Sugar Analogs as Potential Fungicides for Postharvest Pathogens of Apple and Peach

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ABSTRACT

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One-percent solutions of 2-deoxy-D-glucose, D-mannose, raffinose, L-sorbose, and 2-deoxy-D-ribose were tested as potential fungicides in apple and peach fruit wounds inoculated with *Botrytis cinerea* and *Penicillium expansum* in apple and *Monilinia fructicola* in peach. Among the sugar analogs tested, only 2-deoxy-D-glucose was effective in controlling decay in inoculated apple and peach fruit. A slight reduction in lesion diameter was detected with L-sorbose and D-mannose. Radial growth of *B. cinerea, P. expansum, M. fructicola,* and *Rhizopus stolonifer* was completely inhibited in vitro when 2-deoxy-D-glucose was incorporated into a potato-dextrose agar medium at a 1.0% concentration. Severe alterations in fungal growth were also observed including excessive branching, shortening of the hyphal segments, and hyphal swelling. The sugar analog, 2-deoxy-D-glucose, shows promise as a treatment for postharvest diseases. Effective formulations that are safe to humans must be developed before this technology can be used commercially.

Additional keywords: Blue mold, sugars

Because of the withdrawal of key fungicides for the control of postharvest diseases, an urgent need exists for effective alternatives. Recently, the use of antagonistic microorganisms and the induction of resistance in harvested commodities have shown potential for reducing postharvest losses (6,8,21,22). Yet, the degree of control obtained by these methods is often not comparable to that obtained with synthetic fungicides. Therefore, for these methods to gain economic acceptance their activity will need to be enhanced.

Various additives have been shown to increase the effectiveness of some antagonistic microorganisms in controlling postharvest decay (12,15). The addition of $CaCl_2$ to antagonistic yeast suspensions enhanced their biocontrol activity and reduced the populations of yeast required to give effective control (15). Enhancement of biocontrol was also reported in apple fruit by adding nitrogenous compounds to suspensions of the antagonist *Pseudomonas syringae* (12). Several nitrogenous and carbohydrates compounds were evaluated for their ability to enhance the biocontrol activity of *P. syringae*. Although six of the carbohydrates tested, including 2-deoxy-D-glucose, reduced radial growth and spore germination of *Penicillium expansum* Link, they significantly reduced the biocontrol activity of *P. syringae* (12). Recently, however, Janisiewicz (11) reported enhancement of biocontrol activity of two antagonists, *P. syringae* and *Sporobolomyces roseus*, by 2-deoxy-D-glucose. The ability of sugar analogs to control disease development has not been fully explored.

Sugar analogs have long been known to affect metabolic processes in fungal and plant cells (1,2,10,16,18). In several fungi (particularly yeasts) sugar analogs such as sorbose and 2-deoxy-D-glucose reduced growth and caused morphological changes often characterized by excessive branching (14,16). The adverse effect of mannose and its analogs has also been demonstrated in several plant systems (10,19). The ability of sugar analogs to sequester phosphate and consequently reduce ATP synthesis is believed to be the basis of their biological activity in plant tissue (10). This has been recently demonstrated in pear fruit, in which mannose was shown to delay ripening (19). This effect on both the pathogen and the host may confer to sugar analogs a potential as antifungal agents for the control of postharvest rot diseases. Although the antifungal property of sugar analogs is well documented, few attempts have been made to utilize them as fungicides (1,2). This investigation was undertaken to explore the potential of different sugar analogs for the control of postharvest diseases of apples and peaches.

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MATERIALS AND METHODS

Reagents, microorganisms, and plant material. The sugar analogs (2-deoxy-D-glucose, D-mannose, raffinose, L-sorbose, and 2-deoxy-D- ribose) were purchased from Sigma Chemical Co. (St. Louis, MO). Iprodione (Rovral) was obtained from Rhône Poulenc (Research Triangle Park, NC). All other chemicals were of analytical grade. Isolates of *Rhizopus stolonifer* (Ehrenb.: Fr.) Vuill., *P. expansum*, and *Botrytis cinerea* Pers.:Fr. were isolated from infected fruit and maintained on potato-dextrose agar (PDA). Cultures of 2-wk-old *P. expansum* and *B. cinerea* were flooded with sterile distilled water containing 0.1% (v/v) Tween 80 to remove conidia. Sporangiospores of *R. stolonifer* were obtained from 3-day-old PDA cultures incubated at 27 C. Conidia of *Monilinia fructicola* (G. Wint.) Honey were obtained from sporulating lesions of inoculated peach fruit. Spore suspensions from the pathogens were adjusted with sterile water to obtain 10^3 sporangiospores per milliliter for *R. stolonifer*, 10^5 conidia per milliliter for *B. cinerea*, and 10^4 conidia per milliliter for *P. expansum* or *M. fructicola*, and were used in each experiment described below.

