Biological Control of Dollar Spot Disease of Creeping Bentgrass

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ABSTRACT

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Top-dressing creeping bentgrass with sand-cornmeal or chopped grain colonized by fungi or bacteria was tested as a means of suppressing the intensity of epidemics of dollar spot disease incited by *Sclerotinia homoeocarpa*. In a greenhouse, 45- to 90-day-old turfgrass grown in cups was top-dressed with 1,500 cm^3/m^2 of sand-cornmeal infested by mycelium of *S. homoeocarpa*, followed by an equal amount of sand-cornmeal infested by potential antagonists. Four of 24 potential antagonists inhibited the growth of *S. homoeocarpa* and suppressed disease by 25–90%. In 1987, plots on a closely mown sward of creeping bentgrass were treated with inoculum of *S. homoeocarpa* and top-dressed weekly with sand-cornmeal (400 cm^3/m^2) infested by isolates of potential antagonists. Maximum disease intensities (percentage of plot area blighted) were 5, 18, or 44% in plots treated with sand-cornmeal infested by *Fusarium heterosporum*, an *Acremonium* sp., or an unidentified bacterium, respectively, during a 35-day epidemic, compared to 84% in plots not top-dressed and 64% in plots top-dressed with noninfested, autoclaved sand-cornmeal. In another experiment, maximum disease intensities were 31% in plots not top-dressed; 9% in plots top-dressed with noninfested, autoclaved chopped grain; or 3–6% in plots top-dressed with chopped grain infested by potential antagonists. In 1988, treatments at 2-wk intervals with sand-cornmeal infested by *F. heterosporum* (isolate pa 7) at 400 cm^3/m^2 limited disease intensity of a 78-day epidemic of dollar spot to 3%, compared to 18% in nontreated plots. Sterilization of sand-cornmeal infested by *F. heterosporum* (isolate pa 7) by heating to 70 C for 1 h did not significantly ($P = 0.10$) reduce efficacy. Results of laboratory and greenhouse experiments suggest that *F. heterosporum* (isolate pa 7) produces substances toxic to *S. homoeocarpa*.

Dollar spot, caused by *Sclerotinia homoeocarpa* Bennett, is a serious disease of turfgrass on golf course putting-greens, closely mown fairways, bowling greens, and home lawns. Creeping bentgrass (*Agrostis palustris* Huds.) and annual bluegrass (*Poa annua* L.), the two major species in closely mown (<2.5 cm) turf in the northern United States and Canada, are highly susceptible to *S. homeocarpa* (37). In addition, warm-season species including bermudagrass (*Cynodon dactylon* (L.) Pers.) and zoysiagrasses (*Zoysia* spp.) may be seriously affected (34). *S. homoeocarpa* causes straw-colored, sunken spots approximately 5 cm in diameter on closely mown turf. Foliar lesions are typically straw-colored with brown margins (34). In Ontario, rapid disease progress in late summer or early fall coincides with high humidity, prolonged leaf wetness, and temperatures >20 C (5,17). Low soil fertility and drought stress predispose turfgrass to dollar spot (12,34,37).

Dollar spot has been suppressed by high rates of nitrogen fertilization, adequate water supply, avoidance or removal of dew and guttation fluid from turf, and the application of fungicides (34,37). In southern Ontario (L. L. Burpee, *unpublished*) and in the United States (37) more money is spent to manage dollar spot than any other turfgrass disease on golf courses. No dollar spot-resistant cultivars of creeping bentgrass or annual bluegrass are available (37).

Frequent applications of inorganic and synthetic-organic fungi-

cides are cost-effective for control of dollar spot because disease-free golf greens and fairways are highly valued. However, reduction of fungicide use on golf courses is of particular benefit because the courses are used intensively during the growing season; players are in close contact with the turf, maintenance personnel are required to handle fungicides frequently, and fungicide application costs often exceed $170/ha (L. L. Burpee, *unpublished*).

The development and implementation of a biological control for dollar spot may limit fungicide use for the management of this disease. Biological control has been investigated as a means of managing fairy rings (35), Typhula blight (6), brown patch (4), and take-all patch (38,39) on turfgrass swards. Recently, Nelson and Craft (28) reported up to 63% suppression of dollar spot on bentgrass putting greens top-dressed monthly with mixtures of sand-cornmeal infested with strains of the bacterium *Enterobacter cloacae*. In addition, a brief report (18) summarized a study on biological control of dollar spot by *Gliocladium virens* Miller, Giddens & Foster. Applications of a prill formulation of *G. virens* (strain GL21) at 2-wk intervals suppressed dollar spot of bermudagrass by as much as 70%. Our study was designed to test the hypothesis that dollar spot can be reduced by top-dressing turfgrass swards with a medium infested by fungi or bacteria isolated from turfgrass plants, thatch, or soil.

MATERIALS AND METHODS

Acquisition of potential antagonists. Fungi and bacteria were isolated from turfgrass foliage or thatch in Ontario, or obtained from culture collections (Table 1). Parts of turfgrass thatch, grass plants, or unidentified mushrooms collected from turf were placed on BASM (Basidiomycete Agar for Systematics, modified by Smith, 36) in 9-cm-diameter petri dishes. Some pieces were surface disinfested by a brief immersion in 90% ethanol followed by immersion in 10% household bleach for 30 or 60 s and two rinses in sterile deionized water. Mycelia that grew from turfgrass thatch into holes cut through the thatch-layer of a 15-year-old sward of creeping bentgrass were also placed on BASM. Organisms isolated on BASM were cultured on autoclaved grain, air-dried, and stored at −22 C.

TABLE 1. Isolates used in a study of biological control of dollar spot disease of creeping bentgrass

Number and name	Source
5 *Acremonium* sp.	Thatch of bentgrass green, CRS[a]
35 *Diaporthe* sp.	Soybean seed
6 *Fusarium heterosporum*	Lesion on *Festuca* sp., CRS
7 *F. heterosporum*	Lesion on *Festuca* sp., CRS
38 *Lambertella subrenispora* (isolate LMK 5)[b]	*Aster ageratoides*, Japan
41 *Myriosclerotinia scirpicola*[b] (isolate LMK 68)[b]	Necrotic culms of *Scirpus*, GDR
17 *Rhizoctonia* sp.	Necrotic leaf of *Poa pratensis*, CRS
45 *Rhizoctonia* sp. (isolate BnR 165)	*P. pratensis*, Philadelphia, U.S.A.
46 *Rhizoctonia* sp. (isolate BnR 154)	*Stenotaphrum*, Texas, U.S.A.
1 *Sclerotinia homoeocarpa*	Lesion on *P. pratensis* leaf, CRS
12 *S. homoeocarpa*	Necrotic leaf of *P. annua*, CRS
14 *S. homoeocarpa*	Lesion on *P. pratensis* leaf, CRS
18 *S. homoeocarpa*	Lesion on bentgrass leaf, CRS
42 *S. sclerotiorum* (isolate gb 0100)[c]	San Diego, U.S.A.
2 Bacterium (unidentified)	Thatch of bentgrass green, CRS
47 Bacterium (unidentified)	Grain culture of *S. homoeocarpa*
4 Fungus (unidentified)	Thatch of bentgrass green, CRS
8 Fungus (unidentified)	Necrotic bentgrass leaf, CRS
20 Fungus (unidentified)	Rotting bentgrass leaf, CRS
21 Fungus (unidentified)	Symptomless leaf of *P. annua*, CRS
22 Fungus (unidentified)	Lesion on *Festuca* sp., CRS
23 Fungus (unidentified)	Necrotic leaf of *P. annua*, CRS
24 Fungus (unidentified)	Chlorotic bentgrass leaf, CRS
25 Fungus (unidentified)	Mushroom on bentgrass green, CRS
26 Fungus (unidentified)	Necrotic bentgrass leaf, CRS
27 Fungus (unidentified)	Necrotic leaf of *P. annua*, CRS
28 Fungus (unidentified)	Necrotic stem of *Agrostis palustris*, CRS
29 Fungus (unidentified)	Lesion on *P. pratensis* leaf, CRS
30 Fungus (unidentified)	Mushroom on bentgrass green, CRS
31 Fungus (unidentified)	Lesion on *P. pratensis* leaf, CRS

