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Managing *Botrytis* in Greenhouse-Grown Flower Crops

The floriculture industry is extremely diverse, including bedding plants, bulb crops, cut flowers, potted plants, and perennials. It is the fastest growing component of agriculture in the United States (7), with cash receipts for operators with $100 million or more in gross sales totaling $2.83 billion in 1993 (1). Greenhouse-grown floricultural crops are constantly threatened by the plant-pathogenic fungus *Botrytis cinerea* Pers.:Fr. (teleomorph *Botryotinia fuckeliana* (de Bary) Whetz.), which causes gray mold or Botrytis blight. The wet, humid greenhouse environment favors rapid growth and prolific sporulation of *B. cinerea.* While much is known about the general biology of *Botrytis* (6,33), gray mold continues to cause significant losses at all stages of floriculture production. Our objectives are to review recent work on the epidemiology and control of *Botrytis* on greenhouse-grown floricultural crops and offer an integrated approach to disease management.

Disease Symptoms

Symptoms of *Botrytis*-caused diseases include leaf spots; blighting; stem cankers; rots of corms, rhizomes, tubers, and seeds; and damping-off of young seedlings. Blighting may affect leaves (Fig. 1A and B), petioles, blossoms (Fig. 1C and D), and stems (Fig. 1E and F) and is the most common symptom caused by *Botrytis.* Beginning as small, water-soaked spots on leaves, stems, or blossoms, the spots coalesce rapidly, affecting large portions of tissue. Infection of blossoms by *B. cinerea* may cause premature fading and dying of petals, which then drop. Leaf blight may be initiated when infected tissue, such as blighted blossoms, falls onto healthy leaves (Fig. 1G). Stem blight typically begins in a broken or cut stem surface and progresses downward, causing a dieback of the entire stem; in severe cases, the blight extends into the base of the plant and kills it (Fig. 1H and I).

Several important floricultural crops are susceptible to *Botrytis,* including chrysanthemums, poinsettias, New Guinea impatiens, and tetraploid and selected diploid geranium *(Pelargonium* spp.) cultivars, all of which are propagated asexually by cuttings. Disease caused by *B. cinerea* has been implicated as a limiting factor in the storage and shipment of nonrooted and rooted cuttings (5). When cuttings are removed from stock plants, wounds formed at the base of the cutting provide suitable infection sites for *B. cinerea,* which may cause a stem rot and plant death. Stem blight is a common disease caused by *B. cinerea* on stock plants and may decrease the number of growing points that can be removed as cuttings. Leaf blight is also a problem and occurs on wounded, senescent, or stressed leaf tissue.

In seed-propagated ornamentals, *Botrytis* may cause a postemergence or preemergence damping-off. In statice (*Limonium* sp.), *B. cinerea* persists in old flower parts surrounding the seed and penetrates the emerging seedling (59). Bedding plants are produced as plugs in flats that may have hundreds of cells, each containing as little as 1 cm^3 of growing mix. Because plug production requires a high degree of crop uniformity and quality, even a low percentage of disease is unacceptable.

Botrytis frequently causes storage blights of cut flowers, including standard carnations, *Euphorbia fulgens*, gerbera, and roses. When cut roses are stored under high humidity, petal spotting caused by *B. cinerea* may progress rapidly to blighting of the entire flower head (Fig. 1J and K). Gerbera flower blight caused by *B. cinerea* is a limiting factor in production, with symptoms often occurring during storage or transport and shipment, when temperature fluctuations result in high humidity and condensation on the flowers (53).

B. cinerea sporulates readily on necrotic and diseased tissue, appearing as a fuzzy or powdery gray mold (Fig. 1L). When sporulation of *B. cinerea* is extensive on the plant, a cloud of gray conidia typically can be observed if the plant is physically disturbed. This prolific sporulation can be used to distinguish Botrytis blight from blights caused by other plant pathogens.

