to reduce spore production by *B. cinerea* on agar medium. Significant effects on sporulation were observed for several films. The objectives of this study were to verify whether a similar effect could be observed on plant tissue, and to investigate the relationship between the efficiency of the nUV film in inhibiting spore production and the type of plant substrate.

MATERIALS AND METHODS

Films. Six 180-μm-thick polyethylene films were used in the first part of this study. Samples of the experimental films and data on their transmittance spectra were kindly provided by Exxon Chemical International, Inc. (Machelen, Belgium). Five films (nos. 2 to 6) contained additives to absorb nUV light (Fig. 1A). One film (no. 1) contained no such additives and was used as a control. The transmittance of light was highest for film 1, particularly in the range 300 to 390 nm, which is involved in stimulation of spore production by *B. cinerea* (3,10,15,16). Films no. 2 and 3 contained a yellow pigment and absorbed nUV light completely below 340 nm. They differed in their transmittance of visible light above 440 nm, but both had somewhat lower transmittance in part of the violet-blue range (400 to 480 nm) that is known to inhibit the sporulation of *B. cinerea* in vitro (3,10,15,16). Films no. 4, 5, and 6 had identical transmittance spectra above 360 nm, exemplified by film 6 in Figure 1A. Their transmittance of the visible range was almost as high as that of

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film 1, especially in the violet-blue range. They blocked nUV light below 380 nm, with the exception of a short window at 260 ± 10 nm. The three films differed essentially in the size of the transmittance peak at 260 nm: it was highest for film 4 and lowest for film 6 (Fig. 1A).

In order to compare the spectral transmittance of those film samples to plastics already commercially available for greenhouse covers, measurements were made with a Licor LI 1800 portable spectroradiometer (Licor, Inc., Lincoln, Nebraska) in several greenhouses in Southern France. Five commercial films were examined: Celloflex 4S and AI4F (Prosyn Polyane, St. Chamond, France), COPEVA 4S (ID Plastiques, Sartrouville, France) and two PITT S4 films (SMS, Pouancé, France), one of which (PITT S4y) contained a yellow pigment (Fig. 1B). Both PITT S4 films had been in place on a greenhouse for 2 years when the light measurements were performed. The UV-absorbing film samples used in the present study had transmittance spectra somewhat similar to those obtained with three of the commercial films (Fig. 1). However, films 4 to 6 were the most absorbent in the nUV range (lower limit of transmission close to 390 nm) and the least absorbent in the violet-blue range (400 to 480 nm).

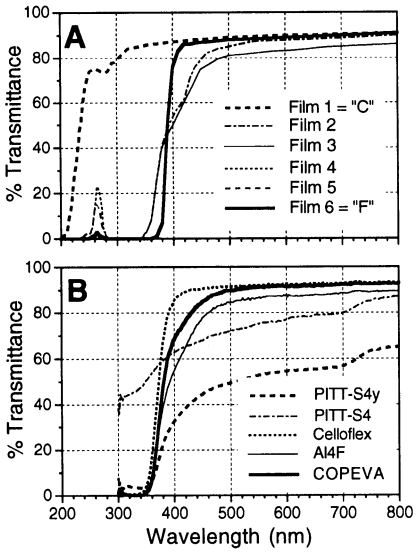

Fig. 1. Transmittance of light in the near-ultraviolet and visible range for plastic greenhouse films: **(A)** films used in the present study; **(B)** films commercially available.

Inoculum production. Strain BC1 of *B. cinerea*, isolated from tomato in a greenhouse, was used throughout this study unless otherwise mentioned. To examine possible differences in the sensitivity of different strains to the inhibition of sporulation by the nUV filter, tests were also conducted with four other strains of *B. cinerea* isolated from the air spora of a tomato greenhouse. Concentrated spore suspensions (ca. 10^7 spores per ml) were kept at –20°C in 40% glycerol, and subcultures were made on PDA medium (Difco Laboratories, Detroit, Michigan) as needed. The inoculum used for both the mycelial growth tests and the spore production tests consisted of 2-mm-diameter mycelial plugs taken from the growing margin of a 2-day-old colony. To ensure homogeneity in the size of the mycelial plugs, they were removed with the help of a sterile cork borer from petri plates containing a constant volume of medium. The 2-day incubation was carried out at 22°C in the dark to avoid possible carryover with the mycelial plug of a (hypothetical) light-induced sporogenic substance, as it has been shown that even very short irradiation periods may lead to subsequent sporulation of a colony (16).

Spores used in the germination tests were collected from colonies on PDA medium after 10 days of incubation at 22°C in the dark. They were suspended in sterile distilled water, and their concentration was adjusted to ca. 10^4 spores per ml.