Tree-ripe apples (cv. Red Delicious) were hand-harvested at commercial maturity and peach fruit (cv. Loring) were picked at the firm ripe stage (5.5–8.5 kg of pressure) at the Appalachian Fruit Research Station, Kearneysville, WV. Fruit were sorted on the basis of size and absence of physical injuries or infections and stored at 0 C for 24 hr prior to their use.

Treatment with sugar analogs. One-percent solutions of 2-deoxy-D-glucose, D-mannose, raffinose, L-sorbose, and 2-deoxy-D-ribose were prepared in sterile deionized water and filter sterilized. Apple fruit were individually wounded as described previously (20). Fifty μl of 1% sugar analog or sterile water was placed in each wound and allowed to be absorbed by wounded tissue. Within 30 min of treatment, wounds were challenged with 30 μl of a conidial suspension of *B. cinerea* or *P. expansum*. Inoculated fruit were incubated under high humidity in enclosed plastic trays containing water. For each treatment, four replicates of 25 fruit were arranged in a randomized complete block design. Fruit were evaluated daily for rot develop-

ment, and lesion diameter and percent infection were determined 3, 7, and 14 days after inoculation. The experiment was repeated three times. The arcsine transformation was applied to the data prior to analyses of variance and mean separation.

Control of postharvest decay with 2-deoxy-D-glucose. The effect of different concentrations (0, 0.05, 0.5, and 1.0%) of 2-deoxy-D-glucose and iprodione (100 μg/ml) on decay of apple inoculated with *B. cinerea* and *P. expansum* and peach inoculated with *M. fructicola* and *R. stolonifer* was investigated. Fruit wounds were treated with 50 μl of different concentrations of 2-deoxy-D-glucose or iprodione (100 μg/ml) and challenged with 30 μl of spore suspension of each postharvest pathogen used in this study within 30 min after treatment. There were four replicates of 25 fruit per treatment with complete randomization. Inoculated fruit were incubated under the same conditions as in the previous test. Lesion diameter and percent infection were determined for each treatment as described above. The tests were repeated four times and the data were analyzed by analysis of variance as in the previous test.

Determinations of sugars in the wounds. Since the inhibitory effect of sugar analogs is known to be reversed by utilizable sugars, in particular glucose (16), the amount and type of sugar available in the wound were determined. Ten apples and 10 peaches were wounded with a sterile nail by making five wounds (5 mm deep × 3 mm wide) per fruit. Within 30 min of wounding, 50 μl of sterile deionized water was applied in each wound and allowed to equilibrate for 10 min. Thereafter, the water and diffusate were pipetted out of 10 wounds, pooled together, and filtered through a membrane (0.22-μm pore diameter). Samples collected were injected into a high-pressure liquid chromatograph equipped with a Waters 410 refraction index detector (H_2O mobile phase at 0.5 ml min^{-1}; column, HPLC carbohydrate Aminex HPX-875C, at 80 C).

Antifungal assays. Inhibitory effects of 2-deoxy-D-glucose were determined on one-fourth strength PDA. Sterile molten PDA was amended with membrane sterilized solutions of 2-deoxy-D-glucose to obtain concentrations of 0, 0.01, 0.1, and 1.0% 2-deoxy-D-glucose, and immediately dispensed into 9-cm-diameter polystyrene petri dishes. Each dish was seeded with a 6-mm-diameter mycelial plug taken from the margin of 4-day-old *B. cinerea*, 2-day-old *R. stolonifer*, or 7-day-old *P. expansum* and *M. fructicola* cultures. Four replicates of four dishes were used for each fungus at each concentration and the dishes were incubated in the dark at 24 C. Growth measurements were determined every 12 hr over a period of 7 days. Growth inhibition was calculated from data of two runs of the experiment.