[a] Ontario Ministry of Agriculture Research Station, Cambridge, Ontario, Canada

[b] Provided by L. Kohn, University of Toronto, isolates LMK 5 and LMK 68, respectively.

[c] Provided by G. J. Boland, University of Guelph, isolate gb 0100.

Preparation of infested topdressings. Inocula were prepared by culturing isolates of fungi and bacteria on a mixture of wheat, corn, oats, and barley, or a mixture of sand and cornmeal (2:1, v/v). A sand mixture of pH 6.5 was sieved to exclude particles >1.0 mm or <0.1 mm, resulting in a mean particle diameter of 0.5 mm and a gradation index of 4. Moist grain or dry sand-cornmeal was placed in 15- × 30-cm cake pans lined and covered with aluminum foil. Grain was autoclaved at 121 C for 30 min and autoclaved again after 24 h. Sand-cornmeal was autoclaved twice for 60 min, then moistened to 6% (v/v) with 1% lactic acid in sterile deionized water. An entire fungal or bacterial colony on 20 ml of BASM in a 9-cm petri dish was cut into 50–100 pieces, placed on 500 cm^3 of the sterile grain or sand-cornmeal, and incubated at 23 ± 2 C. After incubation for 2 wk, cultures were sliced, broken, and dried. Infested grain was chopped and sieved to exclude particles >2.0 mm. Infested sand-cornmeal was forced through a 1.7-mm screen. Infested topdressings were stored at 10 C for up to 2 wk. Samples of inocula of each organism were distributed on agar in petri dishes to ensure viability and purity. Infested sand-cornmeal contained 2–3 × 10^3 cfu/g.

Evaluation of potential antagonists in a greenhouse. Creeping bentgrass cultivar Penncross was seeded at a rate of 21 g/m^2 (210 kg/ha) on fine-textured vermiculite in 8-cm-diameter styrofoam cups. Temperatures were 20 C at night and 20–30 C during the day. Relative humidity (RH) varied between 30 and 80%. Germination was complete at day 6, and the grass was first cut about day 12. The grass was cut with scissors to 1 cm every 4–7 days (clippings were removed). Soluble 30-15-15 (N-P-K) fertilizer was applied with each irrigation, at 7- to 10-day intervals, at a rate of 1.0 ml/L (25 ml/cup). After application of fertilizer, the cups were watered to saturation. Before inoculation, the grass was stressed by withholding water and fertilizer for 10 days to increase the susceptibility of the turf to *Sclerotinia* (37). Each cup of turf was top-dressed with 7 cm^3 (a depth of 1.5 mm) of grain or sand-cornmeal infested by *S. homoeocarpa* (isolate S84), followed by an equal amount of antagonist inoculum or noninfested, sterile topdressing, and then was watered lightly. Cups that received autoclaved, noninfested sand-cornmeal, autoclaved sand, or no topdressing were used as controls. To assess pathogenicity of potential antagonists, all treatments were also applied without *S. homoeocarpa*. Treatments were arranged in a randomized complete block design with five replicates.

The turfgrass was misted daily at 1800 h and kept in a plastic enclosure from 1800 to 0900 h, maintaining near 100% RH. From 0900 to 1800 h, RH was 15–40%. Temperatures were 19–23 C from 1800 to 0900 h and 25–35 C from 0900 to 1800 h. Artificial lighting was not used, and ambient light intensities were not measured. Horsfall-Barratt ratings (20) of disease intensity (visual estimates of percentage of area of turf blighted per cup) were recorded daily at 1800 h when the turf was dry, until disease increase ceased (6–7 days).

Two experiments were conducted. In experiment 1, 15 potential antagonists were used (14 fungi and one bacterium). Sixty-five-day-old creeping bentgrass was top-dressed on 5 May 1987 with sand-cornmeal infested by *S. homoeocarpa* followed by sand-cornmeal infested by potential antagonists. Grass was nutrient-stressed (not fertilized for 10 days) but not drought-stressed. In experiment 2, 16 potential antagonists (15 fungi and one bacterium) were tested, of which four (three fungi and one bacterium) were repeated from experiment 1. Forty-two-day-old grass was top-dressed on 30 June 1987 with sand-cornmeal inocula.

Evaluation of potential antagonists under field conditions.

Experiments were conducted in 1987 at the Ontario Ministry of Agriculture and Food (OMAF) Research Station near Cambridge, Ontario, on a 15-year-old sward of creeping bentgrass cv. Penncross. Methods of maintenance of the creeping bentgrass were similar to those prescribed for golf course putting greens (1). Experimental units were 40 × 40 cm plots. Treatments were arranged in a completely randomized design with six replications. The design included nontreated (control) plots that were alternated in a chessboard pattern, with squares separated by 10-cm-wide buffer strips. Disease intensity from nontreated plots was used as a covariate in the statistical analysis. Topdressings infested by potential antagonists (produced as described in a previous section) were applied with a hand-held shaker and rubbed into the turf by hand. All plots were assessed for disease intensity (percentage of area of turf blighted per plot), using the Horsfall-Barratt rating system, every other day from the first appearance of disease until mid-September.

Two field experiments were conducted with potential antagonists that ranged from weakly to highly disease-suppressive in the greenhouse experiments. In experiment 1, five potential antagonists in sand-cornmeal were top-dressed on creeping bentgrass weekly from 5 June to 11 September 1987 at a rate of 400 cm^3/m^2. Controls were autoclaved sand; autoclaved, noninfested sand-cornmeal; and no treatment. Chopped grain infested by *S. homoeocarpa* was applied at a rate of 20 cm^3/m^2 on 5 August. In experiment 2, five chopped-grain topdressings infested by potential antagonists were applied at a rate of 0.25 kg/m^2 (~400 cm^3/m^2), on 23 August, 31 August, and 10 September 1987. Treatment with isolate pa 2 was repeated in experiment 2. Controls included autoclaved, noninfested chopped grain, and no treatment. Sand-cornmeal infested by *S. homoeocarpa* was applied at a rate of 10 cm^3/m^2 on 5 August.