Quantification of spore germination and mycelial growth. Tests were conducted in vitro on PDA medium. Mycelial growth was assessed by measuring the diameter of colonies developing from a mycelial plug (obtained as described above) placed in the center of the plates. To evaluate the rate of spore germination, aliquots of the spore suspension (0.5 ml) were spread on the surface of the medium. For a given treatment, three to four replicates of at least 100 spores were examined after 24 h. For both tests, the petri plates were placed in trays, each covered with the control film or a film treated to absorb nUV light.

All petri plates used in this study were clear polystyrene plates (Greiner Labortechnik, Frickenhausen, Germany). They were always used with the covers on to avoid dehydration of their contents during incubation. Such plates were used because of the high transmittance of nUV light by polystyrene: it is close to 100% for wavelengths 400 nm and above, 90% near 350 nm, 80% near 320 nm, and it drops sharply below 300 nm, with a lower limit at 260 nm (data provided by the manufacturer).

Incubation took place in a growth chamber at 18°C (darkness) and 24°C (light) with a photoperiod of 14 h. The trays were placed 95 cm below a ceiling of 16 cool-white fluorescent tubes (Philips TLM 40W, Philips, France) and received a total radiation of 65 $\mu mole \cdot m^{-2} \cdot s^{-1}$.

Quantification of spore production. Tests were conducted in vitro on PDA medium and in vivo on stem cuttings, cotyledons, and flowers. The volume of PDA was standardized at 15 ml per 9-cm-diameter petri plate to avoid variability in the amount of nutrients available to the fungus. Stem cuttings, 2 cm long, were excised from tomato plants cv. Monalbo, melon cv. Védrantais, and cucumber cv. Marketer. The plants were grown in a greenhouse and used at an age of 12 weeks (old tomatoes) or 5 weeks (young tomatoes, melon, and cucumber). Cucumber cotyledons were picked fully expanded, 10 days after sowing. Sporulation on tomato flowers was quantified on whole, freshly opened flowers, or on dry residue (petals, stamens, and style) collected 1 day after onset of wilting. For a given species and type of organ, care was taken to select plant material as homogeneous as possible in size and fresh weight. The plant organs were placed in sets of five on sterile water-soaked filter paper (Durieux N° 127, Paris) in 9-cm-diameter petri plates.

Table 1. Effect of incubation under different ultraviolet-filtering films on *Botrytis cinerea* strain BC1 grown on potato-dextrose agar medium

Film[w]	% Germination after 24 h[x]	Colony diam. after 72 h (mm)[y]	Spore prod. ($\times 10^3$) after 9 days[z]
1 = control C	98.1 ab	68.7	119,133 ± 17,564
2	93.3 b	74.3	0 ± 0
3	99.7 a	73.3	0 ± 0
4	98.1 ab	73.3	13 ± 13
5	99.2 ab	71.0	13 ± 13
6 = F	97.1 ab	72.7	0 ± 0

[w] See Figure 1 for characteristics of the films.
[x] Numbers followed by different letters are significantly different ($P < 0.05$) according to Duncan's multiple range test on arcsine transformed data.
[y] No significant differences ($P = 0.15$) according to Fisher's F test.
[z] Data expressed as numbers of spores per petri dish ± standard error of the mean.

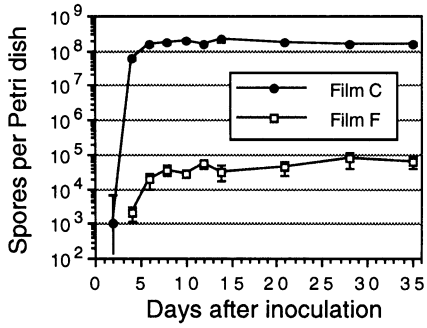

Fig. 2. Kinetics of spore production by strain BC1 of *Botrytis cinerea* on potato-dextrose agar medium incubated under a standard polyethylene film (control film C = film no. 1) and a polyethylene film containing additives that absorb near-ultraviolet light (film F = film no. 6). Error bars indicate the standard error of the mean.

Inoculation was performed by depositing a mycelial plug (obtained as described above) in the center of each PDA plate or plant organ. For each experiment, sets of five PDA plates or plant organs were incubated in trays covered with the films to be tested. Incubation took place in a growth chamber as described above.

To assess spore production on PDA medium, 5 ml of 0.1% Tween 80 (Sigma Chemical Co., St. Louis, Missouri) solution were poured on each plate, and the surface of the colony was gently rubbed to detach all aerial mycelium and conidiophores from the agar. The suspension was transferred to a flask, and another 5 ml of solution was used to rinse the surface of the agar and remove any remaining spores. The final suspension was vortexed for 30 s with 5 g of glass beads (2.5 mm diameter) to separate the spores. With plant material, the plant organs were directly transferred to flasks containing 5 or 10 ml of Tween solution and 5 g of glass beads. Spore concentration was assessed with the help of a hemacytometer following appropriate dilutions, and results were expressed as numbers of spores per plate, per organ, or per gram of fresh tissue.

