Etiology

The Mycorrhizal Fungus *Glomus macrocarpum* as a Cause of Tobacco Stunt Disease

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ABSTRACT

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Tobacco plants inoculated with sievings containing endogonaceous spores from soils suspected of containing the tobacco stunt pathogen developed stunt symptoms identical to those of naturally stunted plants. *Glomus macrocarpum* sporulated first on stunted plants, followed by *G. microcarpum*. Stunting was correlated with sporulation by *G. macrocarpum* and less strongly with sporulation by *G. microcarpum*. Stunting also was correlated with colonization of roots by arbuscules and external hyphae. Isolates of *G. macrocarpum* from soils containing the stunt pathogen caused stunting in tobacco seedlings, but an isolate of *G. fasciculatum* shown to benefit growth of several woody plants did not. Shoots and roots of tobacco seedlings inoculated with single spores of *G. macrocarpum* were stunted, the degree being related to the number of colonization structures (arbuscules, vesicles, external hyphae, or spores) present. These data suggest that *G. macrocarpum* and perhaps *G. microcarpum* cause tobacco stunt disease.

Tobacco stunt is caused by a soilborne pathogen that can be controlled with soil fumigants (13). Affected plants are stunted, delayed in maturity, and reduced in yield and quality. Roots are essentially symptomless, and the disease can be diagnosed only by eliminating other diseases with distinctive symptoms or signs.

The observation by Fox and Spasoff (9) that inoculation with spores of a *Gigaspora* sp. caused stunting of a breeding line of burley tobacco (*Nicotiana tabacum* L.) suggested that an endogonaceous mycorrhizal fungus may be involved. These fungi were noted in tobacco roots in 1924 by Peyronel (25). In Canada, mycorrhizal colonization of tobacco grown in various soils was found to be more prevalent than colonization by other soilborne microorganisms (14). Mycorrhizae have been noted in cultivars of various types of tobacco (5,6,9,25). Effects on plants have varied. Growth has been reported to be stimulated by mycorrhizal fungi (5,6,9,25), but plant response may be conditioned by cultivar (9) or by fertilizer rate (5). The ecological relations of mycorrhizal fungi and tobacco have received scant attention.

Although endogonaceous fungi have not been shown experimentally to cause disease in crops, early researchers associated them with productivity problems (7,14,16,27). Techniques then available were inadequate for investigating the role of endogonaceous fungi in productivity. More recently, Crush

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(4) obtained evidence that *Acaulospora laevis* Gerd. & Trappe, the dominant endogonaceous fungus locally, may be pathogenic to some forage legumes in New Zealand under normal agricultural situations.

The approach in our research was to attempt to identify a pathogen causing symptoms of stunt from soils known to contain the stunt pathogen. Plants were inoculated with soil sievings. Cultures of *Glomus macrocarpum* (Tul. & Tul.) Gerd. & Trappe were obtained from these plants, and pathogenicity was examined.

MATERIALS AND METHODS

Tobacco fields thought to have severe infestations with the stunt pathogen were located by consulting with Agricultural Extension Service personnel. In all cases, the possibility of soil contamination by herbicides used on corn the previous year or of organic matter toxicity caused by late plowing of sod crops was eliminated. Soil was collected from farms in Franklin, Scott, and Garrard counties and from the University of Kentucky South and Spindletop farms in Fayette County. The South farm soil had been shown to be infested with the stunt pathogen (13), but the Spindletop farm soil was considered by agronomists not to have a productivity problem.

The cultivars used for these experiments, KY 15 and KY 17, have "immunity" derived from *N. debneyi* to black root rot, caused by *Thielaviopsis basicola* (Berk. & Br.) Ferraris (24). Use of these cultivars eliminated confusion with black root rot, which also causes stunting.

Bare root tobacco seedlings for experiments were produced by sowing seeds in vermiculite. Three-week-old seedlings were transplanted into river-dredged commercial building sand (see Fang et al [8] for analysis) in 50-ml black plastic growth tubes (8) and subirrigated with full-strength Hoagland's solution (15) for 3 wk. Transplants about 6 wk old and in the four-leaf stage were used for experiments, which were conducted in the black tubes subirrigated with Hoagland's solution.