Effect of *Fusarium heterosporum* on dollar spot. Two field experiments were conducted on a 10-year-old sward of creeping bentgrass cv. Penncross in 1988 to assess the effect of *F. heterosporum* (isolate pa 7) on dollar spot of creeping bentgrass. Sand with a gradation index of 3.2 and a mean particle diameter of 0.35 mm was used to prepare sand-cornmeal (2:1, v/v). Autoclaved sand-cornmeal was moistened to 5.0% (v/v) with 1.0% lactic acid before addition of 5.0-mm-diameter plugs from the leading edge of a colony of isolate pa 7 on BASM. Cultures were incubated 21 days at 23 ± 3 C. For experiment 1, sand-cornmeal topdressing infested by *F. heterosporum* was prepared in May and stored at 5 C for the duration of the experiment (4 mo). For experiment 2, infested sand-cornmeal was stored at 5 C for 5 wk before application. Location, plot size, the use of systematic control plots, and methods of treatment and disease assessment were as described for the 1987 field experiments.

For experiment 1, plots were treated on 5 May 1988 with 4 cm^3/m^2 of chopped grain infested by *S. homoeocarpa* (isolate S84). Beginning 25 May, topdressing infested by *F. heterosporum* (isolate pa 7) was applied at 1-, 2-, and 4-wk intervals at rates of 200, 400, and 800 cm^3/m^2 per application, respectively. The last 1-wk treatment was applied 22 September, and the last 2-wk and 4-wk treatments were applied 14 September. The last 4-wk treatment was applied at half the regular rate so that the same amount of topdressing was applied to all top-dressed plots. For comparison, plots that were not top-dressed and plots treated at 2-wk intervals with heat-killed (70–80 C for 60 min) topdressing were included in the experiment. Treated and nontreated control plots were arranged in a randomized complete block design. A plot was left nontreated adjacent to each randomized plot (systematic controls). Intensity of dollar spot was estimated every other day from 23 May to 30 September using the Horsfall-Barratt rating scale (20).

For experiment 2, four treatments in a 2 × 2 factorial experiment were arranged in a randomized complete block design with six replications. One factor was the presence or absence of artificial initial inoculum (infested grain) of *S. homoeocarpa*. The other factor was the presence or absence of topdressing infested by *F. heterosporum* (isolate pa 7). On 5 May 1988, 75 mg (~10 particles) of chopped grain infested by *S. homoeocarpa* were inserted by hand to the base of the turfgrass canopy in four locations within each of 12 60- × 60-cm plots of creeping bentgrass. From 25 May to 14 September, sand-cornmeal infested by isolate pa 7 was applied at 2-wk intervals at a rate of 400 cm^3/m^2. Grain infested by *S. homoeocarpa* was also applied around the perimeter of the experimental area to provide a more even distribution of subsequent inoculum.

Interaction in vitro between *S. homoeocarpa* and *F. heterosporum*. Disks 5 mm in diameter were taken from the leading edge of cultures of *S. homoeocarpa* (isolate S84) and *F. heterosporum* (isolate pa 7) on BASM, and were placed on opposite sides of five petri dishes (9 cm diameter) each containing BASM, BASM acidified with 0.1% lactic acid (acid-BASM), or 2% water agar. Cultures were incubated at 23 ± 3 C. Disks containing mycelium of *S. homoeocarpa* were placed on BASM, acid-BASM, and water agar opposite colonies of *F. heterosporum* that were 5-, 9-, or <1-day-old, respectively. Colonies were examined macroscopically and microscopically for evidence of interaction between the two fungi. The procedure was repeated with five dishes of acid-BASM.

Disks of *S. homoeocarpa* and *F. heterosporum* on BASM were placed 40 mm apart on 10 microscope slides coated with 3 ml of 2% water agar for microscopic observation of hyphal interaction. In addition, disks of mycelium of *S. homoeocarpa* and *F. heterosporum* from BASM and water agar were placed 20 mm apart on 10 clean slides each, and a glass cover slip (24 mm square) was laid on top of the agar disks. Slides were kept at 23 ± 3 C on moist filter paper in petri dishes. After 5–8 days, when colonies met, and again after 6–12 days, mycelia were examined at magnifications of ×100 and ×400 for evidence of parasitism or lysis.

Data analysis. For the greenhouse and field studies, an area under the disease progress curve (AUDPC) (32) was calculated for all experimental units using the formula $\Sigma[(y_i + y_{i+1})(t_{i+1} - t_i)/2]$ for which $i = 1,2,3,\ldots,n-1$, y_i is the amount of disease, and t_i the time at the ith rating. To provide a measure of mean disease intensity, areas were divided by the period of disease progress. Statistical calculations were performed by Statistical Analysis Software (SAS Institute Inc., Cary, NC) procedures. Areas were subjected to fixed effects analysis of variance. Normality of experimental error was checked using the univariate procedure. Homogeneity of variance was checked by plotting residuals as a function of predicted values and by plotting standard deviations of treatment means as a function of treatment means, using the general linear model (GLM) and PLOT procedures. Data sets that violated these assumptions and could not be corrected by transformation were analyzed using nonparametric procedures (40). For field data, the mean AUDPC of adjacent control plots was included as a covariate in the statistical model using the GLM procedure. For parametric separation of means, the LSD procedure was used.

RESULTS

Acquisition of potential antagonists. Sixty-four fungi from approximately 20 genera (including 15 isolates of *S. homoeocarpa*, all pathogenic) and several bacteria were isolated from turfgrass foliage or thatch in Ontario. Of these, 23 isolates plus seven isolates from culture collections (Table 1) were screened for the ability to suppress dollar spot in the greenhouse, and nine of the 30 isolates were used in field trials.

F. heterosporum was isolated from six of 14 samples of dollar spot-type lesions on leaves of a fine-leaved fescue (*Festuca* sp.) collected at the OMAF Research Station in Cambridge, Ontario, on 16 October 1986. *S. homoeocarpa* was not isolated from any of the 14 samples. Similar lesions from the same location collected 16 September 1987 yielded *S. homoeocarpa* but not *F. heterosporum*.

S. homoeocarpa was not isolated from any of more than 300 samples of thatch, even though 15 of these samples were taken from the center of dollar spot loci in a sward of creeping bentgrass. Dollar spot lesions and necrotic leaves from dollar spot loci readily

yielded *S. homoeocarpa*. Isolates of *S. homoeocarpa* were similar in appearance to descriptions of other isolates from North America (2,11,12,27). Certain isolates consistently produced sterile apothecia on BASM acidified with 0.2% lactic acid.