Favorable Hosts

Certain floricultural crops and plant parts are highly susceptible to *Botrytis.* In northeastern U.S. commercial greenhouses in which *Botrytis* populations were monitored for fungicide resistance (45), geranium (*Pelargonium* spp.) leaves, flowers, and leaf stipules; primula (*Primula* spp.) flowers; and the senescent leaves and true flowers of poinsettia (*Euphorbia pulcherrima*) supported abundant conidial production. Many other major floricultural crops are much less susceptible to *Botrytis.* Pritchard (50) found that the proportion of inoculated geranium leaves infected with *B. cinerea* was much higher than that of either inoculated petunia or impatiens foliage under comparable environmental conditions.

Plant maturity also plays a role in susceptibility to *B. cinerea.* Nearly mature poinsettias had an increased proportion of bracts and foliage infected and supporting sporulating *B. cinerea,* suggesting that disease management strategies should be heightened during crop finishing (50). Sirjusingh et al. (56) determined that sporulation incidence in inoculated geranium leaves was high in 1-week-old leaves, declined as leaves aged to 4 weeks, and increased as leaves aged from 4 to 10 weeks. As geranium flowers aged, sporulation of *B. cinerea* increased (56).

Inocula

In many diseases caused by *B. cinerea,* conidia serve as the initial inoculum. Con-

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idia of *B. cinerea* in the greenhouse can originate from sources inside and outside the greenhouse (36). Peak atmospheric conidial concentrations of *B. cinerea* occur in geranium stock-plant and cutting-propagation greenhouses in association with grower activity, including irrigating, spraying pesticides, and harvesting cuttings (27,29). The mechanical action associated with harvesting and shipping cuttings releases and disperses conidia into the greenhouse atmosphere (27,29). Droplets from pesticide sprays and irrigation disperse dry conidia via air shock waves and turbulent currents (31). In addition to mechanical shock, water and spray droplets may trigger the release of conidia by causing a rapid increase and subsequent decrease in the relative humidity of the plant microclimate (31).

When there is little or no grower activity in the greenhouse, atmospheric conidial concentrations of *B. cinerea* in stock-plant greenhouses display a bimodal periodicity, with peak concentrations occurring at approximately midmorning and midafternoon (26). These peak concentrations most typically coincide with a rapid decrease in relative humidity. Jarvis (31) observed that release of *B. cinerea* conidia is maximum when the relative humidity is rising or falling rapidly between 85 and 65%. Only a 5% change in relative humidity within this 20% range is necessary for vigorous hygroscopic movement of the conidiophores, resulting in conidial release. The availability of conidia for dispersal within the greenhouse appears to be influenced by the magnitude of previous dispersals. Very high concentrations occurring on one day may be followed by low concentrations the following day under otherwise suitable dispersal conditions (26).

Where plants are being vegetatively propagated in greenhouses separate from the stock plants, diurnal fluctuations of atmospheric concentrations of *B. cinerea* conidia may be absent (29). This absence may be a result of frequent relative humidity alterations by misting systems operating on varying cycles or by the intense activity of growers in the propagation area, which triggers the release of conidia.

Although conidia can land on plant surfaces and invade immediately, they may remain dormant for at least 3 weeks before germinating (52). Nongerminated conidia adhere to surfaces relatively weakly, ap-

Fig. 1. Symptoms of disease caused by *Botrytis cinerea* on greenhouse-grown floricultural crops: (A) leaf blight on geranium, (B) bract blight on poinsettia, (C) flower blight on carnation, (D) flower blight on chrysanthemum, (E) stem blight on Exacum, (F) stem blight on tulip, (G) leaf blight on geranium (will be initiated by infected blossoms), (H) stem blight on geranium, (I) stem blight that has progressed into the geranium crown, (J) spotting on rose, (K) extensive blighting of rose, and (L) sporulation on snapdragon.

parently by hydrophobic interactions with the substrate (9). If wet for several hours under conditions conducive to germination, conidial germ tubes and appressoria adhere strongly to either hydrophobic or hydrophilic substrata (10). As a result of its persistence on plant surfaces, the fungus can be shipped from greenhouse to greenhouse.