An isolate of *G. fasciculatum* (Thaxter sensu Gerd.) Gerd. & Trappe, supplied by J. W. Gerdemann, University of Illinois, was used for comparative purposes in one experiment. Spores of *G. fasciculatum* were produced on sorghum-sudangrass hybrid in a mixture of sand and soil. Isolates of *G. macrocarpum* were obtained by inoculating tobacco plants with soil sievings as described previously (8) and growing them for about 40 days in the sand-Hoagland's system. Spores from these infected plants were used to establish cultures.

In some experiments in which plants were inoculated with spores picked out with a Pasteur pipette, the spores were surface-disinfested with Chloramine-T (*N*-chloro-4-methylbenzene-sulfonamide sodium salt) (21). Spores were placed on a sieve with 100-μm openings, dipped into 2% Chloramine-T (w/v) for 4 min, and rinsed in deionized water three or four times. Although the effectiveness of the disinfestation procedure was not evaluated, all contaminating microorganisms may not have been removed (22,26).

Before inoculation, root systems of plants were carefully rinsed free from sand and cut to 4 cm in length. Plants were inoculated by transferring soil sievings or single spores with a Pasteur pipette to the root system 2 cm below the crown. The placement of single spores was observed with a dissecting microscope (25×) (8). The inoculated plant was then transplanted by pouring sand carefully around the root system in the growth tubes (8).

Plants were prepared for evaluation of mycorrhizal development by immersing the root systems in a container of water and removing the sand by gentle agitation. The sand and water were sieved (100-μm openings) to recover spores not attached to roots.

Spores of endogonaceous fungi were identified according to keys and species descriptions (1,10,23).

Roots for colonization determinations were cleared by a no-heat KOH procedure and stained with trypan blue in lactophenol (19). Root colonization was evaluated by a grid-line intercept method (11). Intercepts were rated for arbuscules, vesicles, external hyphae, and endogonaceous fungal spores. Unfortunately, mycelium of mycorrhizal fungi within the root cortex did not retain sufficient stain to permit reliable ratings for internal hyphae.

Statistical analyses were done with the SAS general linear model (12).

RESULTS

After 45 days, the only plants stunted were those inoculated with sievings of soil from the Scott County farm (Table 1). *G. macrocarpum* sporulated profusely on the roots of these plants and also on the roots of plants inoculated with sievings of soil from the South farm. *G. microcarpum* (Tul. & Tul.) Gerd. & Trappe sporulated on roots of plants inoculated with sievings of soil from the Franklin County and South farms. Roots inoculated with sievings of soil from the Franklin County, South, and Scott County farms were heavily colonized with arbuscules and external hyphae.

After 75 days, plants inoculated with sievings of soil from the Spindletop farm were slightly stunted, those inoculated with sievings of soil from the Franklin County and South farms were about one-half the size of uninoculated plants, and plants inoculated with sievings of soil from the Scott County farm were

TABLE 1. Plant growth, spore production, and mycorrhizal colonization structures associated with tobacco plants (cultivar KY 15) inoculated with soil sievings and grown in a sand-Hoagland system for 45 or 75 days