Effect of 2-deoxy-D-glucose on fungal morphology. Preliminary studies showed that 2-deoxy-D-glucose caused morphological alterations in most of the fungi examined. The effect of 2-deoxy-D-glucose on the morphology of *B. cinerea*, *R. stolonifer*, *P. expansum*, and *M. fructicola* was characterized by growing these fungi on PDA amended with 0.1% 2-deoxy-D-glucose. The agar was overlaid with a dialysis membrane, and a 5-mm-diameter mycelial plug of the pathogens was placed on the membrane. To further characterize the effect of 2-deoxy-D-glucose on fungal morphology, the dialysis membrane with attending pathogens was removed, sectioned, and processed for scanning electron microscopy. Mycelial samples were vapor fixed with 2% osmium tetroxide in double-distilled water, air-dried, and sputter-coated with gold. Samples were kept in a dessicator until examination with a Cambridge S-120 SEM (Cambridge, England) at 10 kV and photographed.

RESULTS

Control of postharvest decay with 2-deoxy-D-glucose. Among the sugar analogs tested, only 2-deoxy-D-glucose was

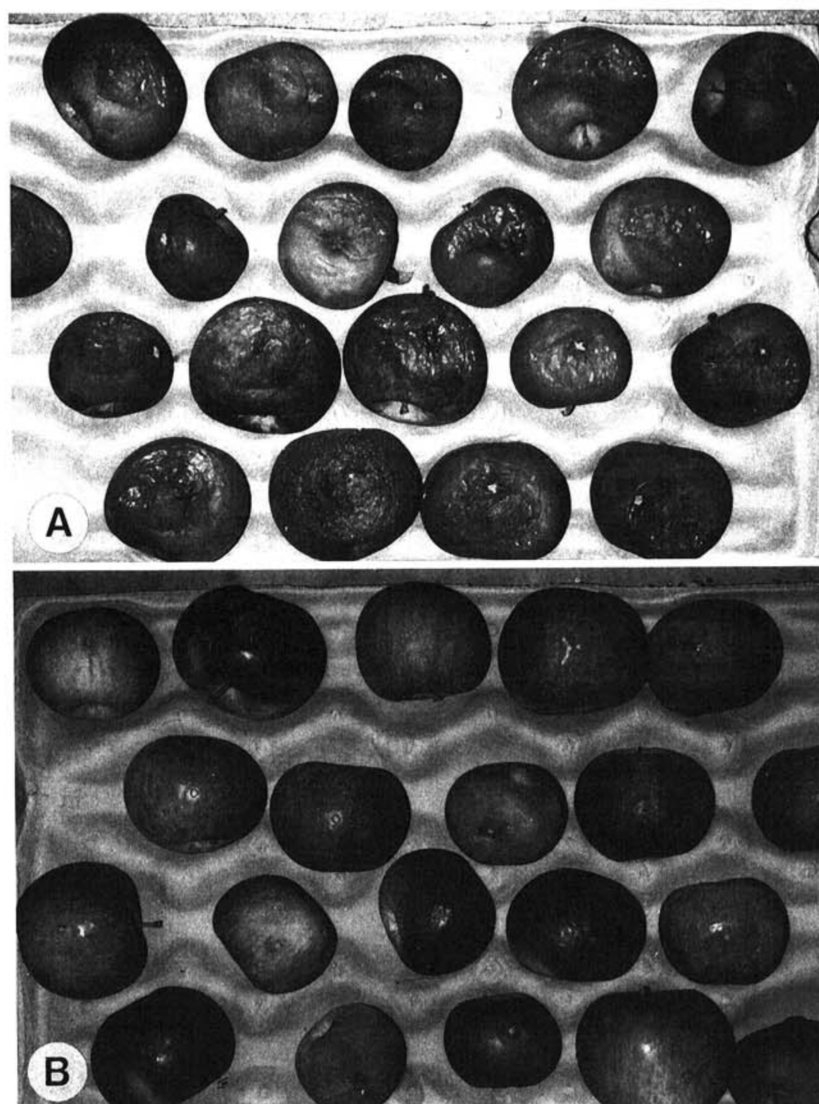

Fig. 1. Apple fruit inoculated with *Botrytis cinerea* and treated with **(A)** deionized water or **(B)** 1.0% 2-deoxy-D-glucose after 7 days at 24 C.