Botrytis conidia or quiescent infections may become active during the postharvest production period due to the physiological or biochemical changes in the plants or the environmental conditions of shipment and storage. Frequently, tight packing of plants reduces air movement and contributes to the environmental conditions necessary for infection by *B. cinerea*. Conidia deposited on leaves during shipping may germinate and infect under the conducive environmental conditions that often occur when shipments are delayed or when plant material is not removed from shipping boxes promptly. If infection begins in the box, it can continue (when conditions are favorable) after plants have been removed from the box and have been potted and placed on greenhouse benches.

When symptomless plant parts from geraniums were evaluated for recovery of *B. cinerea* on the same day the shipments were received, *B. cinerea* was nearly always recovered (5). *Botrytis* was recovered most frequently from the stipules and flower buds. In addition, sporulation of *B. cinerea* was observed on the geraniums within 5 days after shipments of cuttings were received. In a study using field-grown cut flowers including *Alstroemeria*, mums, corn flower, iris, *Leptospermum*, mini- and standard carnations, Shasta daisy, *Gypsophila*, statice, and sweet William, symptomless plant parts were assayed for recovery of *Botrytis* (4). Although symptoms were not evident, *Botrytis* was recovered from iris, mini- and standard carnations, *Leptospermum*, *Gypsophila*, and statice.

Infection can also occur when hyphae grow from infected plant tissue into healthy tissue. Plant parts such as petals and whole senescent flowers, which are easily infected by *B. cinerea*, may drop onto healthy tissue, adhere, and provide a large saprophytic inoculum base. Sirjusingh et al. (56) demonstrated that infection efficiency of *B. cinerea* growing from leaf pieces is 200 times greater than that of conidia. Such inoculum typically is not as dependent on free water for disease establishment as are conidia.

The prevalence and duration of survival of sclerotia in the greenhouse are unknown. In the laboratory, sclerotia readily give rise to mycelia and conidia. It is possible that, following crop-free periods in greenhouses, conidia developing from sclerotia are the initial source of inoculum. *Botrytis* also is known to form thick-walled chlamydospores (60) resistant to drought and bacterial antagonism as well as to nutrient and oxygen deficiency. These, too, may remain in crop debris and give rise to conidia or mycelia when conditions are favorable. However, the introduction of *Botrytis* on new plant material brought into the greenhouse probably overshadows the importance of sclerotia and chlamydospores as sources of the fungus.

Principles of *Botrytis* Management

Sanitation. Infected plant debris should be removed to reduce conidia and vegetative hyphae, which can serve as sources of inoculum. The amount of plant debris within the crop canopy influences atmospheric conidial concentrations, since *B. cinerea* readily sporulates on wounded and senescent plant tissue. In a commercial greenhouse, an increase in wounded and senescent tissue with sporulating *B. cinerea* was associated with increased atmospheric conidial concentrations (27). *B. cinerea* sporulating on necrotic leaves at the base of stock plants grown for cutting production provides a major source of inoculum for infecting geranium stems wounded during harvest of cuttings (27) (Fig. 2A and B). Similarly, the number of airborne conidia of *B. cinerea* trapped increased with the amount of dead gerbera tissue as the crop aged (>6 months) (35). These conidia provided inoculum for flowers, resulting in postharvest blight (34).

Immediate disposal of rogued plant tissue via covered containers may minimize concentrations of airborne conidia (Fig. 3). Such debris typically supports sporulating *B. cinerea* and may litter the benches and floors of the growing or shipping area, allowing continued release and dispersal of conidia. Similarly, plants left over from previously filled orders and being held indefinitely should be removed from the production area. Such mature plants typically exhibit senescent lower leaves with lesions containing sporulating *B. cinerea*. Grower activity near these plants could cause release of significant inoculum for adjacent newly established plants or cuttings. In a study conducted in a commercial greenhouse, *Botrytis* conidia traveled a minimum of 0.762 m (29) by air currents. Jarvis (32) found that conidia-covered water-splash droplets could travel up to about 1 m. Dillon Weston and Taylor (8) found that a single conidia-laden water drop falling onto a *Botrytis*-infected leaf could contaminate an area approximately 2.5 m^2, and a leaf exposed to a rain shower lasting 45 min contaminated an area more than 32 m^2.

