Fungal Photomorphogenesis: A Basis for the Control of Foliar Diseases Using Photoselective Covering Materials for Greenhouses

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One of the consequences of the steady rise in the standard of living in western society is the rapid expansion of the greenhouse industry throughout the world. Cultivation under cover enables year-round supply of a variety of vegetable, ornamental, and fruit crops. It also enables many crops to be produced in regions where they cannot grow outdoors at all, although protected winter production of many crops in cold regions is highly energy-consuming. The decrease in transportation costs and transit time, coupled with extended shelf life of many products, has prompted a shift in production towards areas of milder climates. Even in such areas out-of-season production of several important crops is impossible without protection. Transparent thermoplastic films can supply the required protection at relatively low cost. Many crops are grown during winter in unheated walk-in tunnels in regions with mild winters. Usually, only passive ventilation is provided in walk-in tunnels, and the greenhouse covering materials are designed to moderate nighttime heat losses, while allowing maximum photosynthetically active radiation (PAR) into the greenhouse during the day.

The warm and humid environment in a greenhouse is ideal for the development of many diseases, the most common diseases of which are gray mold caused by *Botrytis cinerea* Pers., downy mildew caused by *Pseudoperonospora cubensis* (Burk. Curt.) Rostow, and alternaria blight caused by *Alternaria solani* Sorauer (Jarvis, 1992).

The spread of plant diseases depends on complex interactions among pathogen, host

and the environment. The dominant environmental factors involved in the pathogenesis of foliar diseases are temperature, light, relative humidity (RH), and their interactions. Air and leaf temperatures, vapor pressure deficit (VPD), air velocity, and evapotranspiration rate affect the likelihood of condensation and the duration of surface wetness. Marios et al. (1988), for example, demonstrated that VPD is linearly and inversely correlated with susceptibility of rose (*Rosa hybrida* L.) flowers to gray mold under controlled temperature conditions. Leaf wetness duration was not assessed in this study. Elad (1989) showed that germination of *B. cinerea* spores is associated with duration of wetting of rose petals.

Yunis et al. (1994) modelled the microclimatic conditions that favor the outbreak of gray mold on cucumbers (*Cucumis sativus* L.) and showed that the unheated, passively ventilated, walk-in tunnel provides even more favorable conditions for foliar pathogens; it is wind-free at night and during part of the day, and the RH is frequently very close to 100% at night. The risk of water condensation in a nonheated greenhouse is higher than in a temperature-controlled greenhouse. Heating and ventilation cannot be used to control climate in walk-in tunnels.

Sporulation, spore production, spore viability and germination, and mycelium growth are the key processes in the life cycle of all fungi and in the epidemiological spread of fungal diseases. These morphogenetic stages are strongly affected by environmental factors such as light, humidity, and temperature. Breaking the cycle of epidemic development, at any of its stages, is a key requirement in any integrated pest management (IPM) strategy for fungal pathogens. This can be accomplished by direct action against the causative organism, e.g., elimination of spores and inhibition of their germination by prophylactic fungicides, or by manipulation of the environment, e.g., by modifying the sunlight spectrum by the materials used for greenhouse covering (Raviv and Reuveni, 1995). Combinations of physical and chemical means are usually more effective than either of these approaches alone.

The continuous use of a narrow range of fungicides in a monocrop system exerts intensive selection pressure for fungicide-resistant races of pathogens. Resistant strains have been

reported for benomyl and metalaxyl (Wolfe, 1981). Once a resistant strain appears, a common practice among growers is to increase the concentration and/or application frequency of the fungicides. The increased selection pressure leads to the establishment of highly resistant pathogen populations and to the need for new, more aggressive (and frequently more expensive) fungicides (Dekker, 1987; Skylakakis, 1983).

The use of increasing dosages of chemicals has negative effects on both the growers' net profit and health. The growing concern about chemical hazards to humans, to nontarget beneficial organisms and to the ecological balance leads to an extensive search for alternative pest control strategies to replace the use of synthetic chemicals. These issues and others that are related to the health and management of greenhouse-grown crops have been thoughtfully discussed by Jarvis (1992) and by Nicot and Baille (1996).

The nonchemical control of diseases in the greenhouse is sometimes difficult. Thoughtful manipulation of the environment is required, so that, despite the availability of favorable conditions for an epidemic, infection may be prevented by a specifically "manipulated" unfavorable condition.

The initial infection by most foliar pathogenic fungi in the greenhouse usually occurs in a film or a drop of water on the plant tissue, and can be prevented (at a certain energetic cost) by maintaining the canopy temperature above dew point, thus preventing spore germination. However, commercial greenhouses in Mediterranean climates are generally unheated, and therefore keeping canopy temperature above the dew point is difficult.

