Reciprocal Translocation of Carbohydrates Between Host and Fungus in Bahiagrass Infected with *Myriogenospora atramentosa*

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ABSTRACT

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The pathogen *Myriogenospora atramentosa* provides an unprecedented model for the study of fungal biotrophy. Both mycelium and stromata of the fungus were entirely epiphytic upon the leaf blades of the host grasses *Paspalum notatum* and *Andropogon virginicus*, and both host and pathogen could be separated along their interface into separate homogeneous fractions for analysis. Successive opposing leaves of the host were commonly bound together at the tips by bridges of fungal stromata. Infected leaves contained less than 4% of the sucrose present in uninfected leaves. The primary carbohydrates present in stromatic extracts were the sugar alcohols mannitol and arabitol. An unidentified low-molecular-weight compound present in extracts of uninfected leaves and stromata was absent from extracts of infected leaves. Greater amounts of ^{14}C label (originally supplied as $^{14}CO_2$) accumulated in compounds in infected leaves than in uninfected leaves. Compounds containing ^{14}C label originally supplied as ^{14}C-sucrose moved from leaf to stromatic bridge to second leaf. Although microscopy showed no alteration of the cuticle separating host and fungus, host epidermal cells beneath the fungus were modified in size and shape.

Additional key words: Clavicipitaceae, fungal physiology, grass parasite.

Myriogenospora atramentosa (Berk. & Curt.) Diehl has been described (9) as producing a superficial infection of grasses that results in development of stromata over the adaxial surface of the midrib in the apical region of the leaf blade. Although penetration of host tissues has not been observed, all leaves may become infected from mycelium present among leaf primordia in the buds. The "tangletop" condition results when the linear stromata on successive opposing leaves in early stages of development fuse at the tips (9, and Fig. 2) into stromatic bridges that bind the leaf blades into a series of loops (9, and Fig. 1). The possibility of separating host and fungus tissues into homogeneous fractions and the connection of host leaves by stromatic bridges suggested that infections by *M. atramentosa* might provide an unusual opportunity for studying translocation between fungus and host. The following objectives, therefore, were established: to examine the interface of host leaf and fungus stroma to ascertain any changes in host tissue in response to infection and to verify the superficial, nonhaustoriate nature of this fungal infection; to determine the nature of the carbohydrates present in host and pathogen tissue; to measure the incorporation of $^{14}CO_2$ by infected plants, and the transport of ^{14}C-labeled compounds into the fungus; and to determine whether there is transport of ^{14}C-sucrose from the plant into the fungus and from the fungus into the plant.

MATERIALS AND METHODS

Source and culture of infected plants. Healthy plants of *Paspalum notatum* Flügge (bahiagrass) and *Andropogon virginicus* L. and plants naturally infected with *M. atramentosa* were dug up at various locations in Georgia, brought to Athens, and planted in 15-cm-diameter plastic pots containing a soil:sand:vermiculite:perlite mix (3:1:1:1, v/v). In the greenhouse, plants were grown at 26 ± 3 C with natural daylight. Plants were watered daily with tap water, and liquid fertilizer (12:6:6) was applied twice a year. Two-year-old healthy and infected pot-grown plants were divided and transplanted to field plots where they were watered as needed and fertilized (10-10-10, N-P-K) twice a year.

Tissue sampling procedure. In all experiments, three sets of tissues were compared: stromatic tissue of the fungus stripped from the surface of infected leaves and freed of all host tissue, uninvaded leaf blade tissue lateral to and on either side of the stromata on infected leaves, and corresponding leaf blade tissue from uninfected leaves. Stromata were removed from host tissue under a dissecting microscope. Pooled samples of stromatic tissue and of host tissue from comparable locations within the infected plant were used for the carbohydrate analyses and for the experiments on the incorporation of $^{14}CO_2$. Pooled samples of stromata contained 40–50 mg (wet weight) of tissue. Individual stromata, ranging from 2 to 10 mg (wet weight) were separately analyzed in translocation experiments.