Evaluation of potential antagonists in a greenhouse. Disease intensity was closely related to the amount of aerial mycelium of *S. homoeocarpa* produced on the turf. Turf inoculated with *S. homoeocarpa* alone was over 90% blighted after 4 days. Four isolates of potential antagonists (pa 7, 2, 5, and 17), of the 27 isolates tested, suppressed disease by more than 25% (Fig. 1). When sand-cornmeal preparations of isolates pa 7 and 2 were mixed with the sand-cornmeal infested by *S. homoeocarpa* before application, disease intensities were 35 and 41%, respectively, compared to 8 and 22% when the preparations of potential antagonists were applied on top of the sand-cornmeal infested by *S. homoeocarpa*.

Treatments common to experiments 1 and 2 gave consistent results in each experiment. Regression of AUDPC/time values in experiment 2 against those of experiment 1, for common treatments, gave an adjusted R^2 of 0.94 and a slope of 1.0.

In each experiment, the surface of the topdressings infested by *F. heterosporum* became orange as the fungus produced abundant sporodochia. When the turf was examined at the end of each experiment, a thin black layer, presumably stroma of *S. homoeocarpa*, was observed between a lower layer of topdressing infested by *S. homoeocarpa* and an upper layer of topdressing infested by *F. heterosporum*. No such black layer and little or no differentiation of layers produced by the pathogen or potential antagonist was observed in cups of other treatments. Increased growth and improved color of turf resulted from application of isolates pa 2, 6, 7, 21, 23, 27, 30, 32, or 47. Isolates pa 46, 45, and 17 (*Rhizoctonia* spp.), isolate pa 42 (*S. sclerotiorum*), and isolates pa 20 and 26 (unidentified fungi) were pathogenic, resulting in disease intensities of 12, 52, 61, 32, 8, and 25%, respectively.

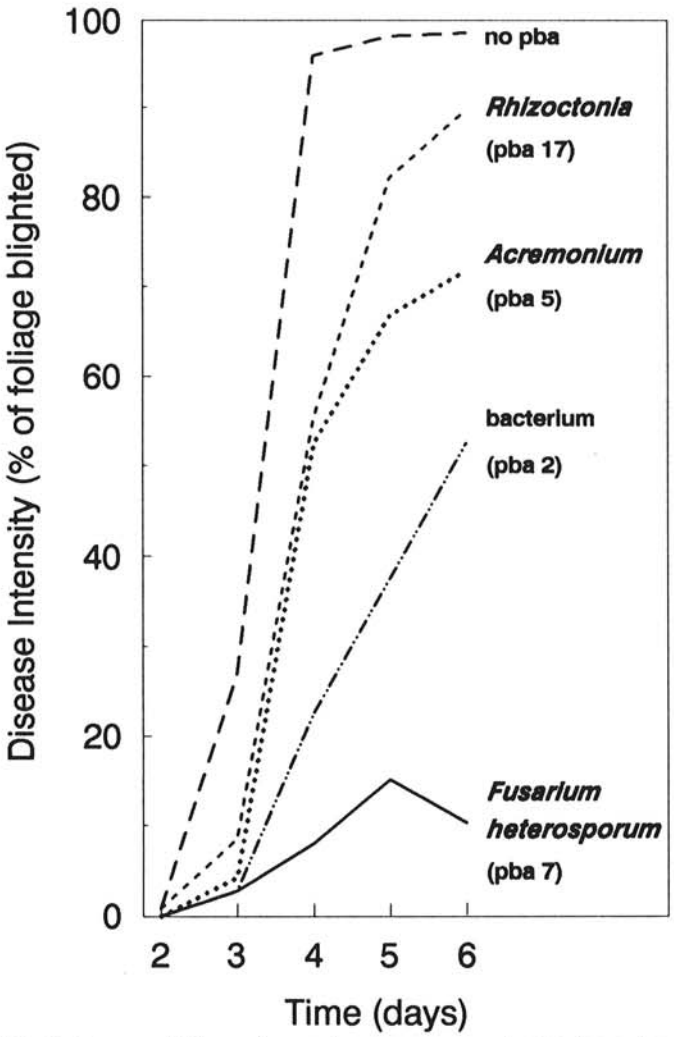

Fig. 1. Progress of disease in greenhouse-grown creeping bentgrass topdressed with a 1.5-mm layer of sand-cornmeal infested by *Sclerotinia homoeocarpa* and covered with an equal amount of sand-cornmeal infested by potential antagonists.

Evaluation of potential antagonists under field conditions. In experiment 1, significantly less disease occurred in plots treated with isolates pa 2, 5, and 7 than in plots treated with autoclaved, noninfested sand-cornmeal (Fig. 2A). In turn, significantly less disease occurred in plots treated with noninfested, autoclaved sand-cornmeal than in plots not top-dressed. The turf in plots treated with sand-cornmeal infested by *F. heterosporum* (isolate pa 7) was the least diseased throughout the epidemic, with <5% of foliage blighted. In green areas of plots treated with *F. heterosporum*, small dollar spot-type lesions were observed on bentgrass leaves. Colonization of these lesions by *F. heterosporum* was not determined.

Residual effects from topdressings of *F. heterosporum* (isolate pa 7) and *Acremonium* (isolate pa 5) were detected the following summer (1988); AUDPC was reduced by 30 and 40%, respectively, compared to nontreated plots. Residual effects were greatest in the first half of the epidemic (18 July–12 August), whereas disease intensities after 45 days were not significantly different in treated and nontreated plots.

In experiment 2, disease intensities in plots treated with pa 2 and 21 were significantly less than in plots top-dressed with autoclaved, noninfested grain (Fig. 2B). There was 50% less disease in plots top-dressed with autoclaved grain than in nontreated plots. At each rating, <3% of turfgrass was blighted in plots treated with isolate pa 21.

All plots in experiment 2 that were treated with potential antagonists exhibited a residual reduction of dollar spot the following summer (1988). Disease intensity (AUDPC) in plots treated the previous year with isolates pa 21 or 31, was 50% less than in nontreated plots. No residual reduction of dollar spot occurred in plots top-dressed with autoclaved grain. As in experiment 1, residual effects were greatest in the first half of the epidemic and not significant at the end of the epidemic.

Potential antagonists ranked similarly in field and greenhouse experiments. Exceptions were isolates pa 2 and 21. Isolate pa 2, an unidentified bacterium, suppressed disease significantly more than the isolate of *Acremonium* (pa 5) in the greenhouse but was significantly less effective than isolate pa 5 in the field. Of the five isolates used in experiment 2, isolate pa 21 was less effective in reducing disease than each of the other isolates in greenhouse experiments but was more effective than each of the other isolates in the field. Topdressing with autoclaved sand-cornmeal (or chopped grain) significantly reduced disease of creeping bentgrass in the field but not in the greenhouse.

Effect of *F. heterosporum* on dollar spot. In experiment 1, dollar spots were first observed on 23 May, 18 days after inoculation with *S. homoeocarpa*. Less than 3% of the foliage was blighted in each plot until 8 July, after which a severe dollar spot epidemic developed (Fig. 3A). In plots treated weekly with pa 7, disease peaked at 20%, compared to a maximum of 80% in plots not treated with *F. heterosporum*. Inspection of plots on several days, shortly after dawn, revealed that on some days mycelium of *S. homoeocarpa* was present in dollar spots in nontreated plots but not in dollar spots in plots treated weekly with pa 7. Disease progress curves were similar for the treatments applied at 1- and 2-wk intervals, with the exception of a temporary increase to 15% disease on 3 August in plots top-dressed at 2-wk intervals.