Light controls the pathogenic processes of several foliar diseases. Light transmitted through the greenhouse covering is therefore a possible controllable factor in the epidemiology of foliar diseases in both heated and unheated greenhouses. Careful modification of the light spectrum may effectively reduce spore production and germination.

This review presents the potential use of greenhouse covers as light filters designed to affect the life cycle of plant pathogens; its authors, in close collaboration with the plastics industry in Israel, are involved in the implementation of this approach at the Newe Ya'ar Research Center.

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LIGHT QUALITY AND FUNGAL GROWTH

Two signal-transducing photoreceptors—phytochrome (absorbing in the 600 to 800-nm band) and the blue-absorbing photoreceptor (absorbing in the 300 to 500-nm band)—are active both in higher plants and in fungi (Kendrick and Kronenberg, 1986). Plants and their fungal pathogens have adapted through evolution to environmental fluctuations and to changes in the natural light spectrum. This has enabled them to survive and flourish, even in habitats where the radiation appears distinctly unfavorable. In fungi, light acts in many cases as a stress-inducing agent and results in morphogenetic changes, including spore production and germination.

Several reviews on the requirement for monochromatic light for sporulation of many fungi have been published since the early sixties (Furuya, 1986; Gressel and Rau, 1983; Kumagai, 1984; Leach, 1971). Sporulation responses to light vary among species and environmental conditions. Ultraviolet (UV) radiation, especially in the 280 to 320-nm waveband (UV-B), affects the sporulation of many pathogenic fungal genera such as *Alternaria*, *Botrytis*, *Cercospora*, *Cercospora*, *Fusarium*, *Helminthosporium*, *Stemphylium*, and *Trichoderma* (Kumagai, 1982; Leach, 1962, 1967; Oncsirosan and Bantari, 1969; Panagopoulos et al., 1992). Blue light may have an inductive effect on sporulation of *Trichoderma viride* Pers.: Fr. g (Kumagai and Oda, 1969b) and *Verticillium agaricinum* Link (Corda) (Osman and Valadon, 1979) or an inhibitory effect, as reported for *Alternaria cichorii* Nattrass (Vakalounakis and Christias, 1981), *Alternaria tomato* (Cooke) G.F. Weber (Aragaki, 1962; Kumagai and Oda, 1969a), and *Helminthosporium oryzae* Breda de Haan (Honda and Sakamoto, 1968). Induction and inhibition of sporulation in *Botrytis cinerea* have been reported for UV-B and for blue light, respectively (Tan, 1974, 1975a, 1975b; Tan and Epton, 1974). Opposing reactions of blue light and of UV radiation in conidiophore production (Kumagai, 1982) and in the terminal phase of sporulation (Honda et al., 1968) in fungi have been reported. Illumination with blue light reportedly inhibits sporangial production of *Pseudoperonospora cubensis* in infected cucumber leaves (Inaba and Kajiwar, 1971).

Short pulses of monochromatic red and far-red light are sufficient to inhibit or enhance sporulation in *B. cinerea*. Although not all isolates of the fungus sporulate under the control of light, Tan and Epton (1973) clearly demonstrated that sporulation occurring in darkness can be inhibited by subsequent exposure to blue light. This inhibition is initiated by conversion of a mycochrome from the M_B form, which induces sporulation, to the M_{NIV} form, which inhibits it (Tan, 1974). For this conversion, continuous narrow-band illumination is needed to obtain almost total inhibition of sporulation. (Tan, 1975a, 1975b). The quantum efficiency needed for such a conversion, however, is lower than that needed for the reverse process (Tan, 1975a, 1975b).

Fig. 1. Light transmission spectra of several common greenhouse covers. (A) Glass; (B) PVC film; (C) UV stabilized commercial polyethylene (PE) film; (D) UV-B absorbing PE film.

Fig. 2A. Severe damage caused by gray mold on tomatoes grown under PE films with high UV transmissivity.

Fig. 2B. The effect of UV-absorbing PE film on the control of gray mold on greenhouse-grown tomatoes.