Histology of infected tissue. Infected leaves and uninfected leaves from healthy plants were mounted in Tissue Tek O.C.T. compound (Ames Division, Miles Laboratories, Elkhart, IN) and sectioned on an American Optical, Spencer model 880, clinical microtome equipped with a specimen-freezing stage (Bailey Instruments, Saddle Brook, NJ). Infected grass segments with stromata attached were sectioned perpendicular to the leaf and above, through, and below the stromata. Frozen specimens were sectioned at 12 μm and stained with one of several fat-soluble stains in the Sudan and Oil Red series. Best results were obtained with Sudan IV prepared by combining a saturated solution of the stain in 95% ethanol with an equal amount of glycerin. Sections were mounted in stain, viewed with bright-field optics under a Zeiss microscope, and photographed on Ektachrome ET-135 film. Comparative histological observations were made on *A. virginicus* infected with *M. atramentosa*.

Gas chromatography of sugars and sugar alcohols. Gas chromatography (GC) was used to identify and quantitate the sugars and sugar alcohols in tissue extracts. The method was based on the rapid one-step gas chromatographic method developed for

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analysis of tobacco leaf carbohydrates by Severson et al (13). Freeze-dried, field-grown tissue was ground and placed in a standard auto-sampler vial with 1 ml of derivatizing agent (a 1:1 mixture of *N,O-bis*(trimethylsilyl)trifluoroacetamide and *N,N*-dimethylformamide) and an internal standard (dimyristin). The vial was sealed, placed in an ultrasonic bath for 45 min at room temperature, and then heated at 76 C for 20 min. This step extracted the leaf carbohydrates, which were converted into volatile trimethylsilyl derivatives. The silyl-sugar derivatives were then separated and quantitated with a Hewlett-Packard 5830 gas chromatograph equipped with an auto-injector and a 0.64×45.7-cm glass Dexsil 300 GC column. Column temperature was programmed 90–330 C at 8 C/min. The injector temperature was 225 C and detector temperature was 350 C. Low-resolution mass spectra were obtained (70 eV) by the direct insertion of probe samples into a Hewlett-Packard model 5930 dodecapole mass spectrometer; probe temperature was 250 C. Sugars and sugar alcohols were identified by comparison of GC retention time and GC-mass spectrometry data of authentic standards.

Incorporation of $^{14}CO_2$. Incorporation of $^{14}CO_2$ was studied by supplying $^{14}CO_2$ to healthy and infected shoots of a potted greenhouse-grown bahiagrass plant. The plant was labeled in a glass chromatography chamber ($30 \times 30 \times 60$ cm). A 15-ml beaker containing 3 ml of 0.1 M $NaH^{14}CO_3$ and seated on a water-driven stirrer was placed in the chamber. The $NaH^{14}CO_3$ (11 mCi/mmole) was purchased from International Chemical and Nuclear Corporation, Cleveland, OH. An open petri dish was placed on the bottom of the chamber to receive the ethanolamine trapping solution. The chamber lid was provided with ports to accommodate tubing for the introduction of water and reagents. The pot of bahiagrass infected with *M. atramentosa* was placed in the chamber, and the chamber lid was sealed. At time zero, $^{14}CO_2$ was generated by injecting 3 ml of 90% (w/v) lactic acid into the $NaH^{14}CO_3$ solution from a 10-ml syringe attached to a Teflon tube leading to the $NaH^{14}CO_3$ solution. The $NaH^{14}CO_3$ solution and lactic acid were mixed with the water-driven stirrer during the 2-hr exposure period, and the plants were illuminated bilaterally from an incandescent light and laboratory overhead fluorescent light for a total of approximately 5,000 lux at 29 C internal chamber temperature. A total of 300 μCi of $^{14}CO_2$ was released into the chamber. After the 2-hr exposure period, 5 ml of ethanolamine trapping solution was introduced into the chamber to absorb excess $^{14}CO_2$ and the plant was removed from the chamber within 5 min and allowed to assimilate the newly formed carbohydrate in the dark for 24 hr.

Stromata, infected leaves with stromata removed, and uninfected leaves were collected at the end of the dark period and macerated in a ground glass tissue homogenizer in 80% ethanol. The homogenate was centrifuged at 1,240 *g* for 5 min, and the supernatant containing the extracted assimilate was saved. The pellet was washed twice with additional portions of 80% ethanol followed by centrifugation. The supernatant and washings from the pellet were combined and evaporated to dryness with a Büchler rotary evaporator. Sample residues were each redissolved in 2 ml of 80% ethanol and tested for radioactivity. Samples were counted in scintillation fluid consisting of napthalene, 60 g; PPO, 4 g; POPOP, 200 mg; dioxane, 1,000 ml. Radioactivity of three separate sample extracts per tissue was measured in a Packard Tri-Carb model 3255 liquid scintillation spectrometer. All counts were quench corrected by external standards ratio. Means of tissue radioactivity and confidence intervals were calculated (Student's *t*-test, 2 df, $P < 0.05$).