Comparison of AUDPC/time values for the period 25 May to 30 September showed that significantly less disease occurred in plots treated with pa 7 than in nontreated plots (Fig. 4A). Disease intensities in plots treated weekly, every other week, or every 4 wk with pa 7 were 86, 81, or 67% less than in nontreated plots, respectively. Disease progress curves and values of

AUDPC/time were not significantly different for pa 7 and for heat-killed inoculum applied at 2-wk intervals (one-tailed, paired Student's t test, $P = 0.10$) (Fig. 4A).

In experiment 2, peak disease intensities were 34% in plots treated with grain inoculum of *S. homoeocarpa* and not topdressed with pa 7, and 18% in nontreated plots (Fig. 3B). Dollar spot was first observed on 23 May, and the disease was still active on bentgrass after 30 September. Disease intensity in plots treated with pa 7 and not treated with inoculum of *S. homoeocarpa* peaked at 3% on 24 September. Dollar spots did not develop until July at all 48 points where grain infested by *S. homoeocarpa* was placed, but disease did develop at 26 of 48 points by 23 May. Half of these 26 points were located in plots that were to be treated with pa 7. Dollar spot was first observed on 12 July in nontreated plots, 7 wk after symptoms were observed in plots treated with *S. homoeocarpa*.

Significantly ($\alpha = 0.05$) more disease (AUDPC/time) occurred in plots treated with inoculum of *S. homoeocarpa* than in corresponding plots not treated with *S. homoeocarpa*; i.e., 340% more disease developed in plots treated with *S. homoeocarpa* and isolate pa 7 than in plots treated with isolate pa 7 alone, and 210% more disease developed in plots treated with *S. homoeocarpa* alone than in nontreated plots (Fig. 4B). For plots not treated with inoculum of *S. homoeocarpa*, disease intensity was 87% less in plots treated with pa 7 than in plots not treated with pa 7. For plots that were treated with inoculum of *S. homoeocarpa*, disease intensity was 80% less in plots treated with pa 7 than in plots not treated with pa 7. According to a one-tailed paired Student's t test, there is weak evidence that these percentage reductions in epidemics were different ($P = 0.13$).

Two unidentified fungi grew on the topdressing infested by pa 7 between 12 July and 7 August. One, which resembled a *Pythium* sp. in appearance of hyphae and growth on agar, was associated with the development of a foliar blight that resulted in brown patches of turf 10–15 cm in diameter. These circular patches developed in a few days and persisted for about a month. The other fungus produced white mycelium that grew over symptomless bentgrass leaves and produced gray-white circles up to 40 cm in diameter. Occasionally, isolate pa 7 produced mycelium or orange sporodochia on the sand-cornmeal topdressing. On 28 July, growth of pa 7 was particularly apparent. Two days later, some plots treated with pa 7 were slightly brown in color due to a change in color of older leaves.

Interactions in vitro between *S. homoeocarpa* and *F. heterosporum*. No morphologically distinct zone of hyphal interaction or zone of inhibition was observed between colonies of *S. homoeocarpa* and *F. heterosporum* (pa 7) on BASM. A small amount of mycelium of pa 7 grew on top of the colonies of *S. homoeocarpa*, but mycelium of *S. homoeocarpa* did not grow into the zone of the medium occupied by pa 7. Stromatization by *S. homoeocarpa* did not occur in a 3- to 4-cm band adjacent to the colony of pa 7. Mycelium of *S. homoeocarpa* became pigmented (brown) in a band 1–3 cm along the leading edge of the colony. A clear zone of inhibition of the mycelium of *S. homoeocarpa*, approximately 10 mm wide, developed on acid BASM. Hyphae at the leading edge of the colony of *S. homoeocarpa* became multi-branched, swollen, and dark, and grew very slowly toward the colony of pa 7. During 3–4 wk, the zone of mycelial inhibition gradually disappeared as a small amount of mycelium of pa 7 grew slowly toward and on top of the leading edge of the colony of *S. homoeocarpa*. As on BASM, a zone of inhibited stromatization of *S. homoeocarpa* occurred, and a