RESULTS

Comparison of UV-absorbing film samples: effect on the development of *B. cinerea* on PDA medium. The germination rate of *B. cinerea* conidia on PDA medium was high (>93%) under all six films (Table 1). While films containing nUV-absorbing additives could not be distinguished statistically from the control, significant differences ($P > 0.05$; Duncan's multiple range test on arcsine transformed data) were found between films 2 and 3 (Table 1). No significant difference was found on colony diameter after 72 h ($P > 0.15$; Fisher's F test). Spore production after 9 days of incubation was much reduced under nUV-absorbing films as compared to the control (Table 1). No spores were detected for three of the films. Based on these data and on the light transmission properties of the nUV-absorbing films, film 6 was selected for further studies. It will be referred to as film F for the remainder of this paper, while control film 1 will be referred to as film C.

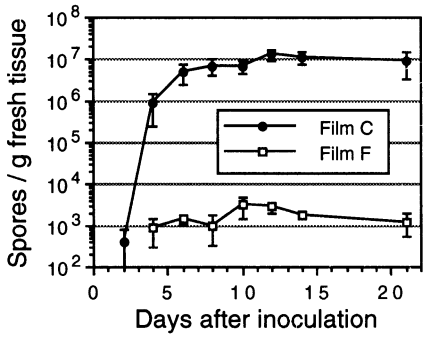

Fig. 3. Kinetics of spore production by strain BC1 of *Botrytis cinerea* on tomato stem cuttings incubated under a standard polyethylene film (control film C = film no. 1) and a polyethylene film containing additives that absorb near-ultraviolet light (film F = film no. 6). Error bars indicate the standard error of the mean.

Kinetics of spore production on PDA medium. Striking morphological differences were observed between colonies growing on PDA under nUV filtering film F and control film C. In all plates incubated under film C, the colonies produced a thick layer of conidiophores. Conidia were first observed 2 days after inoculation (DAI), and production reached a plateau after 6 DAI (Fig. 2). Under film F, the colonies produced abundant aerial mycelium, but very few conidiophores were observed with a dissecting microscope. Conidia were first detected at 4 DAI, and their production reached a plateau after 6 to 8 DAI (Fig. 2). Spore production under film F was sharply reduced in comparison with the control film. It remained less than 0.05% of that under film C for the duration of the experiment.

Kinetics of spore production on tomato stem cuttings. Spore production on tomato stem cuttings was also strongly affected by the type of film. Cuttings incubated under film C rapidly disappeared under a thick mat of fertile conidiophores, whereas those under film F were covered with abundant aerial mycelium showing very scant fructification. The kinetics of spore production under either film (Fig. 3) closely resembled that observed on agar medium. Sporulation on stem cuttings was strongly inhibited under film F and remained less than 0.05% of that of the control starting 4 DAI. The data collected beyond 21 DAI were not used, because spore-forming phyllosphere contaminants (such as *Trichothecium roseau* (Pers.:Fr.) Link, and *Rhizopus stolonifer* (Eremb.:Fr.) Vuill.) developed on the decayed tissue and interfered with the quantification of *B. cinerea*. Attempts were made to surface disinfest the stems prior to the experiments, but this treatment was abandoned because it interfered with the development of *B. cinerea* under both types of films (data not shown).

Spore production on other plant tissues. Spore production was sharply reduced under film F on all plant material tested (Table 2). Because large differences in weight of plant tissue were observed among different types of organs and different species (data not shown), no attempt was made to compare directly the spore counts on different types of organs. Rather, the efficiency of film F in inhibiting sporulation was compared by computing the ratio of spore counts under film C and film F. It differed markedly among host

Table 2. Effect of incubation under a UV-filtering film on spore production by *Botrytis cinerea* strain BC1 on different plant tissues

	Spore counts ($\times 10^3$) per organ under control film C[w]	Spore counts ($\times 10^3$) per organ under nUV-filtering film F[w]	Ratio C/F[x]
Tomato stem[y]			
Young plants	15,702 ± 1,779	6 ± 3.6	2,617
Old plants	15,282 ± 5,201	18 ± 6.8	849
Melon stem	9,280 ± 1,207	7 ± 2.4	1,326
Cucumber stem	8,360 ± 1,254	14 ± 4.5	597
Tomato flowers[z]			
Dry	7,390 ± 1,043	122 ± 60.1	61
Fresh	12,398 ± 1,009	571 ± 78.4	22
Cucumber cotyledons	50,080 ± 1,116	3,192 ± 261.6	16

[w] Data are expressed as numbers of spores per 2-cm stem cutting, flower, or cotyledon ± standard error of the mean (five replicates). Spore production was assessed 7 days after inoculation.
[x] Ratio of spore counts under film C over spore counts under film F.
[y] Young plants: 5 weeks old; old plants: 12 weeks old.
[z] Dry flowers = petal and stamen residues; fresh = whole freshly opened flowers.