Table 1. Effect of sugar analogs on gray mold and blue mold of apple after 7 days at 24 C

	Infected fruit (%)[b]	
Treatment[a]	***Botrytis cinerea***	***Penicillum expansum***
Control	100	100
Glucose	100	100
Mannose	97.0	95.2
L-sorbose	94.3	93.1
Rafinose	98.1	100
Deoxy-D-ribose	99.3	96.4
2-deoxy-D-glucose	0 (21.3)[c]	0 (22.4)[c]
LSD_{05}	4.9	2.9

[a] Wounded fruit treated with 50 μl of different sugar analogs or sterile water and 30 min later were inoculated with 30-μl conidial suspensions of *B. cinerea* or *P. expansum*.
[b] Percentage of infected fruit based on four replicates of 25 fruit.
[c] After 14 days of incubation.

effective in controlling decay of apple caused by *B. cinerea* (Fig. 1, Table 1) or *P. expansum* (Table 1). Deoxyribose and raffinose at 1.0% did not appear to delay lesion development caused by either fungus. Only a slight reduction in lesion diameter was detected with either L-sorbose or D-mannose (data not shown). In fruit treated with 2-deoxy-D-glucose, decay lesions were visible only after 10 days of storage at 24 C, and invading hyphae in the wound appeared attenuated as indicated by reduced lesion size. Lesion development in the 2-deoxy-D-glucose–treated wounds proceeded at a slower rate than in the water control. At the end of 14 days storage, less than 22% of fruit treated with 1.0% 2-deoxy-D-glucose developed small lesions with a diameter of 10 mm (Table 1), whereas all the fruit treated with the other sugar analogs had reached an advanced stage of decay. In the control and fruit treated with sugar analogs other than 2-deoxy-D-glucose, decay lesions were often visible within 48 hr of inoculation. By day 7, 100% of these fruit were infected and lesions reached 30–65 mm in diameter.

In apple fruit, the inhibitory effect of 2-deoxy-D-glucose increased with increasing concentrations (Table 2). At a concentration of 0.05%, 2-deoxy-D-glucose did not affect lesion development caused by either *B. cinerea* or *P. expansum,* while at 0.5%, less than 23% of treated fruit were infected by *B. cinerea* and less than 40% by *P. expansum* after 7 days of storage at 24 C (Table 2). However, afterward decay developed at a rapid rate. Complete control of decay was obtained with 1.0% 2-deoxy-D-glucose for up to 10 days of storage (Table 2). During this period there was no difference between the 2-deoxy-D-glucose or the iprodione treatment in controlling decay caused by *B. cinerea* and *P. expansum*. Thereafter, however, lesion development progressed at a slightly faster rate in apples treated with 2-deoxy-D-glucose than in those treated with iprodione. By the end of the 14-day storage period, more than 20% of the apples treated with 2-deoxy-D-glucose developed lesions while less than 12% of those treated with iprodione were infected. A similar pattern of control was observed in peach fruit treated with different concentrations of 2-deoxy-D-glucose and challenged with *R. stolonifer* and *M. fructicola*. For instance, less than 33% of the peaches treated with 0.5% 2-deoxy-D-glucose were infected by either *R. stolonifer* or *M. fructicola* after 7 days of storage at 24 C. At a concentration of 1.0%, 2-deoxy-D-glucose completely controlled brown rot and Rhizopus rot of peach for up to 8 days of storage.

Determinations of sugars in the wounds. Analysis of sugars at wound sites revealed that in peach the main sugars present were sucrose (10 μg/μl), fructose (16 μg/μl), glucose (5 μg/μl), and sorbitol (0.75 μg/μl). In apple, however, 6.03, 2.02, and 1.85 μg of fructose, glucose, and sucrose per microliter of diffusate, respectively, were detected.