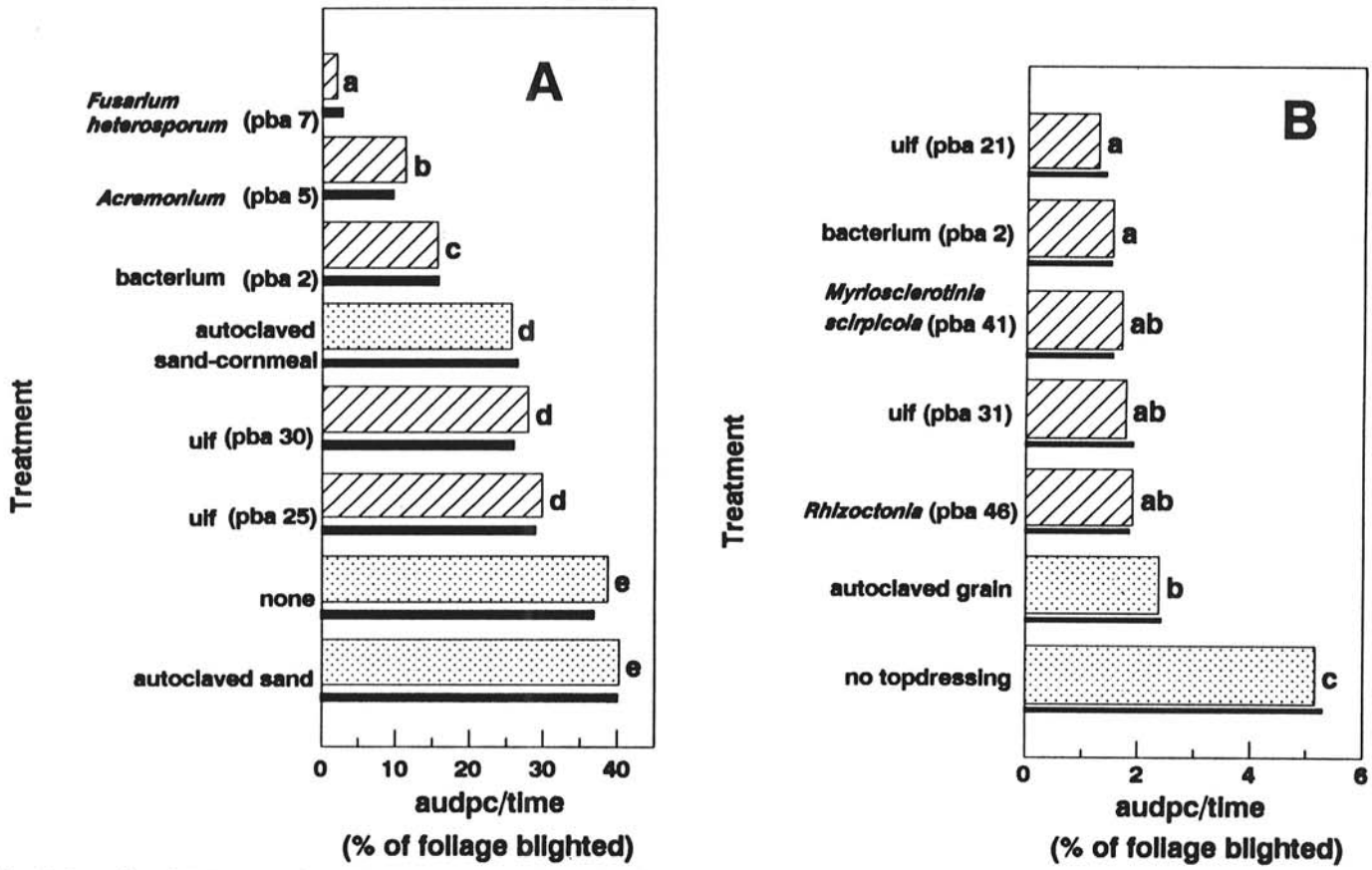

Fig. 2. Intensity of dollar spot in a 15-year-old sward of creeping bentgrass top-dressed with potential antagonists in **A,** sand-cornmeal applied at weekly intervals at 400 cm^3/m^2 from 5 June to 11 September 1987 or **B,** chopped grain applied at 1.6 kg/m^2 on 23 and 31 August, and 10 September 1987. Plots were treated on 5 August with **A,** chopped grain or **B,** sand-cornmeal infested by *Sclerotinia homoeocarpa*. Treatment means of area under the disease progress curve (AUDPC)/time and ln(AUDPC/time) were adjusted for values of AUDPC/time for adjacent nontreated plots by analysis of covariance. Stippled bars represent disease intensities of control treatments. Narrow, black bars represent unadjusted means. Bars followed by the same letter represent values for treatments with Friedman's mean ranks of adjusted ln(AUDPC/time) that do not differ significantly ($\alpha = 0.05$) according to **A,** a Newman-Keuls-type multiple range test or **B,** an LSD multiple-comparison procedure.

brown band of mycelium of *S. homoeocarpa* developed.

Antibiosis, hyphal interference, or parasitism was not evident on water agar in petri dishes, on slides coated with water agar, or on clean slides or cover slips. In dishes of water agar, mycelium of pa 7 extended up to 15 mm into the zone first colonized by *S. homoeocarpa*, but hyphae of *S. homoeocarpa* only grew 2–3 mm into the zone first colonized by pa 7. The largest hyphae of *S. homoeocarpa* in the pa 7 zone were vacuolated.

DISCUSSION

The greenhouse screening technique effectively separated potential antagonists on the basis of their influence on the amount of disease caused by *S. homoeocarpa*. Disease intensity was related to the amount of aerial mycelium of *S. homoeocarpa* that grew from the infested sand-cornmeal 2–4 days after application, suggesting that the protection afforded by topdressings infested by the potential antagonists was due to inhibition of growth of the pathogen and not due to protection of leaf surfaces. Possible modes of antagonism are hyperparasitism, or, more likely, antibiosis. Inhibitory or toxic compounds released by the potential antagonists in the laboratory during colonization of the topdressing media or in the greenhouse during the screening experiment were likely the primary cause of the observed inhibition of growth of the pathogen. Observations of *S. homoeocarpa* and five potential antagonists paired on agar media support this explanation. The isolates (pa 7, 2, and 5) that were most effective in the greenhouse and in the field (1987, experiment 1) inhibited the growth of *S. homoeocarpa* on agar, whereas isolates pa 30 and 25, which had little or no effect in the greenhouse or in the field, showed little or no interaction in vitro. Increased growth and darker green color of turf that was top-dressed with certain potential antagonists (in the absence of *S. homoeocarpa*) presumably were due to conversion of some of the sand-cornmeal culture medium into plant nutrients. Release of nutrients from topdressings infested by potential antagonists probably had little influence on disease intensity, as there was no correlation between the ability of the topdressings to reduce disease and the ability to improve turf color and enhance turf growth in the absence of *S. homoeocarpa*.

Results of topdressing with an isolate of *Aureobasidium* (isolate pa 27) were variable. Isolate pa 27, which resembles *A. pullulans*, an endophyte and epiphyte of plants (9,31) may have colonized leaf surfaces or leaf tissues and interacted with *S. homoeocarpa* there. Disease intensities for treatments with isolates of *Rhizoctonia* (pa 17, 45, 46), *S. sclerotiorum* (pa 42), and an unidentified fungus (pa 20) were influenced by pathogenicity of these potential antagonists observed in the greenhouse.

All isolates that were effective in the greenhouse and were tested in the field significantly reduced field epidemics, but some isolates that were not effective in the greenhouse also suppressed disease in the field. Although the greenhouse screening method seems to be a valuable means of predicting field efficacy, it may primarily detect organisms able to produce substances inhibitory to *S. homoeocarpa*, overlooking organisms that rely on competition or parasitism as modes of antagonism. If a greenhouse screening method is to be used to select isolates likely to be effective in field tests, then more conclusive evidence of correlation of greenhouse and field results is needed. Potential biocontrol agents of varied taxonomy and habitat should be used to determine a general relationship between results of controlled environment and field experiments.

Results of field experiments in 1987 indicated that four of the nine potential antagonists tested could suppress dollar spot