Translocation of ^{14}C-sucrose across stromatic bridges. Excised leaf pairs of field-grown bahiagrass with stromatic bridges formed by *M. atramentosa* were labeled to determine movement of ^{14}C-sucrose across the stromatic bridges. Scintillation vials containing 5 ml of ^{14}C-sucrose labeling solution (International Chemical and Nuclear Corporation, Cleveland, OH; specific activity 0.32 μCi/mg at a concentration of 10 mM) were placed in 4-L beakers and secured with modeling clay. Vials of water were similarly placed in the beakers. Infected shoots with stromatic bridges were excised from the rhizomes at their bases, placed in water, and brought into the laboratory. An additional excision was made under water 2–4 cm further up the shoot. Each excised leaf pair consisted of two leaves bound together at their tips by a stromatic bridge. The leaf pairs were placed with one leaf base in a vial containing ^{14}C-sucrose and the other leaf base in a vial containing water. ^{14}C label was applied to either the older or the younger leaf of the pair. Similarly labeled uninfected leaves served as controls. Uninfected leaves with their bases in water were placed in the same 4-L beakers as labeled uninfected leaves to determine the extent of dark fixation by the leaves of $^{14}CO_2$ respired from the leaves labeled with ^{14}C-sucrose. Uninfected leaves with their adaxial surfaces artificially appressed and held together with sticky tape were similarly labeled to determine whether the stromatic bridge had an active role in the translocation of ^{14}C-sucrose. Each labeling pattern was repeated at least five times. Each beaker contained three vials of ^{14}C-sucrose solution and three vials of water. One leaf base was placed in each vial. The beakers containing the leaves in the vials were placed in the dark for 18 hr to permit assimilation of the label. At the end of this period, the plants were removed from their labeling vials and blotted dry; samples were taken of stromata, infected leaves with stromata removed, and uninfected leaves. Individual stromata were extracted and analyzed separately. The dried residue was taken up in 1.0 ml of 80% ethanol, and 50-μl samples were tested for radioactivity.