Table 3. Differential inhibition of spore production by a UV-filtering film on four strains of *Botrytis cinerea* growing on tomato tissue

	Tomato stem cuttings			Tomato flowers		
Strain	Film C[w]	Film F[x]	Ratio C/F[y]	Film C	Film F	Ratio C/F
M3	10,709[z] a	30.0 a	357	99,892 a	1,337.8 a	75
M4	6,919 a	29.6 a	234	119,487 a	4,781.6 a	25
M10	21,194 a	3.5 b	6,143	169,893 a	797.5 a	213
M11	20,661 a	3.4 b	6,095	103,588 a	2,844.4 a	36

[w] Film C: control film no. 1.
[x] Film F: film no. 6, absorbing near-ultraviolet radiation.
[y] Ratio of spore counts under film C over spore counts under film F.
[z] Data are expressed as thousands of spores produced per gram of fresh tissue at 7 days after inoculation. Within a column, numbers followed by different letters are significantly different ($P < 0.05$) according to Fisher's F test followed, if applicable, by Duncan's multiple range test.

species, plant age, and type of organ (Table 2). The efficiency of film F was greater on young tomatoes than on melon or cucumber stems, and smallest on tomato flowers and cucumber cotyledons.

Differential inhibition of spore production for different strains of *Botrytis cinerea*. Spore production by four isolates from a tomato greenhouse was quantified at 7 DAI on stem cuttings from 5-week-old plants and on fresh tomato flowers, and expressed as the number of spores per gram of fresh tissue (Table 3). On stem cuttings, the isolates did not significantly differ in spore production under film C (Fisher's F test on log-transformed data; $P > 0.05$). Under film F, however, two isolates (M3 and M4) produced approximately 10 times more spores than the others (Table 3). The inhibition efficiency of film F, as measured by the C/F ratio, was reduced close to 20-fold for these two isolates. On tomato flowers, no significant differences were found among isolates for spore production under either film. As observed earlier for isolate BC1, the inhibition efficiency of Film F was lower on flowers than on stem tissue (Table 3). The reduction in efficiency was larger for isolates M10 and M11 than for the others: C/F ratios were 5-, 9-, 29-, and 169-fold lower on flowers than on stem tissue for isolates M3, M4, M10, and M11, respectively.

DISCUSSION

Historically, much effort has been devoted to the study of the effect of light on spore production in vitro by *B. cinerea*. This work was reviewed by several authors (3,9,15). In contrast, similar information for experiments using plant tissue is scant or lacking. In the present study, the incubation of *B. cinerea* under a film containing additives that absorb near-ultraviolet light below 380 nm (film F) resulted in a considerable inhibition in spore production both on an agar medium and on plant tissue. The efficiency of this experimental film on agar medium cultures was comparable to that reported in earlier in vitro studies: ratios of spore counts under control film to counts under film F were ca. 2,000 on PDA medium (Fig. 2), compared to ca. 500 for the most efficient films used in other studies (10). Furthermore, the kinetics of spore production over several weeks after inoculation demonstrated that the altered light spectrum was associated with an inhibition, rather than just a delay in sporulation. This persistence over time of the efficiency of the nUV-filtering film may be a much desired feature for use in agriculture, particularly for greenhouse crops such as tomatoes, which remain in culture for several months.

The efficiency of nUV-filtering film F in inhibiting spore production differed depending on the host species and the plant organ. The fact that it was lowest on flowers and cotyledons, two nutrient-rich organs, supports the hypothesis that nutritional factors may interfere with the effect of light for spore production by *B. cinerea*. These results also lead to speculation that factors affecting the nutritional status of the various plant organs might have an indirect effect on the efficiency of the nUV films in reducing spore production. To evaluate the use of such films for the control of gray mold on greenhouse vegetables, more work is needed to determine the possible effect of fertilization schemes and varietal differences. The epidemiological consequences of the differential inhibition by the nUV film of spore production on flowers and on stems of diseased plants must also be examined. Although flowers represent a small fraction of the plant biomass in a tomato greenhouse, colonization of flower residues by *B. cinerea* is common. This source of inoculum may not be totally negligible, considering that under film F, certain isolates of *B. cinerea* may produce up to 837 times more spores on 1 g of flower tissue than on 1 g of stem tissue (Table 3).

Different strains of *B. cinerea* growing on tomato stem tissue were not equally affected by the altered light spectrum provided by film F. Two strains were less sensitive to the nUV film and produced nearly 10 times more spores than the other strains under film F. While the reduction in spore production provided by the nUV film for those less sensitive strains was still in the order of magnitude of 250- to 300-fold, this aspect clearly deserves more attention, as it may have important practical consequences.

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