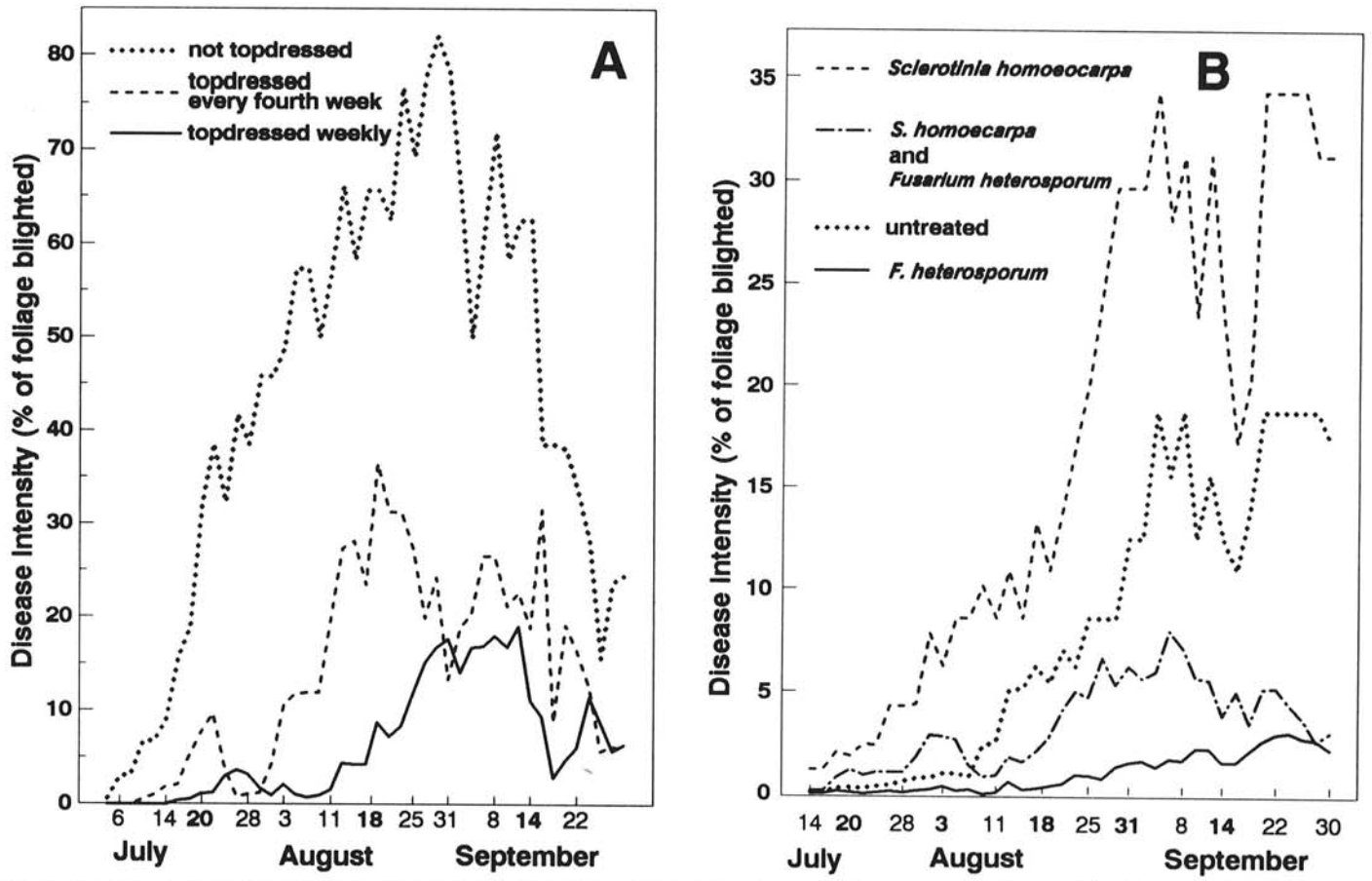

Fig. 3. Progress of dollar spot in a 10-year-old sward of creeping bentgrass top-dressed with sand-cornmeal infested by *Fusarium heterosporum* (isolate pa 7). **A,** plots were top-dressed at rates equivalent to 200 cm^3/m^2 per week. Dates labeled are weekly treatment dates (1988). Dates in bold are dates of 4-wk treatments. All plots were treated on 5 May with chopped grain infested by *Sclerotinia homoeocarpa*. **B,** plots were top-dressed with infested sand-cornmeal at 400 cm^3/m^2 per application on the dates in bold. Specific plots were treated on 5 May with chopped grain infested by *S. homoeocarpa*.

epidemics. Release of nutrients probably did not contribute much to the efficacy of the infested sand-cornmeal, as sand-cornmeal infested by isolates pa 2, 5, or 7 did not stimulate growth and improve color of creeping bentgrass in the greenhouse as much as did sand-cornmeal infested by isolate pa 30, which was not effective in the field. Lower disease intensity in field plots top-dressed with autoclaved, noninfested sand-cornmeal or grain, compared to nontreated plots, may have been due to resident antagonists colonizing the topdressing, or due to nutrient release accompanying decomposition of the topdressing. However, turfgrass that received autoclaved sand-cornmeal was not noticeably greener or faster growing than turfgrass in nontreated plots. Overall, disease intensity in plots top-dressed with sand was not significantly different than in nontreated plots, indicating that physical effects of top-dressing and the sand component of topdressings had little effect on disease.

A 93% suppression in intensity of dollar spot was achieved by top-dressing weekly with 400 cm^3/m^2 of sand-cornmeal infested by an isolate (pa 7) of *F. heterosporum*. Disease intensity was kept below 5%, compared to 80% in plots not top-dressed with *F. heterosporum*. Interplot interference probably increased the amount of disease in plots treated with potential antagonists. A large number of dollar spots developed on noninoculated turf outside the experimental area due to spread of the pathogen from the experimental plots, of which more than half were nontreated and severely diseased.

An increase in the frequency of application of topdressing infested by *F. heterosporum* resulted in greater reduction of dollar spot, most notably during the first half of the dollar spot epidemic of 1988 (4 July–25 August). Although values of AUDPC/time resulting from the application of pa 7 at 1- and 2-wk intervals were not significantly different for the entire period monitored, applications at 2-wk intervals were significantly less effective in suppressing disease than weekly treatments during the period of increasing disease intensity (before 2 September).

Differences in disease progress for experiment 2 (1988) can be explained by the effects of the inoculum of *S. homoeocarpa* that was applied and the effects of the topdressing infested by *F. heterosporum*. The grain infested by *S. homoeocarpa* that was placed in the turfgrass canopy on 5 May served as a excellent source of initial inoculum. Resulting dollar spots developed during the last week of May and remained throughout the next seven weeks. Dollarspots from natural inoculum were not observed until 16 July. Topdressing at 2-wk intervals with 400 cm^3/m^2 of sand-cornmeal infested by *F. heterosporum* controlled disease well, keeping disease intensity below 3%, compared to 18% in nontreated plots.

The two most likely reasons why weekly topdressings were less effective in 1988 (86% suppression) than in 1987 (93% suppression) were because half as much topdressing was applied per m^2 per week in 1988, and because the dollar spot epidemic of 1987 was of shorter duration than in 1988. However, during the first 5 wk after disease intensity reached 3% in nontreated plots in the 1987 and 1988 epidemics, little difference in disease suppression occurred between weekly treatments in each year. Other differences between 1987 and 1988 experiments may also have influenced the efficacy of the *F. heterosporum* treatment. A finer sand from a different source, 17% less water, and less agar colonized by *F. heterosporum* were used for preparation of the 1988 topdressing.