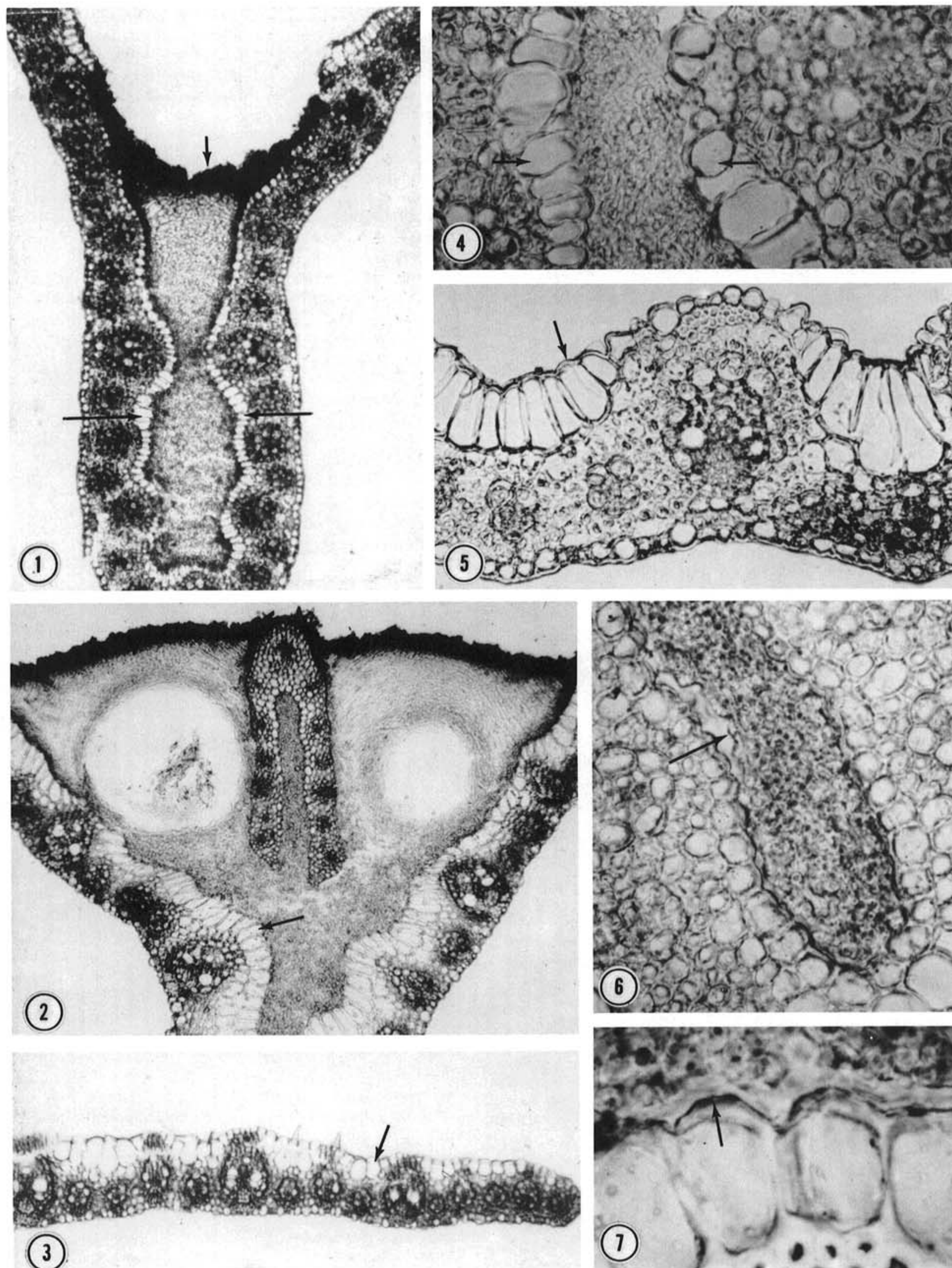
RESULTS

Histology of infected tissue. In cross sections of infected grass leaves the linear stromata of *M. atramentosa* in the apical portions of the leaves appeared as wedge-shaped masses of fungus plectenchyma occupying the cavity created by the upward folding of the leaf. The fungus lay over the midrib, preventing normal expansion of the leaf blade (Fig. 1). The exposed surface of the stroma was covered by a darkened cortex. The rest of the stroma, including the interface with the upper epidermal cells of the host, was hyaline. In shoots exhibiting the tangletop symptom, the folded tip of the younger leaf was immersed in the surface of the stroma on the older leaf (Fig. 2), and fusion of the stromata on the two leaves bridged the gap between the leaves. Abnormalities were evident in the host cells immediately beneath the stroma. In bahiagrass leaves, the epidermal cells beneath the stroma were smaller and more variable in size (Fig. 4) compared with epidermal cells adjacent to the stroma or in healthy leaves (Fig. 5). In leaves of *A. virginicus* infected with *M. atramentosa*, epidermal cells of the host were strikingly elongated in a direction perpendicular to the leaf surface (Fig. 2) as compared with epidermal cells of healthy leaves (Fig. 3).

Microscopy gave no evidence of penetration of host tissue by the fungus, either through the epidermal cell walls or through stromata (Figs. 6 and 7). The Sudan IV stain, specific for lipids, established that a cuticle (Figs. 6 and 7, arrows) was present over the epidermal cells along the interface between host and pathogen. The cuticle was variable in thickness. No differences in thickness or staining reaction, however, distinguished the cuticle along the interface from the cuticle of normal portions of the leaves.

Gas chromatography of sugars and sugar alcohols. Gas chromatography of the sample extracts established that only sucrose and β-galactose were present in extracts of infected leaf tissue (Table 1). Sucrose and β-galactose were also present in healthy leaf tissue along with α- and β-glucose and fructose. Stromata contained mannitol and arabitol as the major carbohydrates, with lesser amounts of fructose, sucrose, and trehalose. Infected leaves differed from uninfected leaves quantitatively as well as qualitatively. Infected leaves contained less than 4% of the amount of sucrose contained in uninfected leaves. β-galactose was present in both infected and uninfected leaf tissue in essentially the same amounts. An unidentified low-molecular-weight compound (retention time, 2.59–2.64 min) was present in healthy leaves and stromata in large quantities. It was entirely absent from infected tissue adjacent to the stromata.