Antifungal activity and effect on fungal morphology. The sugar analog, 2-deoxy-D-glucose, was effective in inhibiting radial growth of the fungi tested with the greatest effect occurring at the highest concentration tested (Fig. 2). At a concentration of 1.0%, 2-deoxy-D-glucose completely inhibited *P. expansum, M. fructicola, B. cinerea,* and *R. stolonifer*. However, only slight growth inhibition was observed at a 0.01% concentration of 2-deoxy-D-glucose. At 0.1%, 2-deoxy-D-glucose reduced the radial growth of *B. cinerea, P. expansum, R. stolonifer*, and *M. fructicola* by over 85% (Fig. 2). Among the fungi tested, *M. fructicola* appeared to be the least sensitive (Fig. 2C) while *R. stolonifer* was the most sensitive to 2-deoxy-D-glucose (Fig. 2A). In addition, 2-deoxy-D-glucose at 0.1% induced severe morphological alterations in the tested fungi as indicated by light microscopy examination. These alterations were characterized by excessive branching, shortening of the hyphal segments, and hyphal swelling. In *R. stolonifer,* 2-deoxy-D-glucose inhibited sporangium formation.

After examination with a scanning electron microscope, untreated hyphal cells of *R. stolonifer, B. cinerea,* and *P. expansum* appeared dense, well preserved and showed no growth alterations (Fig. 3A-B). Hyphal cells of all three fungi treated with 0.1% 2-deoxy-D-glucose appeared shorter and highly distorted (Fig. 3D–G). Swollen hyphal cells often showed signs of cell wall degradation (Fig. 3D) and pitting (Fig. 3F). The alterations observed appeared more pronounced in *R. stolonifer* than in *B. cinerea* and *P. expansum* (Fig. 3D versus Fig. 3E–G). In contrast, hyphal cells of *M. fructicola* treated with 0.1% 2-deoxy-D-glucose showed no apparent signs of alteration. The size and shape of the fungal cells were similar to those

Table 2. Effect of 2-deoxy-D-glucose on gray mold and blue mold of apple

Treatment[a]	Storage (days)	Infected fruit (%)[b] *Botrytis cinerea*	*Penicillum expansum*
Control	7	100	100
0.05% 2-deoxy-D-glucose	7	83.2	90.4
0.5% 2-deoxy-D-glucose	7	22.2	39.0
	14	95.3	97.2
1.0% 2-deoxy-D-glucose	7	0	0
	14	20.1	22.3
Iprodione (100 μg/ml)	7	0	0
	14	10.4	11.2
LSD_{05}		1.8	2.7

[a] Wounded fruit treated with 50 μl of different concentrations of 2-deoxy-D-glucose, iprodione, or sterile water, and 30 min later were inoculated with 30-μl spore suspensions of *B. cinerea* or *P. expansum*.

[b] Percentage of infected fruit based on four replicates of 25 fruit.

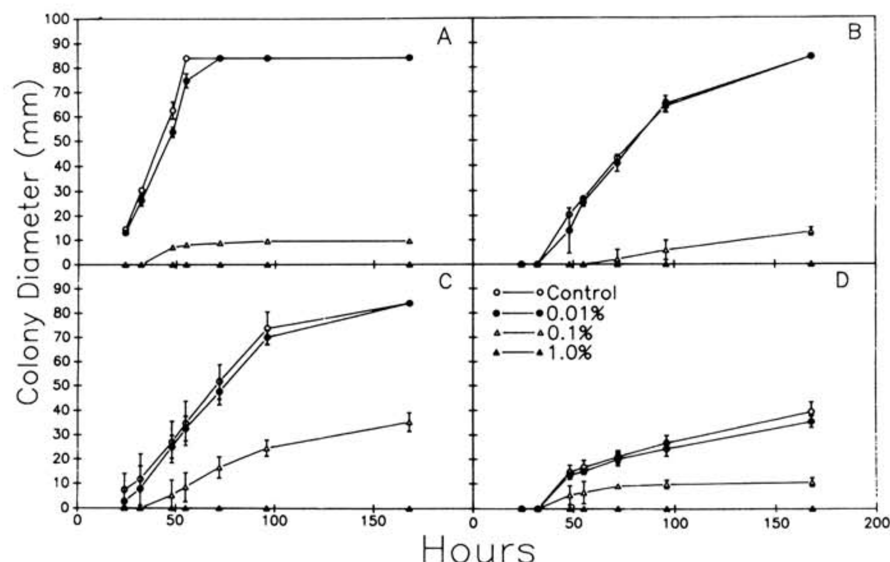

Fig. 2. Inhibition of radial growth of **(A)** *Rhizopus stolonifer,* **(B)** *Botrytis cinerea,* **(C)** *Monilinia fructicola,*and **(D)** *Penicillium expansum* by 2-deoxy-D-glucose at 0.01, 0.1, and 1.0%. Data values are means of four replicates. Vertical bars on data points represent SE values.

observed in the untreated control (not shown).