	Source of inoculum[j]									
	Uninoculated		Spindletop farm		Franklin County farm		South farm		Scott County farm	
Parameter	45 days	75 days	45 days	75 days	45 days	75 days	45 days	75 days	45 days	75 days
Shoot fresh weight (g)	9.6 a[k]	38.2 w	11.6 a[k]	30.4 x	11.9 a[l]	21.9 y	7.8 b[m]	18.7 y	3.1 c[k]	5.7 z
Root fresh weight	1.0 ab	3.8 w	1.6 a	3.0 x	1.5 a	2.0 y	0.9 b	1.7 y	0.4 c	0.7 z
Glomus spp. (spores/plant)										
G. macrocarpum	0	0	0 c	0 z	0.4 c	129.2 y	380.0 b	1,165.5 w	1,029.0 a	537.8 x
G. microcarpum	0 b	0 z	0 b	22.6 y	32.2 a	228.2 x	25.4 a	214.3 x	1.0 b	253.0 x
Unidentified *Glomus* sp.[n]	0	0 z	0	0 z	0	2.2 y	0	0 z	0	0 z
G. etunicatum	0	0 z	0	0 z	0	4.9 y	0	0 z	0	0 z
G. clarum	0	0 z	0	0 z	0	0 z	0	16.2 y	0	0 z
Root colonization (%)										
Arbuscules	0 b	0 z	1.6 b	6.8 y	32.9 a	26.0 x	36.9 a	24.0 x	36.0 a	39.0 x
Vesicles	0 b	0 z	0.3 b	0 z	3.7 a	4.7 z	5.3 a	2.8 z	0 b	0 z
External hyphae	0 b	0 z	2.8 b	6.8 y	37.5 a	30.1 x	22.1 a	27.2 x	45.0 a	46.6 x

[j] Soil collected 26 March 1981; each plant inoculated with sievings from 40 g of soil; sievings passed through sieve with 864-μm openings and retained on sieve with 100-μm openings.

[k] Means of five plants on each observation day. Means followed by the same letter on a line at 45 or 75 days are not significantly different ($P = 0.05$, Duncan's multiple range test).

[l] Means of 15 plants on each observation day.

[m] Means of 10 plants on each observation day.

[n] Produced spores 160–210 μm in diameter.

severely stunted (Table 1). *G. macrocarpum* and *G. microcarpum* sporulated on the roots of plants inoculated with sievings of soil from the Franklin County, South, and Scott County farms, but only *G. microcarpum* sporulated, lightly, on roots of plants inoculated with sievings of soil from the Spindletop farm. *G. etunicatum* Becker & Gerd., *G. clarum* Nicol. & Schenck, and an unidentified *Glomus* sp. sporulated late and sporadically. Extensive colonization of roots by arbuscules and external hyphae, but not vesicles, was associated with stunting and with extensive sporulation by *G. macrocarpum* and *G. microcarpum*. Data from all plants inoculated with soil sievings were subjected to regression analysis. Shoot fresh weight after 75 days was correlated negatively with sporulation by *G. macrocarpum* and *G. microcarpum* and with colonization of roots with arbuscules and external hyphae (Table 2). Colonization of roots with vesicles was not significantly correlated with shoot weight.

Most of the plants inoculated with two or four spores of the isolates of *G. macrocarpum* had this fungus sporulating heavily on their root systems after 40 days (Table 3). In comparison to uninoculated control plants, these plants were stunted 62–74%. Weight of plants inoculated with *G. macrocarpum* but not bearing spores was reduced by 15–45%. The fresh weight of three of these four groups inoculated with *G. macrocarpum* but free from spores was significantly less than that of the uninoculated plants. Inoculation with four spores of *G. fasciculatum* did not result in sporulation or stunting.

These data suggest that a high proportion of plants inoculated with a single spore of *G. macrocarpum* should become infected. Shoot weights of plants inoculated with single spores of *G. macrocarpum* isolated from the Scott County farm soil were one-third the size of uninoculated plants (Table 4). Plants inoculated and colonized were more severely stunted than plants inoculated but not colonized with arbuscules, vesicles, spores, or external hyphae. Plants colonized with arbuscules and external hyphae were stunted more than plants colonized with arbuscules only or not colonized with these structures.

Sizes of root systems somewhat paralleled sizes of shoots (Table 4), and root and shoot weights were correlated closely ($r = 0.94$, $P = 0.0001$). Root system weights were considerably restricted in this growth system, in which root growth was limited physically by the container but plants were never stressed for water or mineral nutrients because of continuous subirrigation with nutrient solution. Even so, root systems of plants with stunted shoots were also stunted, and the shoot:root ratio was rather constant (7–10:1) among the various groups. This relationship was also found when plants were inoculated with soil sievings (Table 1). Roots were not necrotic or discolored.