Incorporation of $^{14}CO_2$. A pot of greenhouse-grown bahiagrass consisting of healthy shoots and shoots infected with *M.*



Figs. 1–7. Cross sections of healthy grass leaves and leaves infected with *Myriogenospora atramentosa*. **Figs. 1 and 4–7,** Leaves of *Paspalum notatum*. **Figs. 2–3,** Leaves of *Andropogon virginicus*. **1,** Infected leaf with hyaline fungus stroma (short arrow) occupying a fold in the center of the leaf blade and bounded on either side by the upper epidermal cells (long arrow) of the host leaf (×360). **2,** Stromatic bridge binding tips of opposing leaves together. The unexpanded tip of the younger leaf appears as a narrow inverted "*U*" embedded in the tip of the *V*-shaped stroma in the older leaf. The large spheres in the stroma are walls of perithecia. The epidermal cells of the host (arrow) are elongated perpendicular to the stroma (×360). **3,** Uninfected leaf showing normal epidermal cells (arrow) (×360). **4,** Stroma in folded leaf. Where the stroma has been pulled away in sectioning, the impressions made by the host epidermis on the stroma are visible. Epidermal cells are small and irregular in shape (arrow) (×720). **5,** Uninfected leaf showing normal epidermal cells (arrow) (×720). **6,** Interface between fungus stroma and host leaf showing impressions of host epidermis on the stroma (arrow) (×720). **7,** Enlargement of interface showing host cuticle stained with Sudan IV (×1440).

atramentosa was used to measure the incorporation of $^{14}CO_2$ by photosynthesis. Incorporation measured in disintegrations per minute per milligram wet weight was 810 ± 46 in infected leaf tissue with stromata removed, 620 ± 35 in uninfected leaf tissue, and 169 ± 41 in stromatic tissue. Incorporation values were higher in the tissue of infected leaves than in uninfected leaves even though large amounts of photoassimilates moved out of infected leaves and into the attached stromata.

Translocation of ^{14}C-sucrose across stromatic bridges. Experiments with excised pairs of leaves joined by stromatic bridges in which the base of one member of the pair was immersed in a solution of ^{14}C-sucrose demonstrated translocation from one leaf into the stromatic bridge formed by *M. atramentosa* and out of the fungus into the second leaf (Table 2). More label was present in the stromata than in the leaves. Overall uptake of the label was less when the label was applied to the older leaf than when the label was applied to the younger leaf. In the two sets of controls used in this experiment there was negligible dark fixation by uninfected, unlabeled leaves of $^{14}CO_2$ that resulted from respiration of leaves labeled with ^{14}C-sucrose and no incorporation by healthy unlabeled leaves attached by sticky tape to healthy leaves whose sheaths were in ^{14}C-sucrose.

DISCUSSION

Microscopy confirmed an earlier report (9) of the complete separation of host and pathogen tissues by the host cuticle and indicated further that the cuticle was not altered by the fungus. Additional indirect evidence for this separation was provided by the absence of the sugar alcohols characteristic of the fungus in infected grass tissue after removal of the stromata. Although no microscopic evidence of alteration of the cuticle beneath the fungus was obtained, results of experiments with ^{14}C-sucrose demonstrated the translocation of carbohydrates from host to fungus and from fungus to host. Further evidence of movement of substances from fungus into host tissues through the apparently intact cuticle is afforded by the host-specific growth alterations in the epidermal cells beneath the fungus stromata.

Although infection enhanced the incorporation of $^{14}CO_2$ by bahiagrass leaves, the finding that less than 4% of the sucrose present in uninfected leaves was present in infected leaves indicates that sucrose or a sucrose derivative was being removed from the host and was being taken up by the fungus. The fact that the unidentified compound was present in large amounts in uninfected leaves and stromata and was absent from infected leaves indicates that it also may have been translocated out of infected leaves and into the stromata. Due to the successful derivatization of this compound prior to gas chromatography, it was postulated to be a carbohydrate, and because the retention time was shorter than the retention times of the five- and six-carbon standards used, it was assumed that the compound had four or fewer carbons and was of low molecular weight. The β-galactose present in both infected and uninfected leaves was probably derived from cell wall material released during the extraction process.