DISCUSSION

Treating wounded apple and peach fruit with 2-deoxy-D-glucose was effective in controlling decay caused by *B. cinerea, P. expansum, R. stolonifer,* and *M. fructicola.* Similar control of blue mold by 2-deoxy-D-glucose has also been reported in apple (11). It seems unlikely, however, that the inhibition observed could be attributed to biochemical processes mediated via the host tissue. In plant tissue, sugar analogs are believed to sequester phosphate and thereby reduce ATP synthesis (10,19). Such an effect is likely to reduce the ability of host tissue to initiate active defense responses. Indeed, 2-deoxy-D-glucose has recently been shown to inhibit active resistance responses designed to restrict fungal invasion, such as callose formation and papilla deposition, in plant tissue (4).

The in vitro results suggest that the observed inhibition is due to direct antifungal properties of 2-deoxy-D-glucose. In fact, at a concentration of 1.0%, 2-deoxy-D-glucose completely inhibited the growth of most of the fungi tested, including *R. stolonifer,* which is known to be insensitive to most fungicides. No apparent inhibition of decay was observed with other sugar analogs that can also act as an inhibitor of glucose metabolism (16). Although the reason for the apparent lack of activity of these analogs is unclear, it may be related to differences in uptake by the pathogen's cells. The sugar analog, 2-deoxy-D-glucose, may have been absorbed more readily than the other analogs tested.

Differential sensitivity to various sugar analogs has also been demonstrated with other microorganisms (16,17). The inhibitory activity of sugar analogs in growth media is often amplified in the absence of carbohydrates and can be reversed by utilizable sugars, in particular glucose (16). However, this does not seem to be the case in the present study, in which the inhibitory activity of 2-deoxy-D-glucose in the wound site, as well as in PDA, was evident despite the presence of sufficient nutrients to sustain pathogen growth. Analysis of sugars in peach wound showed that several sugars are readily available and may constitute an exogenous source of nutrients that are required for *B. cinerea* and *P. expansum* to initiate infection.

Sugar analogs, such as L-sorbose and 2-deoxy-D-glucose, are known to interfere with the growth of several yeasts and some filamentous fungi when used as a sole carbon source (5,17). Their ability to readily form phosphate esters that cannot be further metabolized and that interfere with the metabolic processes implicated in cell wall biosynthesis is believed to be the basis of their antifungal action in yeasts (16). In the case of 2-deoxy-D-glucose, its inhibitory activity has been extensively studied in *Saccharomyces cerevisiae,* in which it was found to affect cell wall-forming enzymes, namely, β-1,3-glucan synthetase (5,14). However, very little information is available on the effect of 2-deoxy-D-glucose on phytopathogenic fungi. In the present study, we demonstrated that 2-deoxy-D-glucose caused severe fungal morphological alterations as indicated by excessive branching in *B. cinerea, R. stolonifer,* and *P. expansum,* three fungi with different cell wall composition (3). Similar alterations were also reported in *R. stolonifer* grown in the presence of chitosan, a β-1,4-glucosamine polymer; these were attributed to a change in balance between the biosynthesis and turnover of chitin (7,9). While the mechanism by which 2-deoxy-D-glucose induces morphological changes needs to be investigated further, it is possible that 2-deoxy-D-glucose may have affected fungal cell wall biosynthesis. This is quite possible since 2-deoxy-D-glucose has been reported to inhibit β-1,3-glucan synthesis in filamentous fungi (23) and in a yeast (14,16).

In conclusion, this study demonstrates the potential of 2-deoxy-D-glucose as an antifungal agent for the control of postharvest diseases. This bioactive compound could represent a useful additive to biological control methods utilizing antagonistic microorganisms by enhancing their activity and providing control comparable to synthetic fungicides. This could be accomplished by selecting for