Sanitation alone, however, is insufficient to control *B. cinerea* because the fungus spreads and increases rapidly through repeated sporulation cycles (48). Under favorable environmental conditions, 2.0×10^4 to 6.0×10^4 conidia per cm^2 can be formed on infected geranium tissue (R. J. Vali and G. W. Moorman, *unpublished*) and 10^5 to 10^7 conidia per cm^2 on strawberry leaves (57).

Environment. High relative humidity (>93%) and free water at the infection site within the canopy are required for invasion by *B. cinerea*. These conditions are common in most greenhouses. Reducing the occurrence of free moisture on the plant

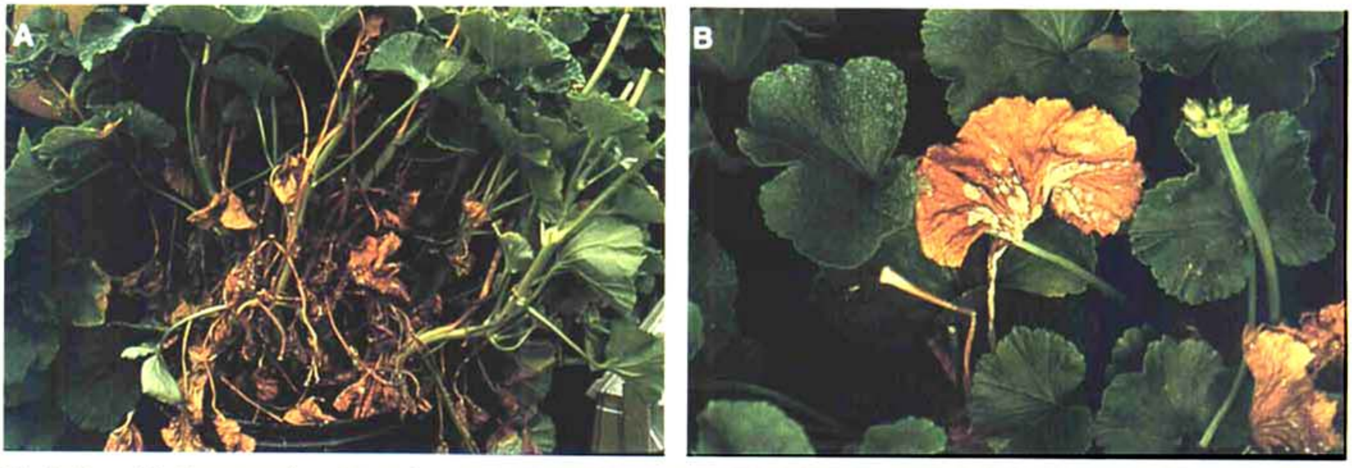

Fig. 2. (A and B) Close spacing of geranium stock plants results in senescence of the lower leaves, which can be readily infected by *Botrytis cinerea*.

surface and the accompanying gray mold may be accomplished via infrared heating systems or trickle, drip, trough, and flood and drain irrigation systems. Reducing relative humidity within the greenhouse may be achieved by venting and heating late in the afternoon to remove humid air before sunset.

It is critical to reduce the relative humidity within the canopy by providing good air flow within the crop. Arranging pots in rows parallel to the air flow with space between rows helps reduce the relative humidity within the crop canopy and results in a less-suitable environment for germination, infection, and sporulation of *B. cinerea* conidia (58). Increasing the space between plants creates a less-dense plant canopy and allows better light penetration, thereby reducing senescence of the lower leaves and removing potential infection and sporulation sites.

An excellent method of reducing the relative humidity within the canopy is to channel heated air under lath, wire mesh, or expanded metal benches to flush the humid air out of the canopy, which may be done with perforated polyethylene tubes such as those commonly used to distribute air above the crop canopy. Forcing heated air into a stock-plant canopy can reduce the incidence of sporulating *B. cinerea* on senescent tissue and reduce atmospheric conidial concentrations (26,30). The conventional method of growing stock plants for cutting production is conducive to stem blight caused by *B. cinerea*. Management practices that promote plant branching in order to form large numbers of shoot meristems that can be removed as cuttings produce short, compact plants with dense canopies that limit light and air penetration and promote senescence of lower leaves. Close spacing of stock plants to maximize cutting production further compounds the problem. *B. cinerea* readily colonizes these senescent leaves and sporulates, providing ample inoculum to infect stems wounded during harvesting of cuttings.