The conversion of carbohydrates produced by host photosynthesis into fungal carbohydrates has been considered a process central to the development of diseases caused by biotrophic fungi (7,14). Gas chromatographic analyses of stromatic extracts of *M. atramentosa* indicated that the predominant carbohydrates present are mannitol, arabitol, and small amounts of trehalose and monosaccharides. These findings are consistent with studies of other fungi (11). A number of roles for the production of these compounds by biotrophic fungi have been suggested, the most prominent of which is the maintenance of a concentration gradient favorable for the passive diffusion of host nutrients into the fungus (7,14). Also, the presence of mannitol and other solutes in the cytoplasm of fungal cells serves to lower the water potential within the fungus, favoring diffusion of water from the host into the fungus. Interconversion of sugars and sugar alcohols may also affect the overall regulation of metabolism (15).

Compounds derived from ^{14}C-sucrose are translocated across stromatic bridges of *M. atramentosa* that join pairs of leaves (Table 2). The fact that there was no translocation in the controls indicates that movement occurs through the stromata. When the younger leaf of the pair was placed in the ^{14}C-sucrose, more label was taken up than when the older, fully expanded leaf was placed in the label. Similarly, more label was translocated across the stromatic bridges into the younger leaves than into the older leaves. This is in agreement with the observation that, in general, half-expanded leaves both export and import carbon, whereas fully expanded leaves export only (10). The younger leaves may have a greater "sink effect" on translocation than older leaves. Translocation of carbohydrates from host to fungus and from fungus to host has been suggested in a study on the replacement disease caused by *Claviceps purpurea* (Fr.) Tul. (8). Intrahyphal translocation between higher plants has been reported as occurring in the fungus associated with the roots of *Monotropa hypopitys* L. (1,5) and in vesicular-arbuscular mycorrhizae (16).

Daly (3) stated that students of carbohydrate movement in plants would be well served to examine the effects of biotrophic pathogens on translocation because the pathogen provides an additional sink for nutrients that can be monitored and defined. Previous investigators have discussed the inherent shortcomings of studying model systems in which it is impossible to separately analyze host and pathogen tissues and to determine their respective contributions to the diseased state (2,4,6). The dissection of bahiagrass shoots infected with *M. atramentosa*, however, resulted in separate sets of tissue consisting solely of either host plant or fungal pathogen. The stromata of this fungus are localized, large, and relatively easy to handle. *M. atramentosa* may be readily maintained in axenic culture or on infected greenhouse plants (12). Students of fungal biotrophy may find that examination of the nature of infection of grasses by *M. atramentosa* in addition to

TABLE 1. Gas chromatographic analysis of sugars and sugar slcohols in tissue extracts of leaves of bahiagrass infected with *Myriogenospora* and uninfected leaves

Sugar (retention time)[b]	Sugars and sugar alcohols in tissue extracts[a] (μg/mg dry wt)		
	Stromata	Infected leaves[c]	Uninfected leaves
Arabitol (7.30)	65.3	0	0
Fructose (8.47)	0.2	0	18.7
α-Glucose (9.34)	0	0	2.9
Mannitol (9.65)	142.4	0	0
β-Galactose (9.71)	0	37.6	38.8
β-Glucose (10.93)	0	0	14.4
Sucrose (16.72)	trace	2.3	73.4
Trehalose (17.61)	trace	0	0

[a] Extracts were prepared from greenhouse-grown material; preliminary work was done on field-grown material and no qualitative differences were obtained compared to greenhouse material.

[b] Retention time was related to standards injected separately and as a total mixture, 200 μg/ml.

[c] Stromata were removed from infected leaves prior to extraction and analysis.

TABLE 2. Translocation of ^{14}C-assimilates in excised leaf pairs of bahiagrass with the leaves bridged by stromata of *Myriogenospora* and ^{14}C-sucrose applied to the younger or older leaves

Type of leaf receiving ^{14}C	DPM/mg wet wt[a]			Percent radioactivity in stromatic bridge
	Younger leaf	Stromatic[b] bridge	Older leaf	
Young	8,061	15,672	165	65
Old	322	1,442	1,290	47

[a] Average of four experiments. DPM = disintegrations per minute.

[b] Each individual stroma joined a pair of leaves consisting of a younger and older leaf.

other more frequently studied biotrophs may add to the understanding of this mode of fungal nutrition as well as to the translocation of carbohydrates in plants.

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