Significant negative correlations with growth were obtained for colonization of roots with arbuscules and external hyphae (Table 5). As with plants inoculated with soil sievings (Table 2), a negative correlation of growth with vesicles approached significance (Table 5). A significant negative correlation with growth was not obtained for spores per root system and spores per gram of root.

TABLE 2. Correlation coefficients (r) and probabilities for significance (P) for relationship between growth of tobacco plants (shoot fresh weight) inoculated with soil sievings and sporulation by mycorrhizal fungi or colonization of roots with mycorrhizal fungus structures after 75 days of growth

Parameter	r[a]	P[b]
Root fresh weight	0.97	0.0001
Spore number		
Glomus macrocarpum	−0.47	0.0011
G. microcarpum	−0.30	0.042
Unidentified *Glomus* sp.[c]	−0.12	0.43
G. etunicatum	0.09	0.57
G. clarum	−0.11	0.46
Root colonization (%)		
Arbuscules	−0.59	0.0001
Vesicles	−0.27	0.069
External hyphae	−0.58	0.0001

[a] Correlations performed on 35 inoculated plants.
[b] Probability of a greater r under the test of the null hypothesis, where $H_0 = 0$. P values less than 0.05 and 0.01 usually considered significant or highly significant, respectively.
[c] Produced spores 160–210 μm in diameter.

TABLE 3. Effect of two isolates of *Glomus macrocarpum* and one of *G. fasciculatum* on growth of tobacco plants (cultivar KY 17) grown in a sand-Hoagland system for 40 days

Isolate[y]	Inoculum level (spores/plant)	Plants with spores: No.	Plants with spores: Fresh weight[z] (g)	Plants without spores: No.	Plants without spores: Fresh weight[z] (g)
Glomus macrocarpum					
SF-1	2	10	3.3 f	2	8.1 bcd
	4	9	3.4 f	3	10.8 ab
GR-1	2	8	4.8 ef	4	7.4 cde
	4	8	3.5 f	4	7.0 de
G. fasciculatum	4	0		12	10.1 abc
None	0	0		4	12.8 a

[y] SF-1 = *G. macrocarpum* from soil from South farm in Fayette County, KY. GR-1 = *G. macrocarpum* from soil from Garrard County farm; *G. fasciculatum* from citrus, California.
[z] Shoot + root. Means followed by the same letter are not statistically different ($P = 0.05$, Duncan's multiple range test).

DISCUSSION

This research shows that a mycorrhizal fungus, *G. macrocarpum*, can cause tobacco stunt disease. Sievings from soils

TABLE 4. Relationship between colonization of roots with mycorrhizal structures and growth of tobacco plants (cultivar KY 15) each inoculated with a single spore of an isolate of *Glomus macrocarpum* obtained from soil from the Scott County farm and grown in a sand-Hoagland system for 75 days

Group	Number of plants	Fresh weight (g): Shoot	Fresh weight (g): Root
Uninoculated	10	41.0 a[x]	3.9 a
Inoculated	80	14.3[y]	1.8[y]
Not colonized	18	25.7 b	3.1 a
Colonized	62	12.0[z]	1.5[z]
Arbuscules	10	24.2 b	3.1 a
Arbuscules, external hyphae	21	10.1 c	1.5 b
Arbuscules, external hyphae, spores	18	8.1 c	1.1 b
Arbuscules, external hyphae, spores, vesicles	13	6.1 c	0.8 b

[x] Means in a column followed by the same letter are not statistically different ($P = 0.05$, Duncan's multiple range test).
[y] Significantly different from uninoculated ($P = 0.0001$, Student's t test).
[z] Significantly different from inoculated but not colonized ($P = 0.01$, Student's t test).