Although using white plastic mulch on top of the pots within a stock-plant canopy can also limit *Botrytis* blight and sporulation, it is not as effective as forced heated air (30). Combining plastic mulch and forced heated air is more effective than the individual treatments. Using plastic mulch alone to reduce Botrytis blight and sporulation may not be cost efficient because the incidence of sporulation can still be relatively high. However, forcing heated air into the plant canopy may be cost effective because the incidence of sporulation on necrotic leaves can be decreased dramatically. Further, the incorporation of forced air could work in management systems in which plants are moved during the growing season, whereas plastic mulch is feasible only in those systems in which plants remain stationary throughout the growing season. In stock-plant growing areas, reducing relative humidity to <60% immediately following harvesting for a minimum of 24 h can decrease the incidence of stem blight even if wounded stems subsequently are inoculated and exposed to environmental conditions favorable for infection (28).

Another factor related to high relative humidity involves the generation of CO_2 for enriching the greenhouse atmosphere. The release of water from CO_2 burners is a known phenomenon, but the increase of relative humidity during CO_2 enrichment in a commercial setting is not well documented (26). While a CO_2 burner may be more economical than liquid CO_2, the long-term impact of the resulting high relative humidity and low vapor pressure deficit may be costly in terms of disease caused by *B. cinerea*. Increased relative humidity and low vapor pressure deficit early in the growing season may allow *B. cinerea* to become established in the senescent lower leaves and other organic material, even though air flow is not yet restricted by a dense plant canopy. Once the pathogen is established saprophytically in senescent material and parasitically in wounded tissue, it is less dependent upon environmental conditions for survival.

Reducing relative humidity during propagation is difficult because of the wet, humid environment established by misting to optimize rooting. Stem rot and leaf blight caused by *B. cinerea* frequently occur on cuttings because the conventional environment for rooting cuttings is conducive to germination of conidia and expansion and coalescence of lesions. Since misting must be provided for the least-mature cutting, grouping cuttings according to maturity within the propagation area will prevent the more-mature cuttings from being kept wetter than necessary, thereby decreasing the potential for *Botrytis* infection and sporulation. At the outset of the propagation cycle, misting periods are frequent and extended, thereby favoring development of *Botrytis* blight. It is critical, therefore, to protect newly planted cuttings from concentrations of airborne conidia by physically separating the new cuttings from older cuttings or established plants that could maintain sporulating *B. cinerea* on senescent leaves.

Covering greenhouses with long-wave infrared-absorbing plastic film may reduce relative humidity by reducing greenhouse cooling during the night. Vakalounakis (61) reported that disease caused by *B. cinerea* on tomatoes was reduced by use of long-wave infrared-absorbing vinyl film compared to use of a common agricultural polyethylene film. A wavelength-selective greenhouse covering that blocks the ultraviolet light and thereby increases the blue–UV ratio also inhibits *Botrytis* sporulation (51). This type of film is produced commercially and can be used as a complete greenhouse covering or a tent over a specific crop within a greenhouse. Reduction of sporulation is reported to be as much as 80% under experimental conditions. However, it should be noted that the effect of light-absorbing plastics on *Botrytis* sporulation can vary with the strain of *Botrytis* that is present and with the plant on which sporulation is occurring (47).

Temperatures in the greenhouse typically are not a limiting factor in the development of *Botrytis* blight. In rose flowers, blighting develops over a wide range of temperatures (11). Conidia of *B. cinerea* germinate on gerbera petals at temperatures ranging from 4 to 25°C (52). The effect of temperature on postharvest *B. cinerea* susceptibility has been investigated. When the influence of day–night combinations of 16, 19, and 22°C on postharvest susceptibility of poinsettia bracts and foliage to *B. cinerea* was investigated, susceptibility was not influenced by the difference in day and night temperature but increased as temperature increased (50). Kerssies (37) determined that temperature had a significant effect on the susceptibility of gerbera flowers, with the number of lesions in the petals increasing at higher temperatures. Similarly, pre-exposing cucumber plants to temperatures as high as 30°C resulted in increased disease on young fruits or leaves compared with plants pre-exposed to 10 to 25°C (19).