EARLY USE OF LIGHT TO CONTROL PATHOGENS

Hite (1973) was probably the first to suggest that modifying light quality could be used to reduce the inoculum potential of *B. cinerea* in the greenhouse. Honda et al. (1977) compared a greenhouse covered with UV- (shorter than 390 nm) absorbing vinyl film to a control greenhouse covered with non-UV-absorbing film and reported partial control of gray mold on cucumber and tomato (*Lycopersicon esculentum* Mill.). UV-absorbing films reportedly inhibit the development of apothecia of *Sclerotinia sclerotiorum* (Lib.) Dby [the causative organism for eggplant (*Solanum melongena* L.) and cucumber stem rot] (Honda and Yunoki, 1977), sporulation of *Alternaria dauci* (Kuhn) Groves & Skolko [causative

organism for leaf blight of carrot (*Daucus carota* L.)], *A. porri* (Ellis) Cif. [alternaria leaf blight of Welsh onion (*Allium fistulosum* L.)], *A. solani* (early blight of tomato), and *Botrytis squamosa* Walker [leaf blight of Chinese chive (*Allium tuberosum* Rotter)] (Sasaki et al., 1985). In *S. botryosum* Wallr., which belongs to another taxonomic group, sporulation induced by blue light was nullified under vinyl UV-absorbing films. (Sasaki et al., 1985; Vakalounakis, 1991). The data presented in these reports indicate a reduction in the blight severity on flowers, fruits, and stems of eggplant and cucumber caused by *S. sclerotiorum* (Honda and Yunoki, 1977), gray mold on cucumber and tomato (Honda et al., 1977), and *Alternaria* and *Stemphylium* leaf spots of various vegetable crops and leaf blight of Chinese chive (Sasaki et al., 1985). Sasaki et

Fig. 3. Light transmission PE films with (2, 4, 6) or without (1, 3, 5) a blue pigment that absorbs part of the yellow-green spectrum (530–600 nm), in combination with various levels of UV-B (280–320 nm) absorbance. (1) Without UV Absorber (UVA); (2) without UVA + blue pigment; (3) commercial sheet with partial UV absorbance; (4) same as 3 + blue pigment; (5) with UV absorber blocking most of UV-B transmittance; (6) with UV absorber blocking most of UV-B transmittance + blue pigment.

al. (1985) claimed that the active part of the UV spectrum in reduction of sporulation in *B. cinerea* is 300 to 340 nm. Similarly, control of early blight of greenhouse tomato caused by *Alternaria solani* has been achieved through inhibition of sporulation by means of UV-absorbing vinyl film (Vakalounakis, 1991). However, Jordan and Hunter (1972) found higher, rather than lower, levels of *Botrytis* infection on strawberries (*Fragaria grandiflora* Ehr.) grown under several colored polyethylene (PE) films than on those under clear PE films or glass. The blue PE may have caused two synergistic phenomena related to *Botrytis* development—etiolation of the plants, and decreased vapor pressure deficit and temperature—both of which may play a role in the enhancement of the disease in this particular case.

The possibility that inhibition of sporulation of *B. cinerea* by UV-absorbing PE films is strain-specific was raised by Nicot et al. (1996) as a result of in vitro experiments. It was postulated that a selection pressure, exerted by absence of UV-B radiation within the green-

house may lead to the establishment of virulent strains that do not require UV-B for sporulation. However, the authors state that the accumulated experience so far does not appear to warrant extreme concern.

Subsequent reports have suggested that the ratio between the intensities of the inductive and inhibitory parts of the solar spectrum may play an important role in keeping the biological balance between certain hosts and their specific (virulent) pathogens, and that modification of the spectral transmissivity of greenhouse covering materials is a practical alternative method for reducing spore production and germination that need not involve excessive interference with PAR. A similar trend by Peterson et al. (1988) showed that inhibition of sporulation of *B. cinerea* in container-grown Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings in greenhouses covered with fiberglass or polyethylene requires a light intensity at 430 to 490 nm that exceeds that in the waveband that induces sporulation (300 to 420 nm).

RECENT IMPROVEMENTS

During recent years, modifications of the commonly used greenhouse covering materials have been suggested and studied (Reuveni et al., 1994). An example is the modified polyethylene (PE) designed to prevent the phenomenon of blackening of rose petals (Raviv et al., 1988); this PE also affects the behavior of *Bemisia tabaci* (Gennadius) (Antignus et al., 1995) and helps to restrict virus diseases transmitted by this insect.

The spectral characteristics of the most commonly used greenhouse cover materials are shown in Fig. 1. Note that glass is not fully opaque to UV-B radiation (Fig. 1a), reinforced PVC absorbs all UV radiation (Fig. 1b), and commercial UV-stabilized PE is UV transparent (Fig. 1c). UV stabilizers that act as free-radical scavengers (hindered amine light stabilizers, or HALS) are currently added during the production process to all plastic films intended for greenhouse use. These stabilizers prevent the rapid degradation of the films, but transmit enough UV light to allow sporulation of fungi such as *B. cinerea*. Adding a UV absorber to the film results in complete absorption of UV-B (Fig. 1d).