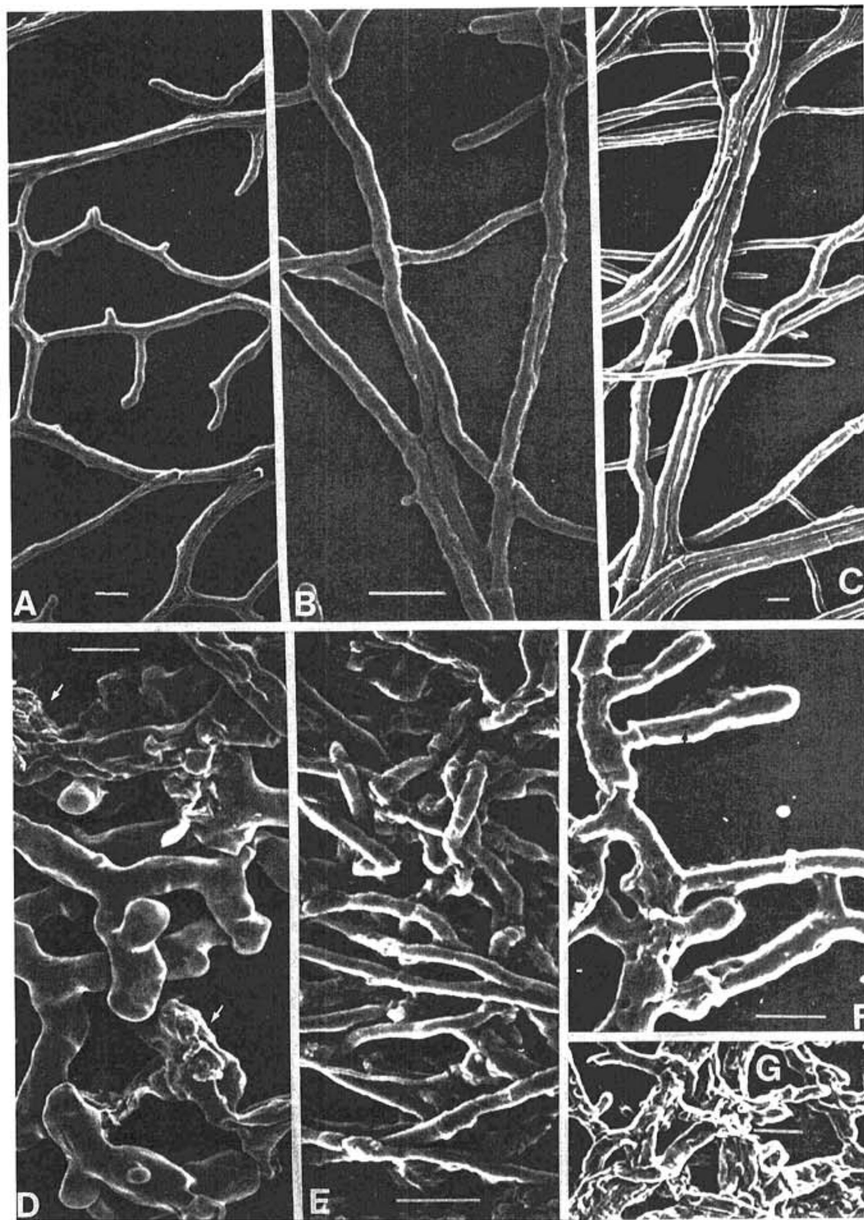

Fig. 3. Scanning electron micrographs of *Botrytis cinerea, Penicillium expansum,* and *Rhizopus stolonifer.* **(A–C)** hyphal cells grown under control conditions (bar = 10 μm). **(A)** *R. stolonifer*; **(B)** *P. expansum*; **(C)** *B. cinerea.* **(D–G)** hyphal cells grown in presence of 0.1% 2-deoxy-D-glucose. **(D)** *R. stolonifer* (bar = 10 μm); **(E)** *P. expansum* (bar = 5 μm); **(F–G)** *B. cinerea* (bars = 5 and 10 μm, respectively).

antagonists resistant to the fungicidal action of the sugar analog. Recently, the combination of 2-deoxy-D-glucose with a mutant of *Sporobolomyces roseus* was shown to reduce by 10-fold the concentration of the antagonist required for the biocontrol of blue mold on apple fruit (11). Additive or synergistic control activity might be realized through the combined application of the antagonist and sugar analog. However, before sugar analogs can be used as fungicides on food their safety for human consumption must be established. Available information suggests that these compounds are regarded as safe by the medical community (13). For instance, 2-deoxy-D-glucose has been utilized in medical research to study insulin metabolism in adults and children at dosages much higher than those tested in this investigation (13).

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