Another tool that can be used to manage the fungus in two very different situations is heat. High temperature, in the form of a thermal dip, has been used successfully as a postharvest treatment of rose flowers (18). A 20- to 40-s thermal dip treatment at 50°C was effective against Botrytis blight. Heat also can be used as a preplanting treatment to reduce the presence of *Botrytis*. Solarization has been used to eliminate the fungus from soil and plant debris in greenhouses during a crop-free period (39).

Fungicide. Fungicides provide protection but do not compensate for poor sanitation practices or poor environmental management, especially if disease pressure is high. Fungicides routinely are applied singly. However, mixtures of two or more fungicides are more effective initially and provide longer protection than do fungi-

Fig. 3. Rogued plant material left in the production area can serve as a source of inoculum to nearby healthy plants.

cides applied singly (41,43,44). In most cases, reduced fungicide rates can be used in mixtures without sacrificing protection. The longer residual activity of fungicide mixtures has become important in the United States recently because now it is mandatory that greenhouse workers be excluded from the greenhouse for 12 to 72 hours after application, depending upon the fungicide used.

Although there appear to be many fungicides available for *Botrytis* control based on trade names, there are actually few modes of action or fungicide classes available. Resistance of *B. cinerea* to fungicides severely limits chemical control options. The first documented case of a fungal population developing resistance to benomyl occurred in *Botrytis* on cyclamen in a greenhouse (2). Resistance to benomyl and cross-resistance to other benzimidazole fungicides in *Botrytis* populations are now common, and multiple resistance to both benzimidazole and dicarboximide fungicides is not unusual (42). The genetic basis of benzimidazole and dicarboximide resistance has been studied (23). Luck and Gillings (40) found that all benzimidazole-sensitive isolates tested have a codon 198 sequence of GAG (Glu), while resistant isolates were GCG (Ala). Based on these findings, a polymerase chain reaction–based test has been developed for rapid identification of benzimidazole-resistant isolates.

Resistant and sensitive strains of *B. cinerea* are often similar in fitness. Vali (62) found that dicarboximide-resistant and -sensitive strains of *Botrytis* differ only slightly in fitness. Therefore, the resistant portion of the population does not decline significantly when the fungicide is no longer used. It was reported that a *Botrytis* population in a greenhouse where benzimidazole use ceased in the 1970s still exhibited resistance 12 years later (24). Alternating fungicides is ineffective in suppressing the buildup of resistance because the resistant portion of the population does not decline significantly during the relatively short period of time that the fungicide is not present (45,62,63). Mixing chemicals with different modes of action is also ineffective in managing resistance if the chemical to which the fungus is resistant is included in the mixture. Although most of the fungicide-sensitive conidia will be killed with such a mixture, the remaining fungicide-resistant conidia will not be completely controlled. Surviving resistant conidia will germinate, infect, and give rise to many more conidia resistant to the fungicide (62,63). Thus, there is no management benefit from using the fungicide once resistance is present.

Even when a particular chemical has never been used in a greenhouse, resistance can inadvertently be brought in on plant material purchased from other operations (45). *Botrytis* conidia on cuttings produced in a greenhouse where a fungicide is used routinely may be resistant, and these cuttings may be sold to an operation where the fungicide has never been used. Thus, each instance of resistance to a previously effective compound is a threat to the entire greenhouse industry.

One glimmer of hope was that *Botrytis* resistant to benomyl was very sensitive to the fungicide diethofencarb, and *Botrytis* resistant to diethofencarb was very sensitive to benomyl, a case of negatively correlated cross-resistance. It was thought that growers could switch back and forth between diethofencarb and benomyl. However, *Botrytis* since has developed resistance to both chemicals (24,34).