The use of sand to top-dress high-quality swards of creeping bentgrass such as golf putting greens is a common cultural practice used to maintain a smooth, firm surface (1). The amount of sand-cornmeal topdressing used in this study (400 cm^3/m^2 = a depth of 0.4 mm) is within the recommended range (1). However, on golf courses applications are usually applied at intervals of 3-

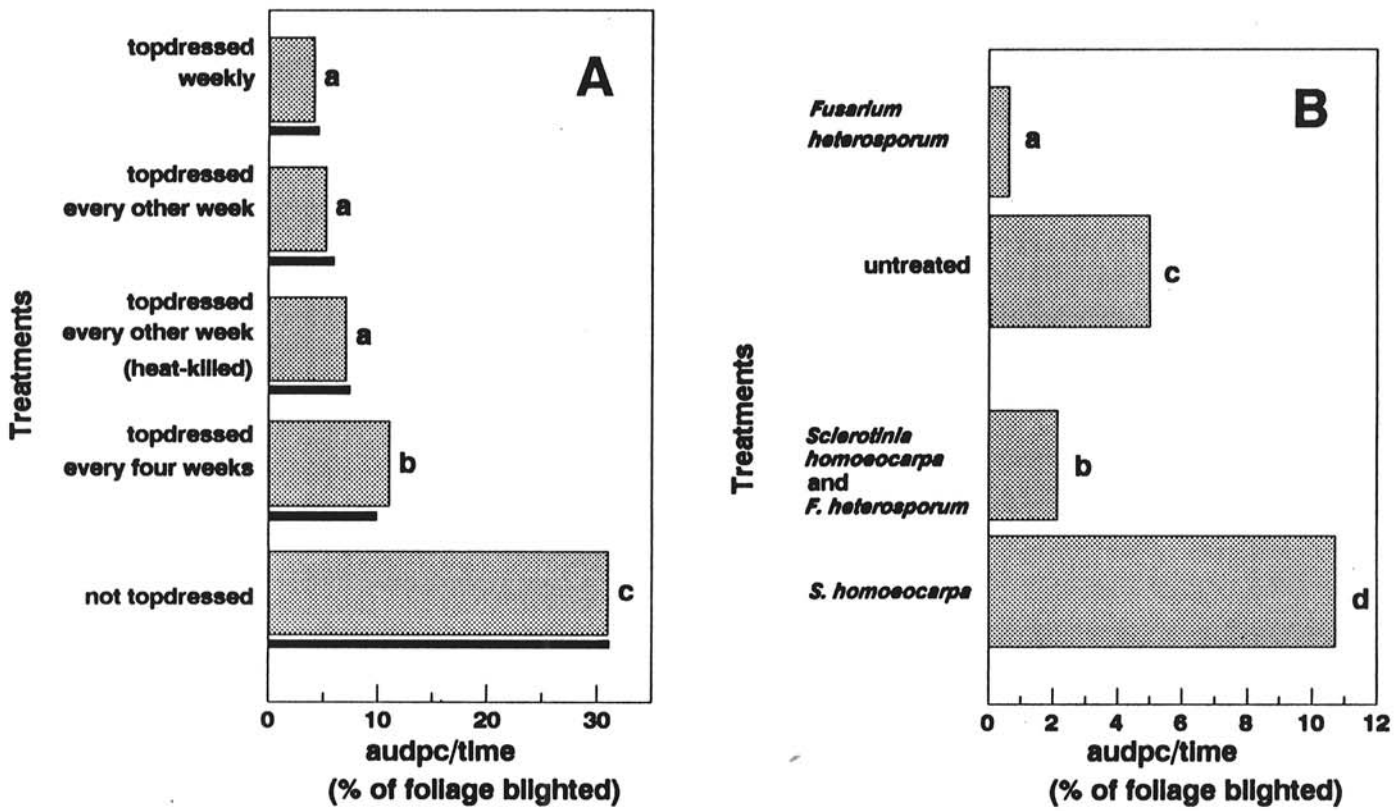

Fig. 4. Intensity of dollar spot (area under the disease progress curve [AUDPC]/time) in a 10-year-old sward of creeping bentgrass top-dressed with sand-cornmeal infested by *Fusarium heterosporum* (isolate pa 7). **A,** plots were top-dressed at rates equivalent to 200 cm^3/m^2 per week. All plots were treated with chopped grain infested by *Sclerotinia homoeocarpa*. Treatment means were adjusted for values of AUDPC/time of adjacent control plots using covariance. Narrow, black bars represent unadjusted means. Bars followed by the same letter represent means that do not differ significantly ($\alpha = 0.05$) according to an LSD multiple comparison. **B,** plots were top-dressed at 2-wk intervals at 400 cm^3 sand-cornmeal/m^2. Specific plots were treated with chopped grain infested by *S. homoeocarpa*. Bars followed by the same letter represent means that do not differ significantly ($\alpha = 0.05$) according to a series of Student's *t* tests.

to 4-wk rather than weekly. A formulation that includes a purely organic carrier of antagonists, such as chopped infested wheat grains, may provide a better nutrient base and allow for lower rates of application.

Autoclaving the dried sand-cornmeal culture of *F. heterosporum* diminished the capacity of the material to reduce the dollar spot epidemic. Surprisingly, there was only 25% more disease (comparing AUDPC) in plots treated with heat-killed topdressing than in plots treated with topdressing that was not killed. Topdressing infested by *F. heterosporum,* heat-killed or not, probably contained a compound(s) toxic to *S. homoeocarpa.* This explanation is consistent with observations of inhibition of the growth of mycelium of *S. homoeocarpa* by *F. heterosporum* in greenhouse screening experiments and in vitro tests. Observations of inhibition of growth, pigmentation, increased branching, and swelling of hyphae of *S. homoeocarpa*, and inhibition of the formation of stroma, when *S. homoeocarpa* (isolate S84) and *F. heterosporum* (isolate pa 7) were paired on acidified BASM, suggest that *F. heterosporum* produced a compound(s) toxic to *S. homoeocarpa.* In addition, metabolites released by *F. heterosporum* were probably the cause of pigmentation and inhibition of stromatization of *S. homoeocarpa* when the fungi were cultured together on BASM. This evidence of antibiosis in vitro also helps to explain the inhibition of growth of *S. homoeocarpa* and formation of a thin black layer between topdressings of *S. homoeocarpa* and *F. heterosporum* in greenhouse experiments.

Further tests designed to characterize antibiosis by *F. heterosporum* should be conducted. The isolates of *F. heterosporum* used in this study probably cannot parasitize *S. homoeocarpa*, based on the absence of hyphal interaction in water agar or on glass, but a small amount of mycelium of *F. heterosporum* grew on mycelium of *S. homoeocarpa* when the two fungi were paired on agar. Parasitic specificity of isolates of *F. heterosporum* toward isolates of *Claviceps purpurea* has been demonstrated (19). Whether isolates of *F. heterosporum* can parasitize *S. homoeocarpa* should be tested further. Isolates of *F. heterosporum* grew on colonies of *C. purpurea* and infected and rotted sclerotia (19). In addition, *F. heterosporum* parasitizes rust fungi (21,24) and has been found on smut-infected ovaries of several grasses (10).

The fact that *F. heterosporum* (isolates pa 6 and 7) was isolated from dollar spot-type lesions may be significant. Reports of *F. heterosporum* (16,22–24,26) suggest that some isolates may be secondary colonizers of diseased plant tissue. The species has most often been found associated with *Claviceps* spp. on inflorescences of grasses (8,10,13–15,19,25,33), and some isolates can kill grass seeds (3,8,13,15,22,23,26,29). Pathogenicity of isolates pa 6 and 7 on seeds is unknown.

Insufficient fundamental information on dollar spot disease and the incitant prevented use of much epidemiological or ecological information to design a strategy for isolation, screening, and field testing of potential antagonists, as is recommended (7,30). Research and development of biological control of dollar spot could be placed on a firm theoretical basis with information from studies on the epidemiology of the disease, the biology of *S. homoeocarpa*, and the microbial ecology of swards of creeping bentgrass.

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