In previous studies by Reuveni, Raviv, and coworkers, spectrally modified PE sheets with various ratios of blue : UV-B transmission were investigated as to their effects on the epidemiology of gray mold caused by the fungus *B. cinerea*. Sheets of PE having a high blue : UV transmittance ratio significantly reduced sporulation of *B. cinerea* (Reuveni et al., 1989), and slowed the development of gray mold (Figs. 2 A and B) on greenhouse-grown tomatoes under PE sheet (Reuveni and Raviv, 1992). The pigments tested in this study absorbed various fractions (up to 100%) of the UV-B waveband and some of the green-yellow waveband (530 to 600 nm). Similar results were reported for roses by Ramirez and Torres (1995).

In Winter 1990, the use of blue polyethylene sheets, rather than commercial IR-absorbing sheets, on commercial walk-in tunnels markedly reduced spread of downy mildew caused by *Pseudoperonospora cubensis* on cucumbers. Under the blue sheet the disease appeared only on the young leaves at the top of the plants, whereas it attacked lower leaves earlier under the IR-absorbing control sheet. This finding led us to a continuing effort to develop a new PE sheet for the control of downy mildew on greenhouse-grown cucumbers, for which the use of spectrally modified films had not been investigated. This research has been conducted over four seasons under both growth chamber and unheated greenhouse conditions, using several PE types, with or without a blue pigment that absorbs part of the yellow-green spectrum (530 to 600 nm), and with several levels of UV-B absorbance. The sheets were manufactured by Ginegar Plastics, Ginegar, Israel, and contained an infrared absorber. Their light transmittances are presented in Fig. 3. Spectroradiometric measurements under sunlight revealed similar light transmittance values.

Fig. 4. The effects of five photosensitive PE films on downy mildew development in cucumbers at three locations (A, B, C) in Israel in 1993. Spectral transmittance of the films is presented in Fig. 3.

We tried to study the effects of several combinations of green-yellow and UV-B absorbing films on two major stages of the life cycle of the pathogen—colonization and sporangium formation. Absorption of UV-B was effective in inhibiting sporangium formation only in combination with absorption of green-yellow wavelengths, but was not effective during the colonization stage. Reducing the intensity of green-yellow light reaching the host-parasite system affected both development stages under growth chamber and greenhouse conditions, and significantly reduced the severity of downy mildew of cucumbers under Mediterranean conditions (Fig. 4, 5 A and B). Despite the reduction in PAR by light absorption in the green-yellow range, yields were not reduced, probably because of the blue films reduced disease severity (Reuveni and Raviv, 1997). We recommend that any commercial sheet based on this approach should be carefully constructed so that PAR absorption is minimal and mainly at wavelengths that are less effective in photosynthesis (Inada, 1976). In practice, a compromise is

necessary between the requirements for 1) wavebands that suppress fungal colonization and sporulation vs. 2) maximal PAR needed for yield.

PROSPECTS FOR THE FUTURE

Currently PE films can be produced with tailor-made spectral characteristics. In some cases these films can be used to reduce the damage caused by diseases and the chemical treatments required to control them. The width of the films is >16 m and their lifetime is up to 3 years. They can consist of two to seven different layers.

The main advantage of a multilayer PE film is the possibility of protecting various sensitive additives, including pigments, from damage. For example, a water-soluble pigment could be sandwiched between two hydrophobic PE layers to prevent leaching by rain or condensation. Similarly, a UV-sensitive pigment could be protected by a UV absorber incorporated in the outer layer.

The increase in the stratospheric transmit-

tance of UV radiation (Bowman, 1988; Heath, 1988; Worrest and Caldwell, 1988) may intensify the risk of UV-induced sporulation in fungi. This possibility should be prominent among further considerations regarding greenhouse pest management.

We suggest that the spectral requirements of key processes in the life cycles of all major greenhouse diseases be investigated, to provide information for research similar to that presented here. These would undoubtedly include additional combinations of pigments, since different fungi may have different spectral needs.

It is hoped that growers soon will be able to buy customized layered films with characteristics that suit not only particular crops, climates, and areas, but also specific pathogens.

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Fig. 5A. The effect of photosensitive PE sheet #5 (with UV absorber blocking most of UV-B transmittance; for spectral transmittance see Fig. 3) on the control of downy mildew on cucumbers. Photographs were taken at the last evaluation of the experiment presented in Fig. 4 at Ahituv.

Fig 5B. The effect of photosensitive PE sheet #6 (with UV absorber blocking most of UV-B transmittance + blue pigment; for spectral transmittance see Fig. 3) on the control of downy mildew on cucumbers. Photographs were taken at the last evaluation of the experiment presented in Fig. 4 at Ahituv.

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