The newer chemicals in the sterol biosynthesis-inhibiting class of fungicides are effective against *Botrytis* (12,46,49). However, since other fungi have developed resistance to this class of fungicides, *Botrytis* also can be expected to develop resistance, as evidenced by the low sensitivity of some *B. cinerea* isolates to fenetrazole and fenethanil (12). Therefore, these chemicals should be used carefully in a way that limits their selection pressure for resistance.

An area that needs greater exploration is the effect of spray mixture additives on the control of fungicide-resistant *Botrytis.* Bourbos et al. (3) reported a synergistic effect between a highly refined horticultural oil and fungicides. Although benzimidazole and dicarboximide fungicides gave less than 10% control and oil only about 50% control of a *Botrytis* strain resistant to both fungicide classes, the combination of oil and a fungicide from either class provided 88 to 100% protection. If oils or other materials have similar synergistic effects with benzimidazole and dicarboximide fungicides, these chemicals may be more useful in *Botrytis* management in greenhouses. Because horticultural oils legally are regulated as insecticides in the United States, they must be registered for use on the crop to be treated. It would not be legal to include them in a spray mixture as if it were just a spreader or sticker additive. This complicating factor coupled with the fact that certain crops or stages of crop development are very sensitive to oils may limit the usefulness of this strategy.

Applications of fungicide must be timed to maximize efficacy, thereby potentially reducing the number of sprays and the threat of resistance. For instance, growers typically delay fungicide application to unrooted plants because the frequent misting and overhead irrigation necessary during propagation may limit fungicide efficacy. However, fungicides should be applied to the stock plants before removing the cuttings or immediately after sticking cuttings, because newly planted cuttings may be exposed to peak atmospheric conidial concentrations (29). Therefore, delaying application of protectant fungicides to unrooted cuttings increases the likelihood that the cuttings will already be infected, although lesions may not yet be visible. Because misting during propagation may reduce fungicide residue on the leaves, selection of fungicides that provide prolonged residual activity may be helpful (41).

Biologicals and Genetic Resistance

Biological controls are being sought actively. Zhang et al. (66) determined that in container production of black spruce seedlings, *Gliocladium roseum* and *Myrothecium verrucaria* suppressed *B. cinerea* as effectively or more effectively than did the recommended fungicides. Infection of rose branches was reduced 50% when *Trichoderma harzianum* was used, but there was no significant control of Botrytis flower blight compared with that of untreated flowers (17). Hammer and Marois (25) successfully used two biological agents to control *B. cinerea* infections on rose flowers during storage at 2.5°C; however, once flowers were removed and exposed to room temperature (21°C), disease was not suppressed. The difficulty in using biological control against *Botrytis* blight on rose flowers may be the latent nature of the disease in this crop.

Further investigations are needed to improve strategies for timing applications of biocontrol agents to optimize control. When leaf populations of *T. harzianum* were studied on tomato, pepper, and geranium plants, population size differed according to plant species, leaf age, length of incubation, atmospheric conditions, and plant nutrition (16). A study by Elad and Kirshner (15) suggested that microclimate conditions influence the establishment and biocontrol activity of *T. harzianum* more than plant nutrition.

Botrytis may develop resistance to biological control agents whose mode of action is to produce antifungal antibiotics. Li and Leifert (38) demonstrated this risk by continuously exposing the fungus to a strain of *Bacillus subtilis* known to produce such chemicals.

Sprays of film-forming polymers have been tested for their ability to protect plants against *Botrytis.* Antitranspirants, developed to act as physical barriers to slow water loss by the plants, also may provide a barrier between the plant surface and the fungal spore. Some antitranspirants reduce Botrytis disease by as much as 60% on geraniums under experimental conditions (13). More work is warranted to determine when such materials are useful under commercial production conditions.

The physiological aspects of crop susceptibility to *Botrytis* and the prospects for developing gray mold–resistant crops have been reviewed (14). Breeding for resistance should be a primary goal for certain highly susceptible crops such as geranium. Not only would such resistance benefit that particular crop, but also other crops grown in the same structure would benefit from the reduced conidial load and disease pressure in the greenhouse.