TABLE 5. Correlation coefficients (r) and probabilities for significance (P) for relationship between colonization of roots with mycorrhizal structures and growth (shoot fresh weight) of tobacco plants (cultivar KY 15) inoculated with single spores of an isolate of *Glomus macrocarpum* obtained from soil from the Scott County farm and grown in a sand-Hoagland system for 75 days

Fungal structure	Mean[a]	r	P[b]
Spores/g root (no.)	101.3 ± 33.4	−0.19	0.10
Spores/root system (no.)	56.3 ± 21.2	−0.089	0.43
Colonization with arbuscules (%)	19.9 ± 2.4	−0.35	0.0015
Colonization with vesicles (%)	2.4 ± 0.5	−0.22	0.052
Colonization with external hyphae (%)	15.5 ± 2.3	−0.38	0.0004

[a] Means ± standard errors; data from plants rated negative for fungal structure not included.
[b] Probability of a greater r under the test of the null hypothesis, where $H_0 = 0$. P values less than 0.05 and 0.01 usually considered significant or highly significant, respectively.

suspected of harboring the pathogen caused typical symptoms of stunt (13). Stunting was correlated with sporulation by *G. macrocarpum* and, less strongly, *G. microcarpum*. Early sporulation by *G. macrocarpum* was related to the severity of stunting induced by soil sievings. Inoculation with surface-disinfested single spores of *G. macrocarpum* resulted in the symptoms of tobacco stunt. Pure cultures of *G. macrocarpum* produced few vesicles in roots, and the correlation of vesicles with stunting induced by soil sievings (Tables 1 and 2) was weak. The extent to which vesicles are produced in tobacco roots by *G. microcarpum* and the other species recovered is not known, however.

There is some evidence that other mycorrhizal fungi, notably *G. microcarpum*, may cause stunting. With long incubation, slight stunting was eventually caused by sievings from soil from the Spindletop farm, and *G. microcarpum* was the only species recovered. The other species were recovered from a single soil sample only, and sporulation was not correlated with stunting. Pathogenicity by *G. microcarpum* has not been evaluated because pure cultures could not be obtained (8).

This study demonstrates a fundamental difference between *G. macrocarpum* isolated from tobacco soils and *G. fasciculatum* (Table 3), an isolate frequently found beneficial to woody plants (20). The difference may be simply that *G. macrocarpum* but not *G. fasciculatum* is able to infect tobacco under these conditions of high mineral nutrition. Unfortunately, colonization was not evaluated in this experiment. The inoculum of *G. fasciculatum* used in this experiment was demonstrated to be viable in other research (18).

The conditions for demonstrating pathogenicity of *G. macrocarpum* to tobacco are quite artificial. However, Jones (17) also demonstrated pathogenicity in soil fertilized with the normal rate of tobacco fertilizer. His experiments also frequently included washes of sievings as control treatments, which are traditional in endogonaceous experiments because of the special problems (obtaining cultures free from other organisms) in satisfying Koch's postulates with obligate parasites.

These experiments do not preclude the possibility that the role of *G. macrocarpum* is that of a vector of another pathogen.

A number of plants were stunted even though no evidence of colonization was obtained (Table 4). The significance of this result is not readily assessed because none of the stains used for mycorrhizal roots is reliable for internal hyphae. Because so many plants were stunted but apparently not colonized by arbuscules or external hyphae, interference with the hormonal control of root initiation may be the mechanism of stunting rather than competition for photosynthate (2,3). The correlation of stunting with colonization by external hyphae, however, supports the photosynthate competition hypothesis. Stunting of many plants without evidence of colonization may be the reason the correlation coefficients are highly significant but relatively low; all colonized plants were stunted. The low correlation coefficients and stunting in the absence of arbuscules, vesicles, and external hyphae indicate that these structures are not involved in the mechanism of stunting. The lower correlations of colonization with growth obtained with single spores than with sievings of soil may be due to inoculum dose. Stunting of plants in the absence of observable colonization has been noted before. One isolate of *G. etunicatum* produced colonization rates on sweetgum as high as 77% and another did not produce detectable colonization, yet both stunted seedlings at high fertility (18). The small size of the tobacco seedlings at the beginning of the experiments may be the reason a single spore was sufficient to stop growth. Plants used commercially for transplanting into the field are much larger, and larger inoculum doses may be required to induce stunting in the field.

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