Botrytis is a highly variable species able to adapt to many environments. The genetic diversity of the fungus is maintained in the multinucleate hyphae and spores and, in some strains, its heterokaryotic condition (22,54). Another source of variation is through sexual reproduction. The frequency of sexual reproduction in the greenhouse is unknown. In the laboratory, the study of recombination in *Botryotinia* has been facilitated greatly by improved methods of inducing apothecial development from sclerotia (20). As a result, it has been demonstrated that sexual compatibility is controlled by a single locus with two alleles (MAT1-1 and MAT1-2). Heterokaryosis explains the fact that some isolates contain both mating-type alleles (21). Genetic variability, along with the potential of quiescent infections and the interactions of the environment, complicate breeding for resistance.

Models

It is possible to monitor and control many environmental factors within the greenhouse with the aid of computers. The influence of temperature, vapor pressure deficit, and radiation on *Botrytis* biology has been studied in some crops (37) and could be used to develop set points for computer-triggered activation of equipment. Commercially available software can be programmed to trigger heating, shading, cooling, irrigation, and venting equipment, based on readings from sensors positioned within the crop. Data from sensors mounted outside the greenhouse to monitor insolation, temperature, humidity, and wind speed and direction can be fed to the computer to be incorporated into the decision-making process of the program.

Modeling epidemics of gray mold has proven to be a difficult task despite the wealth of biological information available (65). A model for predicting outbreaks of gray mold epidemics in unheated cucumber greenhouses was developed using a qualitative approach, whereas a quantitative statistical approach failed to produce a reliable model. Gray mold epidemics were reliably predicted when, on a weekly average, the wetting period of the foliage exceeded 7 h per day and the duration of temperature from 9 to 21°C during 1800 to 0800 HR exceeded 9.5 h per day (65). Sirjusingh and Sutton (55) found that disease incidence on whole geranium flowers increased at 15°C when wetness duration increased from 8 to 24 h, at 21 and 25°C as wetness duration increased from 4 to 12 h, and at 30°C as wetness duration increased from 4 to 6 h. They found that there was no infection at 25°C if wetness duration was less than 4 h. However, Williamson et al. (64) reported that conidia of *Botrytis* germinated and penetrated rose petals within 24 h without free water or appressoria following dry inoculation with conidia when RH was at or above 94%.

Integrating Control

Successful management of *B. cinerea* on greenhouse-grown floricultural crops requires integration of the latest research into current production systems. The floriculture industry is segmented into producers of "young plants" (specialist propagators), "prefinished plants," and "finished, flowering potted plants." Failure to control *Botrytis* at one production stage has negative ramifications for subsequent stages. Conversely, reducing sporulation on the necrotic leaf tissue and blighted stems of geranium stock plants could have a positive effect on the entire production chain. Decreased conidial concentrations within the stock-plant greenhouse could reduce the number of conidia that land on the leaf surface of the cuttings during harvesting, resulting in decreased disease incidence during propagation. Reducing the incidence of *Botrytis* in the propagation greenhouse could reduce the peak conidial concentrations associated with shipping cuttings and thereby decrease incidence of postharvest blight in greenhouses where the finished flowering potted plants are produced.

New opportunities for the control of Botrytis blight are available with the highly sophisticated greenhouses now being used for floriculture production. Heating, venting, fogging, misting, and irrigation can be computer regulated and

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modified to reduce epidemic potential. Overhead radiant heating as well as on-bench and under-bench heating can be used for disease management. Glazing materials that provide for the differential transmission of radiant energy are available. Innovative studies on the epidemiology of *Botrytis* will further explore the potential of these technological advances for disease control.

Ultimately, integrated control of *Botrytis* must be a goal. Sanitation, use of photoselective greenhouse coverings, and minimal use of carefully timed applications of mixtures of fungicides to which the fungus is not resistant will remain important tools. However, humidity control through sensors in the crop canopy linked to computer-controlled air movement and heating systems that flush humid air out of the canopy will become the mainstay of *Botrytis* management in greenhouses. The equipment, methods, and knowledge to enhance *Botrytis* control are already available and will improve in the future as our skill in using these tools increases.

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